ELSEVIER

Crop Protection 18 (1999) 39–45

Crop Protection

The potential for compensation of the effects of the brown planthopper *Nilaparvata lugens* Stal (Homoptera: Delphacidae) feeding on rice

Elsa Rubia-Sanchez*, Yoshito Suzuki, Kenji Miyamoto, Tomonari Watanabe[1]

Laboratory of Pest Management Systems, Kyushu National Agricultural Experiment Station, Nishigoshi, Kumamoto 861-11, Japan

Received 15 September 1998; accepted 26 October 1998

Abstract

A glasshouse experiment investigated the effects of brown planthopper feeding on the physiology of the main shoot and its indirect effects on the primary tiller with Japonica rice Nipponbare and Indica rice Taichung Native 1. Brown planthopper sucking on the main shoot reduced its height, leaf area, average photosynthetic rate of the two upper leaves, leaf and stem nitrogen content, and shoot dry weight. Nipponbare, had a lower photosynthetic rate, and lower nitrogen content of the leaf and stem of healthy plants, and was affected by BPH feeding more than TN1. With the primary tiller kept intact, the effects of brown planthopper feeding on leaf area and shoot dry weight of the main shoot were less than with the removal of the primary tiller. The results suggest that the primary tiller, not infested by the brown planthopper, translocates nutrients and assimilates into the main shoot, to reduce the effects of brown planthopper feeding on the main shoot. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Planthopper; *Nilaparvata lugens*; Compensation; Hopper-rice plant interaction; Tiller

1. Introduction

The brown planthopper (BPH) *Nilaparvata lugens* Stal is an important pest of rice in many Asian countries (Suenaga and Nakatsuka, 1958; Varca and Feuer, 1976; Mochida et al., 1977; Oka, 1979; Kiritani, 1979). The BPH feeds mainly on the stems, and sucks assimilates from the phloem (Sogawa, 1973). Feeding by a large number of BPH may result in drying of the leaves and wilting of the tillers, a condition called hopperburn.

In Japan, BPH invades rice fields at the vegetative stage (Suenaga and Nakatsuka, 1958). The vegetative stage is characterized mainly by formation of tillers (Mae, 1997). Depending on the type of cultivar and environment, the tiller number is positively or negatively correlated with grain yield (Kawano and Tanaka, 1968). Rice plants with a tiller showed better light interception and root development than those without (Ni, 1986). Furthermore, the presence of a tiller increased photosynthetic rate, photorespiration, and carbohydrate accumulation in rice plants.

Tillers play an important role in plant compensation. We define compensation here as the process by which plants respond positively to recover from the effects of pest injury on plant growth. Rice plants compensate for insect injury at the vegetative stage (Binh et al., 1993; Joshi et al., 1992; Shepard et al., 1990; Heong, 1990; Rubia et al., 1989; Navas, 1976). At the early tillering stage, rice plants actively produce tillers, and some tillers including leaves of these tillers may be lost without reducing grain yield because the number of productive tillers is determined at the maximum tillering stage (Matsushima, 1970). The translocation of assimilates from an infested tiller to another tiller is an important mechanism of plant compensation against yellow stem borer injury at the early crop growth stage (Rubia et al., 1996).

Here we investigate the effects of BPH feeding on the physiology of the main shoot and its indirect effects on

*Corresponding author.

[1]*Present address*: Cooperative Research Center for Tropical Pest Management (CRCTPM), CSIRO Division of Entomology, Meiers Road, Private Bag 3, Indooroopilly, Q4068, Brisbane, Australia

0261-2194/99/$ – see front matter
PII: S0261-2194(98)00087-8

the primary tiller of rice cultivars belonging to two groups, a Japonica rice Nipponbare and an Indica rice Taichung Native 1 (TN1). Nipponbare and TN1 are both susceptible to BPH but their response to BPH feeding may vary, so we compared the main shoot and primary tiller response of the two cultivars to BPH injury.

2. Materials and methods

The experiment was conducted inside the glasshouse of Kyushu National Agricultural Experiment Station from June to October, 1997.

