# Photosynthesis and Translocation of Assimilates in Rice Plants Following Phloem Feeding by the Planthopper *Nilaparvata lugens* (Homoptera: Delphacidae)

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**ABSTRACT** Experiments were conducted to measure the effect of feeding by the planthopper *Nilaparvata lugens* (Stål) on photosynthesis and the translocation of assimilates in rice plants, *Oryza sativa* L. We used mature japonica rice plants and applied the $^{13}CO_2$ feeding method to evaluate those physiological effects. The photosynthetic rate was suppressed by *N. lugens* infestation, especially at the lower leaf position, with rates 30% lower than that of control plants at the booting stage. Leaf nitrogen concentration in infested plants was also lower than that in control plants. After flowering, the chlorophyll content and total plant dry weight were reduced by *N. lugens*. Stem and sheath dry weights were significantly reduced by *N. lugens* infestation, whereas panicle dry weight was not affected. Little effect was found on disruption in translocation of assimilates, even when $^{13}CO_2$ was supplied to the infested leaves. Results suggested that removal of assimilates and reduction in photosynthesis by *N. lugens* have the greatest effect on growth and yield of rice plants as compared with the disruption in the translocation of assimilates. Plant death can occur by *N. lugens* infestation if the amount of energy supplied is less than that required for tissue maintenance.

**KEY WORDS** *Nilaparvata lugens*, rice, photosynthesis, translocation of assimilates, stable isotope, $^{13}C$

THE PLANTHOPPER *Nilaparvata lugens* (Stål), a phloem feeder (Sogawa 1982), is a serious pest infesting rice in East Asia. Feeding by this species can cause plant death. *N. lugens* feeding may reduce yield, even if the planthopper population density is not high enough to kill plants (Hirao 1971, Sogawa and Cheng 1979, Watanabe et al. 1997). The amount of dry matter consumed by *N. lugens* accounts for 28% of the total dry matter reduction in rice plants infested at the reproductive stage (after panicle initiation) (Sogawa 1994). A similar relationship was observed during the vegetative stage of rice plants infested with the planthopper *Sogatella furcifera* (Horváth) (Watanabe and Sogawa 1994). These studies show that planthopper infestations cause physiological changes that reduce photosynthesis or alter the translocation of photosynthates. Metabolic changes in rice plants after *N. lugens* infestation were also reported (Sogawa 1971, Cagampang et al. 1974).

Ho et al. (1982) and Rubia-Sanchez et al. (1999) reported that *N. lugens* reduce the photosynthetic activity of young plants of some rice cultivars. Watanabe and Sogawa (1994) reported that photosynthesis of the top leaves decreased with high-density *S. furcifera* infestation at the vegetative stage. Because nymphs and adults of *N. lugens* prefer to feed on the lower leaf sheaths just above the water surface (Kuno 1968), the effect of insect feeding on leaf photosynthesis may change along with the vertical distance from the feeding site to each leaf blade, especially in mature rice plants. However, no studies have been done to assess the changes in the photosynthesis profiles in the canopy of the rice plants at the reproductive stage.

Disruption of the translocation of assimilates has been studied in some homopteran insects (Naito 1977, Kenmore 1980, Naba 1988, Flinn et al. 1990, Nielsen et al. 1990). Naba (1988) found that starch accumulation in the second internode increased as a result of infestation by the leafhopper *Nephotettix cincticeps* Uhler feeding on a flag leaf sheath or topmost internode. Flinn et al. (1990) reported that potato leafhopper, *Empoasca fabae* (Harris), infestation increased leaf total nonstructural carbohydrate of alfalfa from 49 to 465% over that in noninfested plants. Nielsen et al. (1990) reported the disruption of translocation by *E. fabae* feeding by using a $^{14}C$ fixation method. A similar result was observed in ladino clover infested with *Empoasca sakaii* Dworakowska (Naito 1977). Kenmore (1980) reported that the translocation of assimilates was completely blocked by *N. lugens* feeding on rice seedlings. He used the autoradiography method with $^{14}CO_2$. Watanabe et al. (1997) estimated that the translocation of assimilates from stems to panicles was partially disrupted by *N. lugens* feeding. They measured the dry matter weight of each organ in rice

