Physiological Responses to *Nilaparvata lugens* in Susceptible and Resistant Rice Varieties: Allocation of Assimilates Between Shoots and Roots

JING-LAN LIU,[1] JIAN-FEI YU,[1] JIN-CAI WU,[1,2] JIAN-LI YIN,[1] AND HAI-NAN GU[3]

J. Econ. Entomol. 101(2): 384–390 (2008)

ABSTRACT *Nilaparvata lugens* (Stål) is a typical vascular feeder, primarily sucking the phloem sap of host plants. Its feeding on rice, *Oryza sativa* L., plants changes the pattern of allocation of assimilates between roots and shoots, and the root:shoot (R/S) ratio of assimilates is often measured as an index of physiological responses to *N. lugens*. The current study investigated changes in the R/S ratio of biomass, sucrose, and soluble sugar contents of rice plants in a susceptible variety (TN1) and a resistant variety (Xieyou 963). The results demonstrated that root and shoot biomasses in the two varieties linearly decreased with the increase of *N. lugens* infestation density. However, the relationship between changes in the R/S ratio of biomass and *N. lugens* density differed between rice varieties, with the R/S increasing with infestation density in TN1 and decreasing in Xieyou 963. Sucrose and soluble sugar contents and their R/S values were also significantly different between the two varieties. Compared with the control that was not infested by *N. lugens*, the R/S values of sucrose and soluble sugar at 3 days after infestation (DAI) increased but decreased at 6 DAI in TN1. The R/S values of sucrose and soluble sugar were higher at 6 DAI than those at 3 DAI in TN1, whereas these values were lower at 6 DAI than at 3 DAI in Xieyou 963. These contrasting results suggest that physiological responses to *N. lugens* infestation differ between the susceptible and tolerant rice varieties.

KEY WORDS rice, *Nilaparvata lugens*, physiological response, assimilate allocation

The planthopper *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae) is one of the most notorious pests of rice, *Oryza sativa* L., throughout Asia (Dyck and Thomas 1979, Sogawa 1982). *N. lugens* is a typical vascular feeder; primarily sucking the phloem sap (Sogawa 1980) and reducing the chlorophyll, protein content of leaves, and photosynthetic rate (Watanabe and Kitagawa 2000). Both nymphs and adults of *N. lugens* cause economic damage directly by feeding, and severe infestation can lead to a symptom commonly referred to as "hopperburn" (Bae and Pathak 1970).

Previous studies have shown that *N. lugens* infestation can cause physiological changes in rice plants. However, conclusions on the effect of *N. lugens* infestation on allocation of assimilates in rice plants are contradictory. Watanabe and Kitagawa (2000) reported that no obvious disruption in translocation of assimilates was found in the rice plants infested by *N. lugens*, although some other homopteran insects are known to cause such disruption in the infested rice and alfalfa, *Medicago sativa* L., plants (Naba 1988, Flinn et al. 1990, Nielsen et al. 1990). All these studies did not investigate the effect of insect infestations on translocation of assimilates between shoots and roots.

Rice roots not only play a key role in taking up nutrients and water as in other higher plants (Lambers et al. 1998) but also function as sites for the biosynthesis of substances, such as cytokinins, zeatin, and zeatin ribosides, that affect physiological activities (Yang et al. 2000, 2001, 2002). Therefore, the senescence of rice plants, the transportation and distribution of assimilates, grain filling and yield production are closely correlated with the function of their root systems (Ling and Ling 1984; Wang et al. 1992, 1997; Shi et al. 1997; Pang et al. 2000). The growth of roots, in turn, needs energy substances supplied by shoots. Thus, the aboveground organs of rice plants interact with their roots in their functions.

When rice plants are subjected to environmental stresses their roots compete with the shoots for energy substances (Luo and Li 1996, Feng and Luo 1999, Magnani et al. 2000). Recent studies have shown that *N. lugens* infestation reduces the nutrient uptake of rice roots and plant hormone content biosynthesized by rice roots (Wu et al. 2003, 2004; Qiu et al. 2004). Therefore, investigation into the translocation of assimilates between shoots and roots under *N. lugens* infestation is valuable for understanding the holistic physiological response of rice plants, in particular resistance or tolerance of rice varieties to this pest insect. This study was conducted to examine the pattern of allocation of assimilates between shoots and roots in susceptible and tolerant rice varieties that were infested by *N. lugens.*

[1] Plant Protection College, Yangzhou University, Yangzhou, 225009, China.
[2] Corresponding author, e-mail: jc.wu@public.yz.js.cn.
[3] CSIRO Entomology, Black Mountain Laboratories, Canberra, ACT 2601, Australia.