2.1. Rice plants and insects

Fifty plants of cultivars Nipponbare and TN1 were grown at 25/20°C day/night temperatures, 14 : 10 photoperiod and 70% relative humidity. Each cultivar was planted at the rate of one seedling in 1/10 000 a Wagner pots filled with 0.8 g N, 0.8 g P, 0.8 g K per 1.5 l soil.

BPH were reared on seedlings of a susceptible cultivar, Reiho, at 25°C, inside a growth chamber, using a method similar to Yushima et al. (1991). Early fourth instars were used in the experiment to ensure that there are no oviposition effects caused by the BPH.

2.2. Experiment

Plants 21 days after sowing (DAS) of both cultivars, approximately 31 cm plant height, with a main shoot and one primary tiller, were selected. Two treatments were investigated for each cultivar; removal of the primary tiller by cutting its stem at the base, and BPH infestation with 32 nymphs which were caged onto the main shoots. Each treatment was replicated 7 times in the case of Nipponbare because the other plants did not produce tillers at the time of BPH release, and 12 times in the case of TN1. The experiments were laid out in a randomised complete block design for each cultivar.

Five days after infestation, the BPH were removed. The net photosynthetic rate of the first (Leaf 1) and second (Leaf 2) expanded leaves from the top of the main shoot were measured for five plants of each cultivar with a Licor-6200 portable photosynthesis system (LI-COR Inc.). Measurements were made between 1000 and 1200 h when the photosynthetically active photon flux (PAR) was between 1000 and 2000 μmol $m^{-2} s^{-1}$. The middle portion of the fully expanded leaf was enclosed with a 0.25 l chamber. The gas exchange system was operated as a closed system to measure photosynthetic rate during a 20 s period.

The main shoot and the primary tiller were separated. For each tiller, height was measured from the base to the leaf tip. The green leaf area of each tiller was measured using a Licor-3000A portable leaf area meter and a Licor-3050 belt conveyer (LI-COR Inc.). Leaves and stems of each tiller were separated, dried in an oven at 80°C for 3 days, and weighed.

After weighing, dried leaf and stem samples of the main shoots of three replicates were ground to a fine homogenous powder in a high-speed vibrating sample mill (Advantec MFS, Inc.). All samples were weighed and each was placed inside tin boats, folded into cube shaped packets, and sealed. With the aid of vario-E-L software (1995), samples were inserted into the vertical quartz glass combustion tube by means of an automatic sample feeder, and nitrogen was analysed using gas chromatography.

For each cultivar, the average photosynthetic rates of leaves 1 and 2 were calculated. For each tiller, shoot dry weight was calculated by adding the weight of the leaves to the weight of the stems; specific leaf weight was calculated by dividing leaf dry weight by leaf area. Percentage reduction in plant height, leaf area and shoot dry weight of the main shoot and primary tiller caused by BPH feeding were calculated by taking the difference between the control means and the data for each of the BPH-infested plant, divided by the control means and multiplied by 100.

2.3. Statistical analysis

Mean and standard error of each plant growth parameter were calculated for each cultivar and treatment. For measurements made on the main shoot, the data for each cultivar were analysed using analysis of variance (SAS, 1985). Student's *t*-tests were used to compare data for healthy plants vs. BPH-infested plants and healthy plants vs. plants without the primary tiller (SYSTAT, 1992). For measurements made on the primary tiller, the data for each cultivar were analysed using Student's *t*-test. To compare percentage reduction in plant height, leaf area and shoot dry weight of the main shoot and primary tiller of the two cultivars of each treatment, Student's *t*-tests were used.

3. Results

3.1. Plant height

The height of the main shoot of Nipponbare was significantly reduced by primary tiller removal and with BPH injury (Table 1). For TN1, only plants with BPH showed a significantly reduced height of the main shoot. For both cultivars, there was no significant interaction between primary tiller removal and BPH injury.