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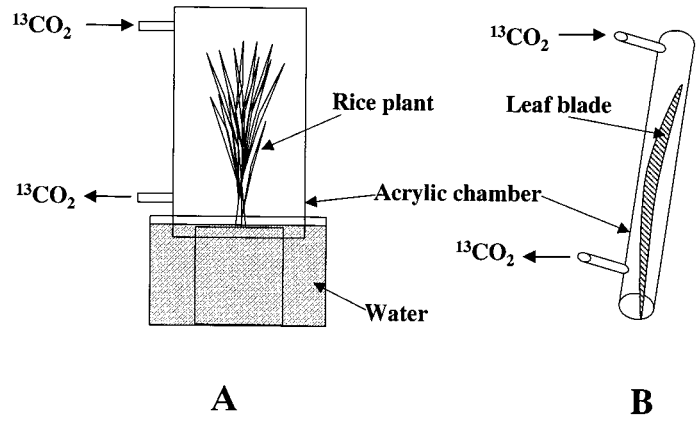


**Fig. 1.** The $^{13}CO_2$ feeding in rice plants. (A) experiment 1. Each plant was enclosed in an acrylic chamber. The $^{13}CO_2$ was circulated by an air pump connected to the chambers. (B) experiment 2. Each leaf blade was placed in a chamber.

plants under field conditions at several times during maturity and estimated dry matter accumulation indirectly. To clarify the feeding effects of *N. lugens* on rice yield and plant death, we need a further and more detailed investigation of the changes in photosynthesis and assimilate disruption during the reproductive stage (after panicle initiation to the harvest).

Tanaka (1958) reported that the $^{14}C$ assimilated in the upper leaves is translocated mainly to the panicles during maturity, but $^{14}C$ assimilated in the lower leaves is mostly translocated to lower parts of the plants and roots. This observation suggests that the effect of disruption of translocation on plant production, such as the accumulation of carbohydrate into panicles, may depend on the positional relationship among the source, planthopper feeding site, and sink.

Watanabe et al. (1997) constructed a rice growth model to evaluate *N. lugens* infestation during grain ripening. They divided the canopy of the rice plants into five leaf layers, with the lowest leaf layer subjected to *N. lugens* feeding. However, the effect of feeding on photosynthesis for each leaf layer and translocation of assimilates between leaf layers was not incorporated into the model (Watanabe et al. 1997). An understanding of the changes to the physiological processes of rice plants caused by *N. lugens* could improve our ability to forecast plant growth and yield under insect infestation. In this study, we used the stable isotope $^{13}C$ to measure the changes in photosynthetic rate of each leaf within a plant and the changes in assimilate translocation from leaf blade to other organs of the rice plant infested with *N. lugens.* We also measured the dry weight of each organ and the nitrogen or chlorophyll content of the leaves.

## Materials and Methods

Two experiments were conducted at the Kyushu National Agricultural Experiment Station, Nishigoshi, Kumamoto, Japan (32° 53′ N, 130° 45′ E). The first experiment, conducted in 1993, examined the effect of feeding by *N. lugens* on the photosynthetic rate. The second experiment, conducted in 1995, examined the effects of *N. lugens* feeding on the translocation of assimilates.

The japonica type rice 'Reiho' is susceptible to *N. lugens* and was used for the first experiment. The japonica type rice 'Hinohikari', which is also susceptible to *N. lugens,* was used for the second experiment. Rice seedlings were transplanted in pots containing high humic volcanic ash soil fertilized with 10 g-N, 10 g-P, and 10 g-K $m^{-2}$. The insects were reared on Reiho seedlings under two 40-W fluorescent lamps in a room at 25°C, 70% RH, and a photoperiod of 16:8 (L:D) h.

For the first experiment, 30-d-old seedlings of Reiho were transplanted singly in 200-$cm^2$ pots on 8 August 1993. Plants were grown under natural temperature and daylength conditions in a greenhouse with a glass roof and wire net sides to prevent natural pest infestations. At the booting stage (66 d old), 100 fourth- to fifth-instar *N. lugens* nymphs were released on each plant enclosed in white nylon mesh and allowed to feed for 11 d, from 13 to 23 September. Based on the field observation, 200 or more *N. lugens* per plant cause plant death (Watanabe 1994). We set the density of 100 nymphs per plant with the expectation of severe infestation but not the death of plants. Control plants were covered with nylon mesh but not infested with *N. lugens.* There were five replicates for each treatment and control.