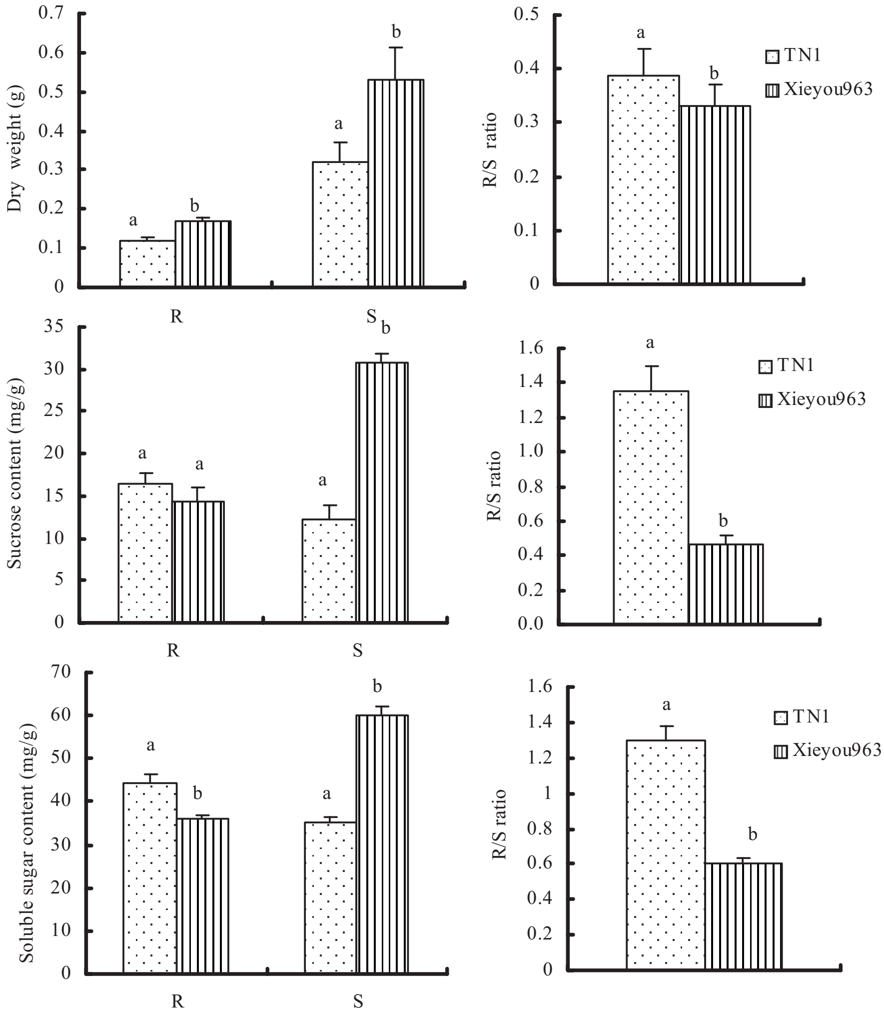

Fig. 1. Several indexes of dry weight, sucrose, and soluble sugar contents and their R/S ratio for TN1 and Xieyou 963 before *N. lugens* infestation. Bars with different letters in the same organ indicate that means were significantly different at $P < 0.05$ (*t*-test). R and S indicate rice root and shoot, respectively.

Materials and Methods

Rice Varieties and Planthoppers. Two varieties of rice, TN1 (Indica rice) and Xieyou 963 (Indica rice) that are known to be susceptible and resistance to *N. lugens*, respectively, were used in this study. Seeds of these varieties were sown in cement tanks (60 by 100 by 100 cm) at the experimental farm of Yangzhou University. After washing off soil with tap water, 30-d-old seedlings bearing six leaves were immediately transplanted into pots (35 cm in diameter and 50 cm in height) containing Espino hydroponics culture solution. Six seedlings as a hill were planted in these pots. Details of the cultivation method were described in Wu et al. (2003). All the rice plants were grown in a greenhouse under natural temperature and photoperiods.

Experimental insects were derived from the population of *N. lugens* maintained in a greenhouse of Yangzhou University. Before the experiment started, the *N. lugens* colony was reproduced for two generations in an insect nursery covered with cages under natural conditions.

Release of *N. lugens*. To investigate the effect of *N. lugens* feeding on allocation of assilimates between shoots and roots, rice plants at 7 d after transplantation were subjected to different densities of the *N. lugens* infestation. The fifth instars were released onto each hill within a nylon cage (30-mesh), as described in Wu et al. (2003). Rice plants without any *N. lugens* infestation were used as a control. Insect mortalities were checked at 24 h after the release of nymphs, and dead nymphs (if any) were replaced with live nymphs at the same age to maintain a given density. The experiment was arranged in a randomized complete block design with four replicates for each treatment and control. Sucrose and soluble sugar contents in both rice roots and shoots were quantified at 3 and 6 d after infestation.