BPH feeding indirectly affected the growth of the primary tiller. With BPH feeding on the main shoot, the

Table 1
Average height, leaf area, specific leaf weight and shoot dry weight of the main shoot[a] of healthy and BPH-infested plants of Nipponbare ($n = 7$) and TN1 ($n = 12$), with and without the primary tiller

Cultivar	Treatment	Height (cm)		Leaf area (cm^2)		Specific leaf weight (mg cm^{-2})		Shoot dry weight (mg)	
		Healthy $\bar{X} \pm$ SE[c]	BPH-infested[b] $\bar{X} \pm$ SE[c]	Healthy $\bar{X} \pm$ SE[c]	BPH-infested[b] $\bar{X} \pm$ SE[c]	Healthy $\bar{X} \pm$ SE[c]	BPH-infested[b] $\bar{X} \pm$ SE[c]	Healthy $\bar{X} \pm$ SE[c]	BPH-infested[b] $\bar{X} \pm$ SE[c]
Nipponbare	Healthy	45.5 ± 0.6a(a)	38.0 ± 1.6b(a)	38.6 ± 2.3a(a)	24.6 ± 0.8b(a)	2.8 ± 0.1b(a)	3.1 ± 0.1a(a)	175.2 ± 8.2a(a)	114.3 ± 4.2b(a)
	No primary tiller	43.7 ± 0.7a(b)	33.4 ± 0.6b(b)	38.4 ± 1.3a(a)	18.9 ± 0.6b(b)	2.8 ± 0.1a(a)	2.6 ± 0.3a(b)	171.4 ± 8.6a(a)	72.1 ± 5.2b(b)
TN1	Healthy	37.5 ± 0.5a(a)	32.8 ± 0.7b(a)	29.8 ± 1.1a(b)	24.6 ± 0.8b(a)	3.1 ± 0.1a(a)	2.7 ± 0.2b(a)	138.9 ± 7.0a(a)	95.6 ± 5.0b(a)
	No primary tiller	38.7 ± 0.4a(a)	32.6 ± 0.9b(a)	32.4 ± 0.9a(a)	21.6 ± 3.3b(a)	3.0 ± 0.1a(a)	2.6 ± 0.2b(a)	151.3 ± 5.3a(a)	82.1 ± 3.0b(a)

[a]For each cultivar and treatment, mean values of each measurement in a row followed by a common letter (not enclosed in parenthesis) are not significantly different at 5% level by *t*-test. For each cultivar and measurement, mean values in a column followed by a common letter (enclosed in parenthesis) are not significantly different at 5% level by *t*-test.
[b]32 BPH on the main shoot.
[c]Mean ± standard error.

primary tiller height growth of Nipponbare was 53% lower than the control treatments whereas for TN1 it was 25% lower than the control treatments (Table 2). Reduction in primary tiller height was greater in Nipponbare than in TN1 (Table 3).

3.2. *Leaf area and specific leaf weight*

The green leaf area of the main shoot of both cultivars with BPH injury was significantly reduced compared to healthy plants (Table 1). With the primary tiller kept intact, the leaf area reduction relative to the control, of the BPH-infested main shoot of Nipponbare was half that of TN1 (Table 3). With the removal of the primary tiller, the leaf areas of the main shoot of BPH-infested Nipponbare and TN1 were reduced by 51% and 33%, respectively, compared with control treatments. For TN1, the interaction between primary tiller removal and BPH injury was significant ($p < 0.01$).

The green leaf area of the primary tiller was indirectly affected by BPH feeding on the main shoot. Reduction in leaf area of the primary tiller of Nipponbare was greater compared to that of TN1 (Tables 2 and 3).

The specific leaf weight of the main shoot of BPH-infested plants without the primary tiller was lower than that of healthy plants (Table 1). For TN1, the specific leaf weight of the main shoot of BPH-infested plants with and without the primary tiller were 13% lower than that of control treatments. The specific leaf weight of the primary tiller of BPH-infested TN1 was 4% lower than that of control treatments.

3.3. *Leaf photosynthetic rate of the leaves of the main shoot*

For Nipponbare, the leaf photosynthetic rates of leaves 1 and 2 were reduced by BPH feeding (Table 4). The average photosynthetic rates of the two leaves were 17 and 27% lower with and without the primary tiller, respectively, compared to the control treatments. Primary tiller removal alone did not significantly affect photosynthetic rate of either leaf.