After the planthoppers were removed, each plant was exposed to $^{13}CO_2$ for 20 min. The $^{13}CO_2$ was introduced using a procedure similar to that of Kitagawa et al. (1992). Each plant was enclosed in a 21.4-liter acrylic chamber and placed in a water tank with water at the same height as the pot to prevent air leaking from the basal part of the chamber (Fig. 1). Two acrylic chambers, containing an infested and a control plant, were connected with vinyl tubes. An air pump and a 1.0-liter glass flask were also connected to those chambers so that the air could circulate within them. $Ba^{13}CO_3$ powder (200 mg) was placed inside the flask. The air inside the chamber was circulated at 6.0 liters/min to reduce the normal $CO_2$ concentration before feeding the plants $^{13}CO_2$. Five min-

utes later, 1.5 ml of 10% lactic acid was injected into the flask to generate $^{13}CO_2$, followed by 1 ml of lactic acid applied twice at 5-min intervals. Two and a half milliliters of 25% lactic acid was injected to convert the remaining $Ba^{13}CO_3$ to $^{13}CO_2$. Feeding of $^{13}CO_2$ was made at >1,200 $\mu$ mol $m^{-2}s^{-1}$ PAR (photosynthetically active radiation).

Each leaf was clipped immediately after the $^{13}C$ feeding. Leaf area was measured using a leaf area meter (AAM-7, Hayashi Denko, Tokyo). The leaves were oven dried at 80°C for 48 h and weighed. All leaf samples were ground to a fine homogeneous powder with a high-speed vibrating sample mill. The $^{13}C$ concentration of each leaf was determined with an infrared $^{13}C$ analyzer (EX-130S, Japan Spectroscopic, Tokyo). The total leaf nitrogen content was determined using an NC analyzer (Sumigraph model NC-80, Sumitomo Kagaku, Tokyo).

For the second experiment, 2-d-old seedlings of Hinohikari were transplanted singly in 100-$cm^2$ pots on 25 June 1995 and grown inside a controlled greenhouse at 25°C and 70% RH under natural daylength. Tillers were clipped at the maximum tillering and booting stages to retain a main stem. Four days after flowering on 17 September, five leaves, from the flag leaf (terminal leaf) to the fifth leaf (counting from the flag leaf downward), were kept on a main stem and the other leaves were trimmed. Twenty-fourth instar *N. lugens* were enclosed on the fifth leaf sheath using cylindrical cages (6 cm diameter and 17 cm high). Hoppers were removed after 6 d. Control plants were caged but not infested. We used a SPAD-502 chlorophyll meter (Minolta, Tokyo) to measure the relative amount of chlorophyll in each leaf after leaf infestation. Because the SPAD reading, which is an index of chlorophyll content, is associated with leaf nitrogen content, it has been widely used to estimate leaf nitrogen content (Takebe and Yoneyama 1989, Turner and Jund 1991, Peng et al. 1996). After infestation, both infested and control plants were divided into three groups, with $^{13}CO_2$ fed to the flag leaf, third leaf, and fifth leaf, respectively. Each leaf blade that was to be supplied with $^{13}CO_2$ was placed into an acrylic cylinder (2 cm diameter and 40 cm long) and fed $^{13}CO_2$. Two chambers, each containing an infested leaf and a control leaf, were connected with tubes and $^{13}CO_2$ was fed to each simultaneously. Fifty milligrams of $Ba^{13}CO_3$ powder was used, with a 1.5-h feeding period. The procedure for generating $^{13}CO_2$ in the flask was the same as described in the first experiment. Forty-eight hours after feeding, the $^{13}C$ concentrations on treated and untreated leaf blades, sheaths and stem, panicle, and roots were measured. There were five replicates for each treatment and for the controls.

The natural abundance of $^{13}C$ is 1.11 atom% of the total carbon atoms in the plants. We calculated the "$^{13}C$ atom% excess" in the plant, which refers to the extra distribution of $^{13}C$ in the plants after $^{13}CO_2$ exposure, as follows:

$$^{13}\text{C atom\% excess} = {}^{13}\text{C atom\% of sample} - {}^{13}\text{C atom\% of natural abundance},$$

where $^{13}C$ atom% = (number of $^{13}C$ atoms/total number of carbon atoms) × 100. The natural abundance of $^{13}C$ was estimated for plants not fed $^{13}C$. For the first experiment, we calculated the $^{13}C$ mg excess in each leaf, which is given as follows:

$$^{13}\text{C mg excess} = \text{dry weight of each leaf (mg)} \times {}^{13}\text{C atom\% excess of the leaf}/100 \times (13/12).$$