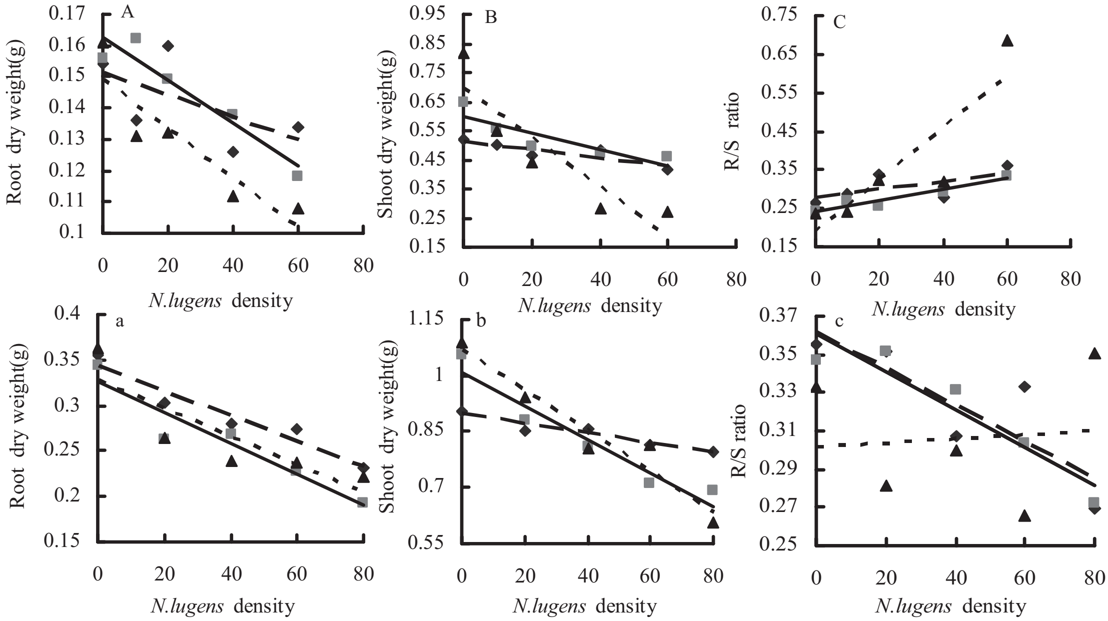

Fig. 2. Effects of *N. lugens* infestations on dry weight in roots and shoots and R/S ratio for TN1 (A, B, and C) and Xieyou 963 (a, b, and c). DAI-Days after infestation. 3 DAI(◆), 6 DAI (□), and 9 DAI(▲). (A) Root: 3 DAI, y = −0.0004x + 0.1512, r = −0.593*; 6 DAI, y = −0.0007x + 0.1625, r = −0.956*; and 9 DAI, y = −0.0008x + 0.1494, r = −0.906*. (B) Shoot: 3 DAI, y = −0.0014x + 0.5136, r = −0.883*; 6 DAI, y = −0.0028x + 0.5999, r = −0.871*; and 9 DAI, y = −0.0084x + 0.6932, r = −0.905*. (C) R/S ratio: 3 DAI, y = 0.0011x + 0.2763, r = 0.653*; 6 DAI, y = 0.0014x + 0.2417, r = 0.953*; and 9 DAI, y = 0.0068x + 0.1846, r = 0.884*. (a) Root: 3 DAI, y = −0.0014x + 0.3444, r = −0.968*; 6 DAI, y = −0.0017x + 0.3266, r = −0.948*; and 9 DAI, y = −0.0016x + 0.3674, r = −0.858*. (b) Shoot: 3 DAI, y = −0.0013x + 0.898, r = −0.959*; 6 DAI y = −0.0045x + 1.0092, r = −0.962*; and 9 DAI, y = −0.0055x + 1.0708, r = −0.964*. (c) R/S ratio: 3 DAI, y = −0.001x + 0.3614, r = 0.843*; 6 DAI, y = −0.001x + 0.3608, r = 0.941*; and 9 DAI, y = 0.0001x + 0.302, r = 0.094*.

Measurement of Sucrose in Shoots and Roots. The sucrose level was measured using the method of Xue (1985). All rice plants were cut and leaves were removed. Shoots and roots were dried in an electric oven at 80°C for 24 h and then ground. Eight milliliters of 80% alcohol was added into a flask with 0.1 g of ground plant materials and then extracted in water bath at 80°C for 30 min. The supernatant was absorbed and centrifuged at 2,000 × *g* for 15 min. This extracted process was replicated three times. The supernatant was collected, and then 24 ml of such supernatant put into 100-ml measuring flask for being decolorized and filtered by addition of 0.1 g of active carbon. One milliliter of the filtered solution was absorbed into a test tube, in which 0.1 ml of 2 N NaOH was added, bathed in boiling water for 10 min, and then cooled in running water. Finally, 3.5 ml of 30% HCl and 1 ml of 0.1% resorcin were added, and the mixture was placed in bathing water at 80°C for 10 min of development before being cooled in running water. Optical density $(OD)_{500}$ values were detected in the UV755B spectrometer (Shanghai Precision Science Instrument Ltd. Co., Shanghai, China).