For TN1, the photosynthetic rate of Leaf 1 was not affected by BPH feeding in intact plants, but the same leaf showed a significant reduction in photosynthetic rate in plants with the primary tillers removed (Table 4). The photosynthetic rate of Leaf 2 was significantly reduced by BPH feeding in both treatments (Table 4). Without the primary tiller, the average photosynthetic rate of the two leaves decreased by as much as 58% with BPH feeding. Like Nipponbare, primary tiller removal alone did not affect the photosynthetic rate of either leaf.

Table 2
Average height, leaf area, specific leaf weight and shoot dry weight of the primary tiller[a] of healthy and BPH-infested plants of Nipponbare ($n = 7$) and TN1 ($n = 12$)

Cultivar	Height (cm)		Leaf area (cm^2)		Specific leaf weight ($mg\,cm^{-2}$)		Shoot dry weight (mg)	
	Healthy $\bar{X} \pm SE$[c]	BPH-infested[b] $\bar{X} \pm SE$[c]	Healthy $\bar{X} \pm SE$[c]	BPH-infested[b] $\bar{X} \pm SE$[c]	Healthy $\bar{X} \pm SE$[c]	BPH-infested[b] $\bar{X} \pm SE$[c]	Healthy $\bar{X} \pm SE$[c]	BPH-infested[b] $\bar{X} \pm SE$[c]
Nipponbare	25.5 ± 1.1a	11.9 ± 1.4b	11.2 ± 1.1a	3.5 ± 0.6b	2.7 ± 0.1a	2.8 ± 0.2a	54.9 ± 0.2a	15.1 ± 0.4b
TN1	20.5 ± 1.4a	15.4 ± 1.0b	11.3 ± 1.1a	6.3 ± 0.8b	2.6 ± 0.1a	2.5 ± 0.1a	47.5 ± 0.4a	23.3 ± 0.4b

[a]For each cultivar, mean values of each measurement in a row followed by a common letter are not significantly different at 5% level by *t*-test.
[b]32 BPH on the main shoot.
[c]Mean ± standard error.

Table 3
Percentage reduction in plant height, leaf area and shoot dry weight of the main shoot and primary tiller of Nipponbare and TN1 caused by BPH feeding on the main shoot

Treatment	Cultivar	Percentage reduction					
		Main shoot[b]			Primary tiller		
		Height (cm) $\bar{X} \pm SE$[c]	Leaf area (cm^2) $\bar{X} \pm SE$[c]	Shoot dry weight (mg) $\bar{X} \pm SE$[c]	Height (cm) $\bar{X} \pm SE$[c]	Leaf area (cm^2) $\bar{X} \pm SE$[c]	Shoot dry weight (mg) $\bar{X} \pm SE$[c]
Healthy	Nipponbare	16.64 ± 3.6	36.19 ± 2.2	34.78 ± 2.4	53.22 ± 5.6	68.66 ± 5.1	72.57 ± 4.3
	TN1	12.61 ± 1.9	17.57 ± 2.6	31.14 ± 3.6	25.20 ± 4.6	41.34 ± 5.1	46.47 ± 3.5
Prob[a]		0.448	0.003**	0.014*	0.006**	0.006**	0.004**
No primary tiller	Nipponbare	23.50 ± 0.2	50.76 ± 1.5	57.93 ± 3.0	—	—	—
	TN1	15.80 ± 0.5	33.44 ± 1.7	45.72 ± 2.6	—	—	—
Prob[a]		0.063	0.001**	0.012*	—	—	—

[a] ** and * significantly different at 1 and 5% level by t-test, respectively.
[b]32 BPH on the main shoot.
[c]Mean ± Standard error.