Next, we calculated the "fixed $^{13}CO_2$ per unit leaf area per second" ($\mu$mol $^{13}CO_2/m^2/s$), which is an index of the photosynthetic rate in each leaf, is given by which

$$\text{Photosynthetic rate in each leaf} = \text{fixed } \mu\text{mol } {}^{13}CO_2/\text{leaf area } (m^2)/1{,}200\ (s).$$

The total photosynthetic rate of the plant was calculated as follows:

$$\text{Canopy photosynthetic rate} = \text{total fixed } \mu\text{mol } {}^{13}CO_2/\text{total leaf area } (m^2)/1{,}200\ (s).$$

For the second experiment, we calculated the distribution of $^{13}C$ excess in each plant organ 48 h after $^{13}CO_2$ feeding, which is given by:

$$^{13}\text{C\% excess in each plant organ} = {}^{13}\text{C mg excess in each plant organ}/\text{total } {}^{13}\text{C mg excess in the plant} \times 100.$$

For the first experiment, we evaluated the infestation effects on leaf area, photosynthetic rate, and nitrogen content in each leaf within a split-plot design with treatments (TR) as a main factor, and leaf positions nested within treatment (LP) as a second-stage factor using PROC GLM (SAS Institute 1990). The effect of the treatments was tested against the interaction between the treatment and the replication (TR × R), and the effect of $^{13}C$-fed leaf position (LP) and the interaction TR × LP were tested against the interaction between the replication, treatments, and leaf position (R × TR × LP). Wilcoxon's two-sample test was used to compare the total photosynthetic rate and the total nitrogen content for the controls and the infested plants.

For the second experiment, the SPAD reading value was analyzed within a split-plot design with treatments as a main factor, and the leaf positions nested within treatment as a second-stage factor. The effect of the treatments was tested by TR × R, and the effect of leaf position was tested using the interaction R × TR × LP.

The total weight of tagged $^{13}C$ and the percentage of $^{13}C$ remaining in the fed leaf (after arcsine transformation) were analyzed within a split-plot design with treatments as a main factor, and $^{13}C$-fed leaf position nested within treatments (LP′) as a second-stage factor. The effect of the treatments was tested against TR × R, and the effect of $^{13}C$-fed leaf position

**Table 1. ANOVA table for the effect of *N. lugens* infestation on leaf area, photosynthetic rate and nitrogen content of leaves (experiment 1)**

| Source of vairation | df | Leaf area | | Photosynthetic rate | | Nitrogen content | |
|---|---|---|---|---|---|---|---|
| | | *F* | *P* | *F* | *P* | *F* | *P* |
| Treatments (TR) | 1 | 1.07 | 0.3762 | 24.37 | 0.0159 | 14.37 | 0.0322 |
| Leaf position (LP) | 4 | 43.03 | 0.0001 | 63.72 | 0.0001 | 27.38 | 0.0001 |
| TR × LP | 4 | 2.28 | 0.0856 | 1.83 | 0.1517 | 1.15 | 0.3538 |

was tested using the interaction R × TR × LP′. We used Wilcoxon's two-sample test to compare the dry weight of the controls and the infested plants.

## Results

In the first experiment, *N. lugens* nymphs became adults during the infestation period. Hoppers fed near the stem base. The leaf area, photosynthetic rate, and nitrogen content in each leaf differed significantly according to leaf position (Table 1). The total leaf area of infested plants was reduced to 89% of the leaf area of the controls, but the differences between the controls and infested plants were not significant (Table 1).

The total photosynthetic rate of infested plants (11.55 ± 0.86 [mean ± SE] $\mu$mol$^{13}CO_2$/m$^2$/s) was lower than that of control plants (16.74 ± 0.41) by Wilcoxon's two-sample test ($P < 0.05$). The photosynthetic rate of individual leaves decreased gradually from the top to the bottom leaves in both the control and the infested plants (Fig. 2). The planthopper feeding had a significant effect to alter the photosynthetic rate. Leaf N concentration decreased from the top to the bottom in infested and control plants, and the treatment effect was also significant (Fig. 3; Table 1).