Measurement of Soluble Sugar in Shoots and Roots. The same process as described above was used to extract soluble sugar from rice shoots and roots. One milliliter of distilled water and 4 ml of 0.2% anthrone were put into 1 ml of extraction solution, bathed in boiling water for 15 min, and then cooled. OD_{620} values were detected with the UV755B spectrometer (Shanghai Precision Science Instrument Ltd. Co.).

Comparison of Root/Shoot (R/S) Ratio for Sucrose and Soluble Sugar Contents. Percentage of increase or decrease of R/S ratios for sucrose and soluble sugar contents at 3 and 6 d after *N. lugens* infestation (3 DAI and 6 DAI) for TN1 and Xieyou 963 was calculated as follows:

$$\text{Percentage of increase or decrease} = ((\text{R/S ratios for sucrose and soluble sugar contents at 6 DAI} - \text{the ratios at 3 DAI})/\text{ratios at 3 DAI}) \times 100.$$

Statistical Analysis. Data for dry biomass, sucrose and soluble sugar contents, and their R/S ratios were analyzed with a one-way analysis of variance (ANOVA). To compare differences in the response of the two varieties to different levels of *N. lugens* infestation, the R/S ratios of sucrose and soluble sugar contents were analyzed with a two-way ANOVA. Means were compared using Tukey's honestly significant difference (HSD) test (α = 0.05). All these statistical analyses were conducted using the SPSS program (SPSS Inc. 2002).

Table 1. Changes of sucrose and soluble sugar contents (milligrams per gram) in rice plants for TN1 under *N. lugens* infestation

Sugar	DAI	*N. lugens* density	Shoot (S)	Root (R)	R/S
Sucrose	3	10	34.7 ± 2.0a	14.3 ± 4.0a	0.33 ± 0.03a
		20	30.3 ± 2.5ab	12.7 ± 2.1ab	0.36 ± 0.03a
		40	31.0 ± 1.2ab	11.2 ± 1.6abc	0.33 ± 0.04a
		60	27.2 ± 4.6b	8.9 ± 1.9bc	0.34 ± 0.06a
		CK	35.8 ± 1.1a	7.2 ± 1.6c	0.20 ± 0.02b
	6	10	27.2 ± 4.1abc	11.7 ± 0.7ab	0.41 ± 0.02ab
		20	33.4 ± 3.8ab	11.8 ± 0.8a	0.38 ± 0.02ab
		40	26.6 ± 0.7bc	10.6 ± 1.9ab	0.43 ± 0.03a
		60	23.4 ± 3.0c	9.7 ± 1.1b	0.37 ± 0.03b
		CK	34.0 ± 3.2a	10.2 ± 0.7ab	0.32 ± 0.02c
Soluble sugar	3	10	40.6 ± 2.4c	11.9 ± 1.8b	0.29 ± 0.05bc
		20	51.2 ± 1.4b	26.7 ± 1.7a	0.52 ± 0.02a
		40	52.8 ± 4.0b	27.2 ± 3.5a	0.52 ± 0.08a
		60	40.6 ± 4.3c	15.1 ± 4.2b	0.40 ± 0.02b
		CK	61.4 ± 4.2a	13.7 ± 1.3b	0.24 ± 0.03c
	6	10	37.9 ± 5.4c	23.3 ± 0.6a	0.65 ± 0.05a
		20	58.7 ± 1.5a	25.5 ± 2.0a	0.44 ± 0.03b
		40	47.1 ± 2.8b	20.3 ± 6.4a	0.49 ± 0.09b
		60	35.7 ± 3.3c	22.7 ± 3.4a	0.63 ± 0.05a
		CK	49.8 ± 2.2b	24.8 ± 3.7a	0.47 ± 0.07b

Means ± SE followed by different letters within a column of the same sugar and DAI are significantly different at the 5% level.

Results

Dry Weight and Sugar Contents in Roots and Shoots from Uninfested Rice Plants. Dry weights of roots and shoots from the resistant variety Xieyou 963 were significantly greater compared with the susceptible variety TN1 when they were not infested by *N. lugens*, although the R/S weights did not show significant differences between the two varieties (Fig. 1). Significantly higher sucrose content in shoots from Xieyou 963 than from TN1 led to significant differences in the R/S ratio between the two varieties (Fig. 1). However, soluble sugar content in roots was significantly higher for TN1 than for Xieyou 963, but inversely that in shoots was lower for TN1 than for Xieyou 963; hence, the R/S ratio of soluble sugar content was significantly higher for TN1 than for Xieyou 963 (Fig. 1).