Table 4
Average photosynthetic rates of Leaf 1 and Leaf 2 ($n = 5$), and leaf and stem nitrogen content ($n = 3$) of the main shoot[a] of healthy and BPH-infested plants of Nipponbare and TN1, with and without the primary tiller

Cultivar	Treatment	Photosynthetic rates (μmol CO_2 m^{-2} s^{-1})				Nitrogen content (g kg^{-1} dry weight)			
		Leaf 1		Leaf 2		Leaf		Stem	
		Healthy	BPH-infested[b]	Healthy	BPH-infested[b]	Healthy	BPH-infested[b]	Healthy	BPH-infested[b]
		$\bar{X} \pm$ SE[c]	$\bar{X} \pm$ SE[c]	$\bar{X} \pm$ SE[c]	$\bar{X} \pm$ SE[c]	$\bar{X} \pm$ SE[c]	$\bar{X} \pm$ SE[c]	$\bar{X} \pm$ SE[c]	$\bar{X} \pm$ SE[c]
Nipponbare	Healthy	16.96 ± 1.3a(a)	13.38 ± 1.4b(a)	16.11 ± 0.8a(a)	14.03 ± 1.5a(a)	49.85 ± 0.7a(a)	38.12 ± 2.2b(a)	28.55 ± 1.4a(a)	26.52 ± 3.1a(a)
	No primary tiller	15.94 ± 1.0a(a)	11.53 ± 1.4b(a)	17.90 ± 1.5a(a)	13.11 ± 1.6b(a)	50.49 ± 0.4a(a)	40.39 ± 2.4b(a)	28.45 ± 0.6a(a)	25.01 ± 2.6a(a)
TN1	Healthy	16.94 ± 2.7a(b)	17.62 ± 2.3a(a)	21.88 ± 2.8a(a)	9.70 ± 1.7b(a)	51.34 ± 2.1a(a)	41.76 ± 0.6b(a)	37.47 ± 0.6a(a)	31.08 ± 0.3b(a)
	No primary tiller	23.52 ± 3.2a(a)	8.71 ± 2.9b(b)	20.70 ± 2.1a(a)	9.63 ± 0.6b(a)	52.22 ± 2.0a(a)	38.43 ± 1.0b(a)	37.64 ± 1.6a(a)	29.81 ± 0.4b(b)

[a] For each cultivar and treatment, mean values of each measurement in a row followed by a common letter (not enclosed in parenthesis) are not significantly different at 5% level by *t*-test. For each cultivar and measurement, mean values in a column followed by a common letter (enclosed in parenthesis) are not significantly different at 5% level by *t*-test.
[b] 32 BPH on the main shoot.
[c] Mean ± standard error.

3.4. Leaf and stem nitrogen content

Leaf and stem nitrogen content of BPH-infested main shoots were lower than that of healthy plants for Nipponbare and TN1 (Table 4). Cutting the primary tillers did not significantly decrease leaf and stem nitrogen content of the main shoots. In general, there was greater reduction in leaf nitrogen content caused by BPH feeding, with the removal of the primary tiller. There was no significant interaction between primary tiller removal and BPH feeding ($p > 0.05$).

3.5. Organ dry weights

Without BPH, no significant decrease in the shoot dry weight of the main shoot of both cultivars was observed after removing the primary tiller (Table 1). BPH feeding significantly decreased the shoot dry weight of the main shoot of both cultivars ($p < 0.01$), with shoot dry weight reduction greater for plants without the primary tiller than for intact plants (Table 1). The interaction between primary tiller removal and BPH feeding was significant ($p < 0.05$). Reduction in shoot dry weight was greater for Nipponbare than for TN1 (Table 3). The shoot dry weight reduction of the primary tiller of Nipponbare was significantly greater than that of TN1 with BPH feeding on the main shoot (Tables 2 and 3).

4. Discussion

BPH feeding on the main shoots of Nipponbare and TN1 reduced its growth by causing a decrease in leaf area, leaf photosynthetic rate and other growth parameters. Whereas BPH feeding decreased leaf photosynthetic rate and nitrogen content of infested shoots, tiller removal did not affect these parameters. BPH sucks phloem sap which contains sucrose and nitrogen compounds (Chino et al., 1987), and the data presented here suggest that removal of these nutrients will affect normal growth and development of the main shoot.

Reduction in leaf nitrogen content, which may be partly responsible for reduction in the growth of the main shoot, is a possible major mechanism for BPH damage. An abundant supply of nitrogen in the leaf increases the amount of CO_2-fixing enzyme, RuBisCO, which plays an important role in photosynthesis (Makino et al., 1985; Mitsui and Ishii, 1938). The reduction in leaf nitrogen content caused by BPH feeding probably led to the reduction in leaf photosynthetic rate. The decrease in photosynthetic rate probably limits the amount of assimilates produced and translocated to other tillers.