In the second experiment, the SPAD readings at each leaf position decreased from the top to the bottom of both control and infested plants (Fig. 4, $F = 305.45$; df = 4, 112; $P = 0.0001$). *Nilaparvata lugens* infestation significantly decreased SPAD readings (Fig. 4, $F = 22.61$; df = 4, 14; $P = 0.0003$). *Nilaparvata lugens* infestation also significantly reduced total dry weight, with results of 5.46 ± 0.09 (mean ± SE) g in infested plants and 5.75 ± 0.10 g in controls (Wilcoxon's two-sample test, $P < 0.05$). That difference of dry weight was mainly caused by the weight differences of leaf sheaths and stem of infested plants and those of control plants (2.39 ± 0.05 g in infested plants and 2.56 ± 0.06 g in controls, Wilcoxon's two-sample test, $P < 0.05$). The dry weight of other organs, panicle, leaves, and roots was not significantly different between the infested plants and the controls.

The total amount of $^{13}C$ remaining 48 h after $^{13}CO_2$ feeding was significantly different according to leaf position in plants fed $^{13}CO_2$ ($F = 24.4$; df = 2, 16; $P = 0.0001$), but significant differences in $^{13}C$ amounts were not found between the infested and the control plants ($F = 1.36$; df = 1, 4; $P = 0.3079$). The distribution pattern of labeled assimilates varied depending upon leaf position of $^{13}CO_2$ feeding (Fig. 5). About 80% of $^{13}C$ assimilated by the flag leaf was translocated into the panicle, whereas 0–5% of $^{13}C$ translocated when $^{13}CO_2$ was fed to the fifth leaf. In contrast, the amount of $^{13}C$ translocated into the roots from the $^{13}CO_2$ feeding site decreased from the bottom leaf to the top leaf.

The percentage of $^{13}C$ remaining in the fed leaf was significantly different according to leaf position of $^{13}CO_2$ feeding ($F = 14.32$; df = 2, 16; $P = 0.0003$), but it was not significantly different between the infested and the control plants ($F = 0.03$; df = 1, 4; $P = 0.8611$). This means that planthopper infestation does not block or change the assimilate translocation from infested leaves to other parts of the plant.

## Discussion

One-hundred fourth to fifth instar nymphs of *N. lugens* feeding mainly on the leaf sheaths of the fifth leaf reduced the photosynthestic rate, especially that

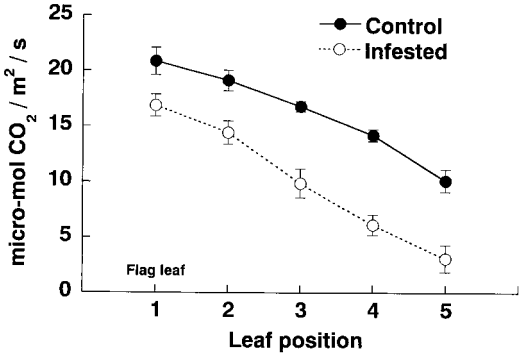


**Fig. 2.** The photosynthesis rate (mean ± SE) of each leaf (experiment 1).

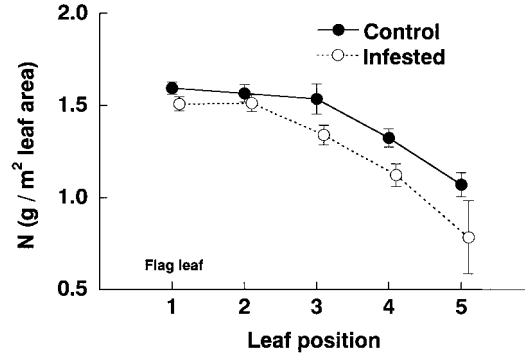


**Fig. 3.** The nitrogen concentration (mean ± SE) of each leaf (experiment 1).

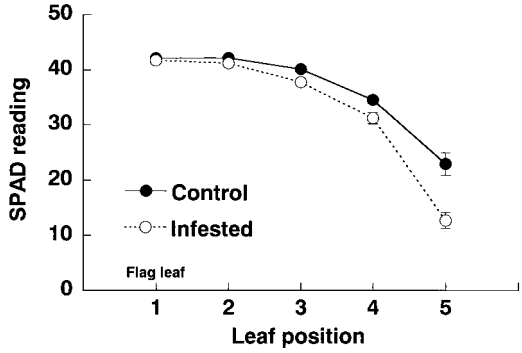


**Fig. 4.** The SPAD reading (mean ± SE) of each leaf. Control and infested plants, 6 d after infestation (experiment 2).