Changes in Dry Weight of Roots and Shoots Due to *N. lugens* Infestation. The dry weight of both shoots and roots in both rice varieties declined linearly with the increase of *N. lugens* densities (Fig. 2), although the coefficients of regression between reduction in dry weight and the density of *N. lugens* varied with the duration of infestation. However, the two varieties apparently had different relationships between the R/S ratio of dry biomass and *N. lugens* densities. The R/S for TN1 increased with the increase of infestation densities, especially as measured at 9 DAI, whereas that for Xieyou 963 decreased with the

Table 2. Changes of sucrose and soluble sugar contents (milligrams per gram) in rice plants for Xieyou 963 under *N. lugens* infestation

Sugar	DAI	*N. lugens* density	Shoot (S)	Root (R)	R/S
Sucrose	3	20	29.5 ± 1.3b	17.5 ± 2.1a	0.65 ± 0.02a
		40	21.9 ± 0.4c	12.8 ± 1.6b	0.55 ± 0.03b
		60	28.1 ± 3.4b	16.9 ± 2.8ab	0.57 ± 0.04b
		80	29.1 ± 0.8b	17.1 ± 2.1a	0.65 ± 0.04a
		CK	34.6 ± 2.2a	18.6 ± 1.8a	0.56 ± 0.01b
	6	20	26.6 ± 2.7ab	11.7 ± 1.5a	0.44 ± 0.02ab
		40	31.1 ± 3.3ab	12.0 ± 1.4a	0.38 ± 0.03bc
		60	30.4 ± 2.2ab	7.5 ± 0.7b	0.23 ± 0.02d
		80	23.9 ± 0.2b	4.9 ± 1.6b	0.29 ± 0.08cd
		CK	32.4 ± 6.1a	14.2 ± 2.2a	0.52 ± 0.06a
Soluble sugar	3	20	39.5 ± 1.4a	25.1 ± 3.1b	0.64 ± 0.07b
		40	38.6 ± 5.8a	24.9 ± 2.7b	0.69 ± 0.09ab
		60	40.0 ± 3.1a	30.9 ± 1.5a	0.800 ± 0.05a
		80	47.2 ± 2.1a	28.3 ± 0.9ab	0.62 ± 0.05b
		CK	32.6 ± 3.4c	13.5 ± 1.0d	0.44 ± 0.03bc
	6	20	38.0 ± 3.1abc	21.5 ± 2.2b	0.51 ± 0.04b
		40	43.6 ± 4.3a	18.2 ± 1.2bc	0.42 ± 0.05bc
		60	35.8 ± 3.5bc	15.2 ± 3.0cd	0.36 ± 0.03c
		80	42.7 ± 0.7ab	28.0 ± 1.5a	0.67 ± 0.04a
		CK	49.8 ± 2.2b	24.8 ± 3.7a	0.47 ± 0.07b

Means ± SE followed by different letters within a column of the same sugar and DAI are significantly different at the 5% level.