The data also suggest two possible mechanisms whereby plants may recover from BPH injury, viz., translocation of assimilates from tillers with no BPH and increase in photosynthetic rate of some leaves. Rice plants may recover from BPH injury with the help of tillers which have few BPH. Here, the effects of BPH feeding were much greater on the main shoots without the primary tillers. Hence, the primary tiller does not compete with BPH for assimilates produced by the main shoot, rather it helps the main shoot counter the effects of BPH sucking. As a consequence, the growth of the primary tiller is reduced. A tiller becomes autotrophic after the third leaf has completely emerged (Ishizuka and Tanaka, 1963) so it is capable of producing carbohydrates and absorbing nutrients. Thus, a tiller could translocate assimilates to other tillers when there is defoliation (Wang and Hanada, 1982) and stem borer injury (Rubia et al., 1996).

The increase in photosynthetic rate was observed in Leaf 1 of BPH-infested intact TN1 plants (Table 3). Our earlier study using 26 d-old intact plants ($\geqslant 2$ tillers) infested by the same number and age of BPH showed varying effects of BPH on leaf photosynthetic rate (Unpublished data). It showed an increase in Leaf 1 photosynthetic rate of BPH-infested Nipponbare and an increase in leaves 1 and 2 photosynthetic rates of BPH-infested TN1. In the case of another phloem feeder *Aphis craccivora* Koch, photosynthesis was depressed on leaves with aphids whereas adjacent leaves with no infestation showed an increase of 18–34% over control leaves of healthy plants (Chang and Thrower, 1981). For yellow stem borer, green leaves adjacent to stem borer-killed leaves showed a higher photosynthetic rate than the same leaves in healthy plants (Rubia et al., 1996).

Lastly, BPH feeding effects were generally greater for Nipponbare than for TN1 suggesting that the former is more susceptible to BPH injury. Healthy Nipponbare showed lower leaf photosynthetic rates and leaf and stem nitrogen content than TN1 so that the amount of assimilates produced by Nipponbare may be less and the energy spent to counter the effects of BPH feeding may be greater. We observed that TN1 seedlings grow faster and tiller earlier than Nipponbare seedlings, a sign that at early plant growth TN1 produces assimilates faster than Nipponbare.

In conclusion, the effects of BPH feeding on the main shoot were greater for plants without the primary tiller suggesting that tillering is an important component in BPH–plant interaction. BPH-susceptible cultivars with few tillers may not be able to compensate sufficiently for BPH injury at the vegetative stage. In the case of yellow stem borers, plants compensate by production of new tillers (Rubia et al., 1996). Moreover, cultivars with higher photosynthetic capacity and faster translocation ability may suffer less from BPH injury than cultivars with lower photosynthetic capacity and slower translocation ability. Photosynthesis and the transfer of nutrients and assimilates from tiller to tiller remains as an important aspect in rice plant compensation to insect injury.

Acknowledgements

This work was financially supported by the Japan Science and Technology Agency. We appreciate the assistance of colleagues in the Laboratory of Pest Management Systems. Thanks to Mrs Yamada for rearing BPH. Thanks to Mr Maruyama for giving advise on the use of the LI-COR 6200 leaf photosynthesis meter and to Mr Arakawa for teaching us carbon and nitrogen analyses. Thanks to Drs Anthea Cook and Frits Penning de Vries for their valuable comments on the paper.

References

Binh, N., Tuc, L.M., Hoa, T.T.H., Heong, K.L., 1993. Managing thrips in the Mekong Delta, Vietnam. Int. Rice Res. Newslett. 18, 31.

Chang, L.H., Thrower, L.B., 1981. The effect of *Uromyces appendiculatus* and *Aphis craccivora* on the yield of *Vigna sesquipedalis*. Phytopathol Zeitschrift. 101, 143–152.

Chino, M., Hayashi, H., Fukumorita, T., 1987. The chemical composition of rice phloem sap and its fluctuation. J Plant Nutr. 10, 1651–1661.