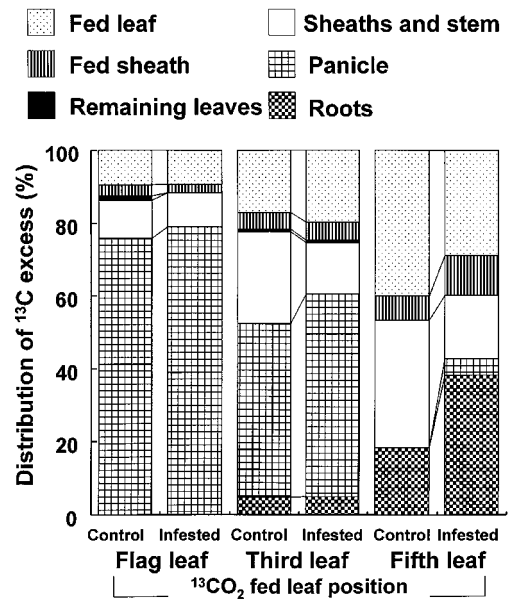


**Fig. 5.** The distribution pattern of $^{13}C$ excess in the plant parts 48 h after $^{13}CO_2$ feeding. Plants were divided into six parts: fed leaf, $^{13}CO_2$-exposed leaf blade; fed sheath, $^{13}CO_2$-exposed leaf sheath; remaining leaf, nonexposed leaf blade; sheaths and stem, nonexposed leaf sheath and main stem; panicle; and roots.

of the lower leaves, which was reduced by 30% (Fig. 2 and Table 1). Sato and Kim (1980) reported that the net photosynthesis of leaves three, four, and five were ≈60–70%, 30–50%, and 10%, respectively, of the net photosynthesis of the flag leaf in healthy plants under field conditions. At night, respiration by the lowest leaves resulted in the consumption of 40% of the photosynthates produced by the same leaves during the day (Sato and Kim 1980). Respiration plus *N. lugens* feeding may lead to a deficit of carbohydrates and cause senescence and partial death of the lowest leaves (Figs. 2 and 3).

Photosynthetic activity is highly correlated with leaf N concentration (van Keulen and Seligman 1987, Sinclair and Horie 1989, Hasegawa and Horie 1996). However, our results showed that the reduction in photosynthesis resulting from *N. lugens* feeding was greater than the corresponding reduction in leaf N content (Figs. 2 and 3). Photosynthesis is more highly correlated with soluble protein content than with total nitrogen or chlorophyll content (Makino et al. 1983, Oritani et al. 1979). More than half of the total soluble protein is composed of Ribulose-1,5-biphosphate (RuBP) carboxylaze, which is the main enzyme to execute $CO_2$ assimilation in photosynthesis (Makino et al. 1984). *Nilaparvata lugens* infestation causes an increase in free amino acids and a decrease in soluble protein in leaves (Sogawa 1971, Cagampang et al. 1974). Cagampang et al. (1974) also showed severe reduction in chlorophyll content of leaf blades with an increase in *N. lugens* density, whereas the total nitrogen content did not change one week after infestation. We conclude that *N. lugens* infestation accelerates the decomposition of RuBP carboxylaze to amino acids, and photosynthesis reduction starts before the reduction of total nitrogen in the leaf blade.

Leaf sheath and stem dry weight reduction were significant in *N. lugens* infested plants, whereas panicle dry weight was not reduced significantly. Rice plants usually do not produce any new organs after flowering and instead accumulate assimilates in the stem as nonstructural carbohydrate (NSC). Translocation of NSC to the panicle occurs during the grain ripening period. *Nilaparvata lugens* ingests sucrose from the leaf sheath and consequently reduces NSC accumulation in the stem. Reduction of photosynthesis by *N. lugens* feeding may also decrease the accumulation of NSC. The lack of differences in panicle weight between infested and control plants suggests that the translocation rate of NSC from the stem to the panicle may not be affected by *N. lugens* feeding as long as a certain amount of NSC remains in the stem.