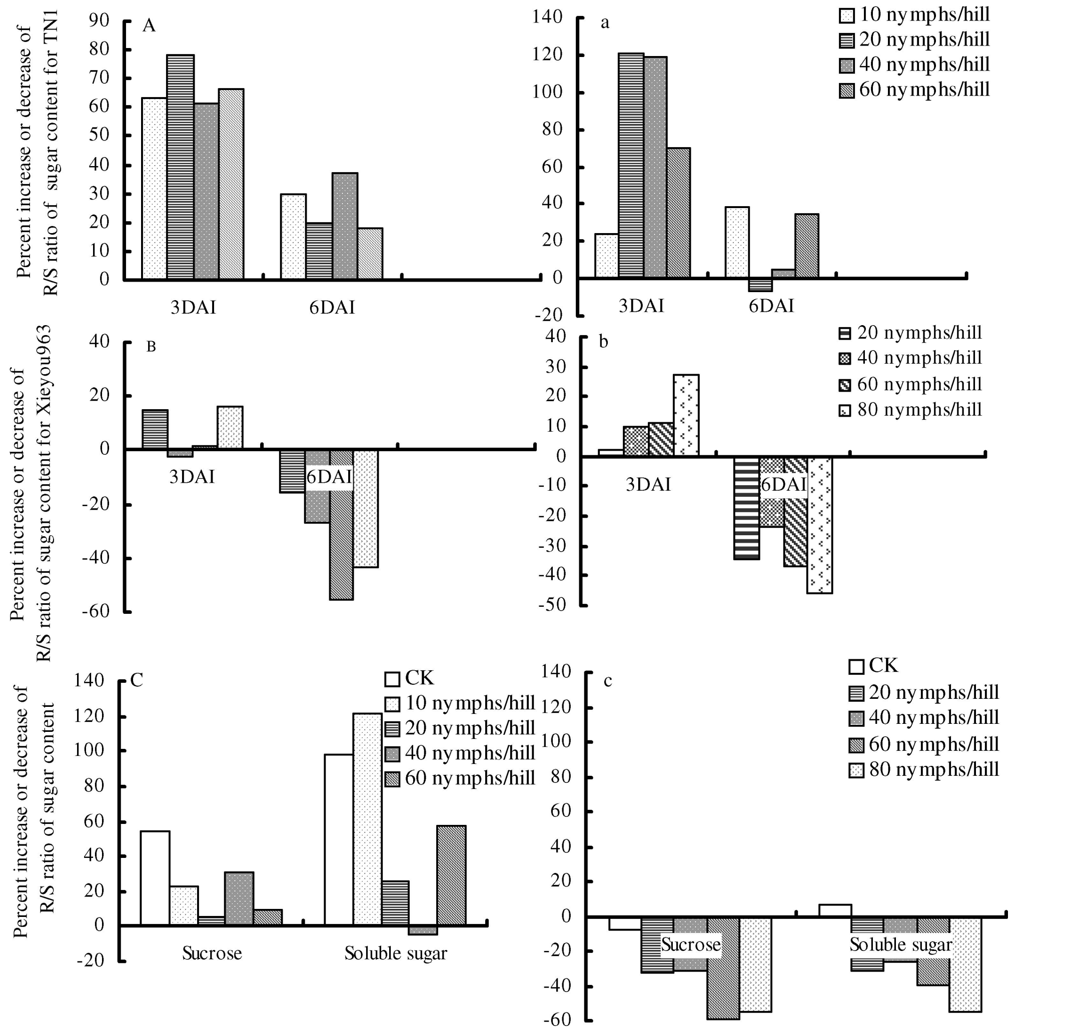

Fig. 3. Percentage of increase or decrease of R/S ratio for sucrose and soluble sugar contents in TN1 and Xieyou 963 plants under *N. lugens* infestation compared with R/S ratio of controls. (A) – sucrose and (a) – soluble sugar for TN1 at 3 and 6 DAI. (B) – sucrose and (b) – soluble sugar for Xieyou 963 at 3 and 6 DAI. (C) – TN1 and (c) – Xieyou 963 at 6 DAI compared with 3 DAI.

increase of infestation densities at 3 DAI and 6 DAI, although a weak positive relationship between these two variables was shown at 9 DAI (Fig. 2).

Changes in Sugar Contents in Roots and Shoots after *N. lugens* Infestation. Feeding by *N. lugens* caused significant changes in the sugar content of roots and shoots in the two rice varieties. However, the pattern of these changes in response to the pest infestation was somehow different between the two varieties. Sucrose and soluble sugar contents in the shoot of infested TN1 plants largely decreased, whereas those in their roots did not change or even increased compared with the control (Table 1). In comparison with the control, less significant changes in sucrose and soluble sugar contents were found in Xieyou 963 infested by *N. lugens* (Table 2). These differences between the two rice varieties are well reflected in their R/S ratios in sucrose and soluble sugar contents. First, the R/S ratios were generally smaller in TN1 than in Xieyou 963. Second, the R/S ratios in TN1 infested by *N. lugens* were all significantly increased compared with the control (Fig. 3), with few exceptions, whereas the R/S ratios in the infested Xieyou 963 plants only increases slightly at 3 DAI, and even significantly decreased at 6 DAI compared with the control (Fig. 3).

Discussion

Plants take up nutrients and water that essential for the growth of shoots largely through their root system, whereas the growth of roots relies on the energy supplied by photosynthesis of shoots. Thus, roots and shoots interplay to perform their functions. However, roots and shoots compete with each other for nutrient substances to grow when the plants are facing with environmental stress (Luo and Li 1996, Feng and Luo 1999). Therefore, whether roots and shoots interplay or compete depends on environmental conditions. When environmental factors favor the growth of both roots and shoots, they interplay; otherwise, they are in competition (Magnani et al. 2000). Such a dynamic relationship between roots and shoots is often reflected in the allocation of assimilates between the above- and underground organs (Hunt et al. 1998, Zerihun et al. 2000, Hebert et al. 2001). Infestation by *N. lugens* is often one of the major environmental stresses for rice plants, which are known to alter the allocation of assimilates between roots and shoots (Sogawa 1971, 1982; Watanabe and Kitagawa 2000).

The current study demonstrated, for the first time, that changes in the R/S ratios of sucrose and soluble sugar content in rice plants varied with not only the duration of *N. lugens* infestation but also variety. The R/S ratios of sucrose and soluble sugar content after *N. lugens* infestation on the susceptible variety TN1 initially increased compared with the control but declined with the increase of infestation duration. However, these ratios in the resistant variety Xieyou 963 little changed at 3 DAI and reduced at 6 DAI. This result indicated that the two varieties showed significant different physiological responses to *N. lugens* infestation. Thus changes in the R/S ratio of some biochemical substances in rice plants under *N. lugens* infestation can be considered as an index of susceptibility to this pest.