Heong, K.L., 1990. Feeding rates of the rice leaffolder, *Cnaphalocrocis medinalis* (Lepidoptera: Pyralidae), on different plant stages. J Agricl. Entomol. 7, 81–90.

Ishizuka, Y., Tanaka, A., 1963. Nutrio-physiology of tillering. Nutrio-Physiology of Rice Plants. Yokendo, Tokyo, 30 pp.

Joshi, R.C., Angela, C.J., Ukwungwu, M.N., 1992. Yield losses due to stalk-eyed fly (SEF) Nigeria. Int. Rice Res. Newslett. 17, 15.

Kawano, K., Tanaka, A., 1968. Growth duration in relation to yield and nitrogen response in the rice plant. Japan J. Breed. 18, 46–52.

Kiritani, K., 1979. Pest management in rice. Ann. Rev. Entomol. 24, 279–312.

Mae, T., 1977. Physiological nitrogen efficiency in rice: nitrogen utilization, photosynthesis, and yield potential. Plant Soil 196, 201–210.

Makino, A., Mae, T., Ohira, K., 1985. Enzymatic properties of ribulose-1, 5-bisphosphate carboxylase/oxygenase purified from rice leaves. Plant Physiol. 79, 57–61.

Matsushima, S., 1970. Crop Science in Rice. Fuji Publ. Co., Ltd, Tokyo, 365 pp.

Mitsui, S., Ishii, Y., 1938. Effects of different application amounts of three major nutrients on the photosynthetic efficiency of rice seedlings. J. Sci. Soil Manure, Japan 12, 287–289.

Mochida, O., Suryana, T., Wahyu, A., 1977. Recent outbreaks of the brown planthopper in Southeast Asia (with special reference to Indonesia). The Rice Brown Planthopper, pp. 170–191. Food Fert. Technol. Cent. Asian Pac. Reg, Taipei, 258 pp.

Navas, D., 1976. Fall armyworm in rice. Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage vol. 6, pp. 99–106.

Ni, W., 1986. Studies of some physiological characteristics of rice plants with a tiller. Acta Agron Sinica 12, 57–62.

Oka, I.N., 1979. Implementing the brown planthopper integrated control program. Indon. Agricul. Res. Dev. J. 1, 14–20.

Rubia, E.G., Heong, K.L., Zalucki, M., Gonzales, B., Norton, G.A., 1996. Mechanisms of compensation of rice plants to yellow stem borer *Scirpophaga incertulas* (Walker) injury. Crop Prot. 15, 335–340.

Rubia, E.G., Shepard, B.M., Yambao, E.B., Ingram, K.T., Arida, G.S., Penning de Vries, F.W.T., 1989. Stem borer damage and grain yield of flooded rice. J. Plant Prot. Tropics 6, 205–211.

Shepard, B.M., Justo Jr., H.D., Rubia, E.G., Estano, D.B., 1990. Response of the rice plant to damage by the rice whorl maggot *Hydrellia philippina* Ferino (Diptera: Ephydridae). J Plant Prot. Tropics 7, 173–177.

SAS Institute, 1985. SAS User's Guide: Statistics, 5th ed. SAS Institute, Cary NC.

Sogawa, K., 1973. Feeding of the rice plant- and leafhoppers. Rev. Plant Prot. Res. 6, 31–43.

Suenaga, H., Nakatsuka, K., 1958. Review on the forecasting of leaf- and planthoppers infesting rice. Spec. Rep. Forecasting Dis. Insects, Japan. Minist. Agric. For. No. 1. 468 pp.

SYSTAT. Statistics, Version 5.2 ed. SYSTAT Inc., Evanston, IL,1992, 724 pp.

Varca, A.S., Feuer, R., 1976. The brown planthopper and its biotypes in the Philippines. Plant Prot. News 5, 1–4

Wang, Y.C., Hanada, K., 1982. Translocation of ^{14}C-assimilate among main stems and tillers in rice plants. Japan. J Crop Sci. 51, 483–491.

Yushima, T., Kamano, S., Tamaki, Y., 1991. Rearing methods of insects. Nippon Shokubutsu Boueki Kyokai, Tokyo, 392 pp.