Contrary to our observation, the complete blockage of the translocation of assimilates in infested plants by *N. lugens* was reported by Kenmore (1980). The difference in findings may be caused by the different stage and size of rice plants studied. We used matured plants while Kenmore (1980) employed 3-wk-old plants with no tillers. The impact of *N. lugens* feeding in his study may be much greater than that in our experiment. Severe disruption of translocation by insect feeding was observed with alfalfa infested by potato leafhoppers, *E. fabae* (Nielsen et al. 1990). Kabrick and Backus (1990) observed abnormal cell divisions and swelling in the vascular cambium and phloem of alfalfa infested with *E. fabae.* The disruption of translocation of assimilates may eventually lead to hopperburn (Kabrick and Backus 1990). A similar enlargement of cells in the phloem tissues was reported with alfalfa infested with *E. sakaii;* however, disruption of assimilates started before the cells enlarged (Naito 1977). Necrotic lesions and occlusion in the vascular tissues by *N. lugens* were reported in the rice plant (Sogawa 1982). However, *N. lugens* usually do not feed on inner leaf sheaths and internodes,

which are normally covered with lower leaf sheaths. Therefore the *N. lugens* infestation has a small effect on assimilate translocation from the upper leaf position and internodes to panicles during the grain ripening period. Our results suggest that the removal of assimilates and reduction in photosynthetic rate of leaves by the hopper feedings have the greatest effect on growth and yield on rice plants as compared with the disruption in the translocation of assimilates. The results also support the assumption that Watanabe et al. (1997) introduced in their model: *N. lugens* feeding does not change the translocation rate of carbohydrates from source to panicle.

The destination of assimilated $^{13}C$ depends on the $^{13}CO_2$-fed leaf position (Fig. 5, Tanaka 1958). The reduction in assimilate production of lower leaves by planthopper feeding may change the amount of the carbohydrates that maintain root activity and may impede the uptake of nutrients from roots. The respiration of rice plants might be changed by the planthopper infestation, but our experiments did not show any information about the respiration. Further investigation will be needed to clarify those physiological changes in rice plant caused by *N. lugens.*

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## References Cited

**Cagampang, G. B., M. D. Pathak, and B. O. Juliano. 1974.** Metabolic changes in the rice plant during infestation by the brown planthopper, *Nilaparvata lugens* Stål (Hemiptera:Delphacidae). Appl. Entomol. Zool. 9: 174–184.

**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.

**Hasegawa, T., and T. Horie. 1996.** Rice leaf photosynthesis as a function of nitrogen and crop developmental stage. Jpn. J. Crop Sci. 65: 553–554.

**Hirao, J. 1971.** Bionomics of the two injurious planthoppers in a paddy field and suitable timing of insecticide application. Bull. Chugoku Natl. Agric. Exp. Stn. Ser. E. 7: 19–48.

**Ho, D. T., E. A. Heinrichs, and F. Medrano. 1982.** Tolerance of the rice variety Triveni to the brown planthopper, *Nilaparvata lugens.* Environ. Entomol. 11: 598–602.

**Kabrick, L. R., and E. A. Backus. 1990.** Salivary deposits and plant damage associated with specific probing behaviors of the potato leafhopper, *Empoasca fabae,* on alfalfa stems. Entomolo. Exp. Appl. 56: 287–304.

**Kenmore, P. E. 1980.** Ecology and outbreaks of a tropical insect pest of the green revolution the rice brown planthopper, *Nilaparvata lugens* (Stål). Ph.D. dissertation, University of California, Berkeley.

**Kitagawa, H., K. Shimotsubo, O. Matsumura, and M. Yasuniwa. 1992.** The trial manufacture of $^{13}CO_2$ asimilating device for measuring photosynthetic rate under rice plant population. Rep. Kyushu Br. Crop Sci. Soc. Japan 59: 75–77.

**Keulen, H. van, and N. G. Seligman. 1987.** Simulation of water use, nutrition, and growth of spring wheat crop. Pudoc, Wageningen. pp. 310.

**Kuno, E. 1968.** Studies on the population dynamics of rice leafhoppers in a paddy field. Bull. Kyushu Agric. Exp. Stn. 14: 131–246.

**Makino, A., T. Mae, and K. Ohira. 1983.** Photosynthesis and ribulose-1,5-bisphosphate carboxylase in rice leaves: Changes in photosynthesis and enzymes involved carbon assimilation from leaf development through senescence. Plant Physiol. 73: 1002–1007.