It has been reported that *N. lugens* and *Sogatella furcifera* (Horvath) feeding on rice plants suppresses photosynthesis and other physiological process (Wang et al. 1998, Watanabe and Kitagawa 2000). *N. lugens* feeding removes assimilates and water from phloem, and thus the effect of *N. lugens* on rice plants could be regarded as an extra "sink" for photosynthates (Sogawa 1982). However, the amount of plant sap sucked by *N. lugens* varies with rice variety, being significantly lower in resistant varieties than in susceptible ones (Zeng and Wung 1984). Chen et al. (2003a) demonstrated that more assimilates were detained in the rice plants of a susceptible variety after *S. furcifera* infestation compared with a resistant variety, indicating that downward (roots) transportation of assimilates in the susceptible variety under *S. furcifera* infestation is blocked and the R/S of assimilates reduced. For example, *S. furcifera* infestation reduced soluble sugar content in the roots of the resistant variety by 34.16%, whereas by 16.83% in the susceptible variety (Chen et al. 2003a). The resistant variety is characterized by compensation through the increase of tillers and growth for the damage of *N. lugens* infestation (Chen et al. 2003b). The results of this study suggested that ssimilates that were transported to roots significantly decreased, or that assimilates in roots were transferred upward for the growth of shoots in Xieyou 963; thereby, the R/S ratio of sucrose and soluble sugar contents significantly reduced in the resistant variety. By comparison, TN1 did not show such a transference mechanism so that a relatively high content of assimilates remained in roots, leading to a significant increase in the R/S ratio of sucrose and soluble sugar in the susceptible variety.

Acknowledgments

We thank two anonymous referees and the editor for corrections and comments on an early version of the article. This research was supported by National Natural Science Foundation of China (grant No. 30670323) and Natural Science Foundation of Ministry of Education of China (grant No. 20061117001).

References Cited

Bae, S. H., and M. D. Pathak. 1970. Life history of *Nilaparvata lugens* (Homoptera: Delphacidae) and susceptibility of rice varieties to its attacks. Ann. Entomol. Soc. Am. 63: 149–155.

Chen, J. M., X. P. Yu, J. W. Chen, Z. X. Lu, J. A. Cheng, L. Y. Tao, X. S. Zheng, and H. X. Xu. 2003a. Relationship between photosynthesis changes in leaves of rice plants infested by whitebacked planthopper, *Sogatella furcifera* Horvath and its resistance. Acta Agric. Nucleatae Sin. 17: 423–426.

Chen, J. M., X. P. Yu, J. A. Cheng, Z. X. Lu, X. S. Zheng, and H. X. Xu. 2003b. Evaluation for tolerance and compensation of rice varieties to infesting of brown planthopper, *Nilaparvata lugens.* Chin. J. Rice Sci. 17: 265–269.

Dyck, V. A., and B. Thomas. 1979. The brown planthopper problem, pp. 3–17. *In* International Rice Research Institute, brown planthopper: threat to rice production in Asia. Los Banos, Philippines.

Feng, G. L., and Y. P. Luo. 1999. Simulation on functional equilibrium of winter wheat root and shoot under different soil water regimes. Acta Ecol. Sin. 19: 96–103.

Flinn, P. W., A. A. Hower, and D. P. Knievel. 1990. Physiological response of alfalfa to injury by *Empoasca fabae* (Homoptera: Cicadallidae). Environ. Entomol. 19: 176–181.

Hebert, Y., E. Guingo, and O. Loudet. 2001. The response of root/shoot partitioning and root morphology to light reduction in maize genotype. Crop Sci. 41: 363–371.

Hunt, H. W., J. A. Morgan, and J. J. Read. 1998. Simulation growth and root-shoot partitioning in prairie grasses under elevated atmospheric CO_2 and water stress. Ann. Bot. 81: 489–501.

Lambers, H., F. S. Chapin, III, and T. L. Pons. 1998. Plant physiological ecology. Springer, New York.

Ling, Q. H., and L. Ling. 1984. Studies on the functions of roots at different node positions and their relation to the yield formation in rice plants. Sci. Agric. Sin. 5: 3–11.

Luo, Y. P., and Y. Z. Li. 1996. Roots and soil system and N- and water-use efficiency of water and nitrogen in crop. China Agricultural Press, Beijing, China.

Magnani, F., M. Mencuccini, and J. Grace. 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. Plant Cell Environ. 23: 251–263.

Naba, K. 1988. Studies on the sucking damage to rice plants caused by the green rice planthopper, *Nephotettix cincticeps* Uhler. 3. Physiological responses of rice plants to sucking in panicles. Jpn. Appl. Entomol. Zool. 32: 31–36.