**Makino, A., T. Mae, and K. Ohira. 1984.** Relationships between nitrogen and ribulose-1,5-bisphosphate carboxylase in rice leaves from emergence through senescence. Plant and Cell Physiol. 25: 429–437.

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

**Naito, A. 1977.** Studies on the feeding habits of some leafhoppers attacking the forage crops. III. Relation between the infestation by leafhopper and its feeding habits—Interruption of assimilates in the plant body by the feeding of *Empoasca sakaii* Dworakowska (Homoptera: Cicadellidae). Jpn. J. Appl. Entomol. Zool. 21: 1–5.

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

**Oritani, T., T. Enbutsu, and R. Yoshida. 1979.** Studies on the nitrogen metabolism in crop plants. 16. Changes in photosynthesis and nitrogen metabolism in relation to leaf area development of several rice cultivars. Jpn. J. Crop Sci. 48: 10–16.

**Peng, S., F. V. Garcia, R. C. Laza, A. L. Sanico, R. M. Visperas, and K. G. Cassman. 1996.** Increased N-use efficiency using a chlorophyll meter on high yielding irrigated rice. Field Crops Res. 47: 243–252.

**Rubia-Sanchez, E., Y. Suzuki, K. Miyamoto, and T. Watanabe. 1999.** The potential for compensation of the effects of the brown planthopper *Nilaparvata lugens* Stal (Homoptera: Delphacidae) feeding on rice. Crop Protection 18: 39–45.

**SAS Institute. 1990.** SAS/STAT user's guide, version 6, 4th ed., vols. 1 and 2. SAS Institute, Cary, NC, USA.

**Sinclair, T. R., and T. Horie. 1989.** Leaf Nitrogen, photosynthesis and crop radiation use efficiency: a review. Crop Sci. 29: 90–98.

**Sato, K., and J. M. Kim. 1980.** Relationship between environmental conditions and production and consumption activities of individual leaves in the population of rice plant in a paddy field. I. Changes in photosynthesis and dark respiration of individual leaves under field conditions. Jpn. J. Crop Sci. 49: 243–250.

**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. 1982.** The rice brown planthopper: Feeding physiology and host plant interactions. Annu. Rev. Entomol. 27: 49–73.

**Sogawa, K. 1994.** Feeding behaviour and damage mechanism of the rice planthoppers, pp. 143–154. *In* A. Elings and E.G. Rubia [eds.] Analysis of damage mechanisms by

pests and diseases and their effects on rice yield. SARP Res. Proceedings. Wageningen.

**Sogawa, K., and C. H. Cheng. 1979.** Economic thresholds, nature of damage, and losses caused by the brown planthopper, pp. 125–142. *In* Brown planthopper: Threat to rice production in Asia. International Rice Res. Institute, Manila.

**Takebe, M., and T. Yoneyama. 1989.** Measurement of leaf color scores and its implication to nitrogen nutrition of rice plants. JARQ 23: 86–93.

**Tanaka, A. 1958.** Studies on the characteristics of physiological functions of the leaf at a definite position on a stem of the rice plant. II. Asimilation capacity and translocation of assimilates in differently positioned leaves. J. Science Soil Manure, Japan. 29: 327–333.

**Turner, F. T., and M. F. Jund. 1991.** Chlorophyll meter to predict nitrogen topdress requirement for semidwarf rice. Agron. J. 83: 926–928.

**Watanabe. T. 1994.** Population dynamics of long distance migratory rice planthoppers, *Nilaparvata lugens* Stål and *Sogatella furcifera* Horváth, and growth and yield analysis of rice plants infested with these planthoppers. Ph.D. dissertation, Kyoto University, Japan.

**Watanabe. T., and K. Sogawa. 1994.** Growth and yield analysis of rice plants infested with long-distance migratory rice planthoppers. III. Quantitative evaluations of vegetative growth of rice plants infested white-backed planthopper, *Sogatella furcifera* Horváth (Homoptera: Delphacidae). Jpn. J. Appl. Entomol. Zool. 38: 275–281.

**Watanabe, T., L. T. Fabellar, L. P. Almazan, E. G. Rubia, K. L. Heong, and K. Sogawa. 1997.** Quantitative evaluation of growth and yield of rice plants infested with rice planthoppers, pp. 365–382. *In* M.J. Kropff et al. [eds.] Applications of Systems Approaches at the Field Level. Kluwer Academic Publishers, Dordrecht.

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