Nielsen, G. R., W. O. Lamp, and G. W. Stutte. 1990. Potato leafhopper (Homoptera: Cicadallidae) feeding disruption of phloem translocation in alfalfa. J. Econ. Entomol. 83: 807–813.

Pang, X., C. J. Li, and F. S. Zhang. 2000. Effect of partial-root supply of P nutrient on the growth and assimilate distribution of wheat seedlings. Acta Agron. Sin. 26: 719–724.

Qiu, H. M., J. C. Wu, G. Q. Yang, B. Dong, and D. H. Li. 2004. Changes in the uptake function of the rice root to nitrogen, phosphorus and potassium under brown planthopper, *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae) and pesticide stresses, and effect of pesticides on rice-grain filling in field. Crop Prot. 23: 1041–1048.

Shi, Q. H., Y. J. Huang, M. Y. Li, Y. Q. Xu, X. M. Tan, and P. L. Zhang. 1997. Studies on the heredity of root characteristics and correlation between the characteristics of roots and upperground parts in rice. Acta Agric. Sin 30: 61–67.

Sogawa, K. 1971. Effects of feeding of the brown planthopper on the components in the leaf blade of rice plants. Jpn. J. Appl. Entomol. Zool. 15: 175–179.

Sogawa, K. 1980. Chemical nature and excretory activity of honeydew in the brown planthopper, *Nilaparvata lugens* (Homoptera: Delphacidae). Proc. Assoc. Plant Prot. Hokuriku 28: 30–35.

Sogawa, K. 1982. The rice brown planthopper: feeding physiology and host plant interactions. Annu. Rev. Entomol. 27: 49–73.

SPSS Inc. 2002. SPSS 11 for Mac OS X. SPSS Inc., Chicago, IL.

Wang, R. F., X. N. Chen, and Y. D. Zhou. 1998. Effect of *Nilaparvata lugens* and *Sogatella furcifera* infestations on vegetable growth of 1 rice plants. Chin. J. Appl. Ecol. 9: 51–54.

Wang, Y. L., J. Z. Cai, J. S. He, L. Chen, J. K. Xu, and Y. Bian. 1992. The relationship between spikelet-root-activity and grain filling and ripening in rice (*Oryza sativa*). Acta Agron. Sin. 18: 81–89.

Wang, Y. L., Y. L. Yao, B. Y. Liu, Z. L. Lu, J. Y. Huang, J. K. Xu, and J. Z. Cai. 1997. Effect of nitrogen supplying levels and timing on the development of roots in hybrid indica rice. Acta Agron. Sin. 23: 699–706.

Watanabe, T., and H. Kitagawa. 2000. Photosynthesis and translocation of assimilates in rice plants following phloem feeding by the planthopper *Nilaparvata lugens* (Homoptera: Delphacidae). J. Econ. Entomol. 93: 1192–1198.

Wu, J. C., H. M. Qiu, G. Q. Yang, B. Dong, and H. N. Gu. 2003. Nutrient uptake of rice roots in response to infestation of *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). J. Econ. Entomol. 96: 1798–1804.

Wu, J. C., Z. H. Qiu, J. L. Ying, B. Dong, and H. N. Gu. 2004. Changes of zeatin riboside content in rice plants due to infestation by *Nilaparvata lugens* (Homoptera: Delphacidae). J. Econ. Entomol. 97: 1917–1922.

Xue, Y. L. 1985. Experimental manual of plant physiology. Shanghai Science and Technology Press, Shanghai, China.

Yang, J. C., S. B. Peng, R. M. Visperas, A. L. Sanico, Q. S. Zhu, and S. L. Gu. 2000. Grain filling pattern and cytokinin content in the grains and roots of rice plants. Plant Growth Regul. 30: 261–270.

Yang, J. C., S. B. Peng, S. L. Gu, R. M. Visperas, and Q. S. Zhu. 2001. Changes in zetin and zetin riboside content in rice grains and roots during grain filling and the relationship to grain plumpness. Acta Agron. Sin. 27: 35–42.

Yang, J. C., J. H. Zhang, Z. Q. Wang, Q. S. Zhu, and L. J. Liu. 2002. Abscisic acid and cytokinins in the root exudates and leaves and their relationship to senescence and remobilization of carbon reserves in rice subjected to water stress during grain filling. Planta 215: 645–652.

Zeng, L., and J. T. Wung. 1984. The resistance of rice varieties to the brown planthopper, *Nilaparvata lugens* (Stål). Acta Entomol. Sin. 7: 375–383.

Zerihun, A., V. P. Utschick, and H. Assirirad. 2000. Compensatory roles of nitrogen uptake and photosynthetic N-use efficiency in determining plant growth response to elevated CO2: evaluation using a functional balance model. Ann. Bot. 13. 86: 723–730.

Received 26 March 2007; accepted 8 October 2007.