Nutrient Uptake of Rice Roots in Response to Infestation of *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae)

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ABSTRACT This study investigated the uptake of three macronutrients, including nitrogen (N), phosphorus (P), and potassium (K), by rice roots in response to different infestation levels of *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae). Hydroponics experiments were conducted on the rice variety 'Zhendao 2' (moderately resistant to *Tryporyza incertulas*, Lepidoptera: Pyralidae) and the variety 'Xiushui 63' (susceptible to *N. lugens*). In 'Zhendao 2', *N. lugens* infestation significantly influenced the uptake of P and K but not N, with P and K uptake decreasing as the duration of *N. lugens* infestation increased. In 'Xiushui 63', *N. lugens* infestation influenced N, P, and K uptake to a different degree, depending on the infestation level, in which infestation for 2, 4, 6, and 8 d at a density of 60 nymphs did not affect N uptake, but such infestation levels significantly influenced the uptake of P and K. After the removal of *N. lugens* from rice plants, the N uptake recovered from infestation faster than that for P and K in the variety 'Zhendao 2', whereas the recovery rate of K uptake was faster than that for N and P in the variety 'Xiushui 63'. The recovery rate of the nutrient uptake was negatively correlated to the density and duration of infestation. The experimental results demonstrated that N, P, and K uptake of rice roots were largely not influenced by *N. lugens* infestation when the pest density was controlled below 15 nymphs per hill. This infestation level was in agreement with the proposed economic thresholds for control measures against the *N. lugens* infestation on rice plants.

KEY WORDS *Nilaparvata lugens*, infestation, rice root, nutrient uptake

Nilaparvata lugens (Stål) (Homoptera: Delphacidae) is a serious pest insect of rice, *Oryza sativa* (Graminales: Poaceae), throughout Asia (Dyck and Thomas 1979). Both nymphs and adults aggregate and feed on leaf sheaths at the basal portion of rice plants, causing economic damage to rice crops (Sogawa and Cheng 1979). When the *N. lugens* population densities are high, the feeding damage can lead to drying of rice leaves and wilting of the tillers, a symptom named as hopperburn; and even a lower level of *N. lugens* feeding on rice plants can result in fewer panicles per unit area and fewer grains per panicle when the infestation occurs before maximum tilling stage, or reduce the percentage of ripened grain and grain weight when the infestation takes place after heading stage (Bae and Pathak 1970). The symptom of hopperburn first appears as yellowing of the older leaf blades of rice plants and extends progressively to all aboveground parts of the plants (Sogawa 1982). Hopperburn is catastrophic to rice plants; for example, all plants can be burnt on the 10th day of infestation by a single pair of adults per plant if such infestation occurs 30 d after transplanting, and even a complete yield loss after such infestation at 30 and 70 d after transplanting (Sarma and ChannaBasavanna 1980).

Because *N. lugens* infestation imposes a serious threat to rice production, many previous studies have been conducted to investigate its feeding process, including salivary secretions, probing stimulant, ingestion and honeydew excretion, sucking stimulant, and causes of hopperburn (Sogawa 1982). These studies have been focused on the effect of *N. lugens* feeding on the physiology and biochemistry of rice plants, with a particular reference to the aboveground shoot tissues, such as leaf blades and leaf sheaths. The impacts of *N. lugens* feeding on these tissues are considered as a direct effect or as a one-way effect on rice plants. However, little is known about the effect of *N. lugens* feeding on the function of rice roots, especially on the uptake of macronutrients in response to *N. lugens* infestation at different densities and for different feeding durations, although this knowledge is necessary for insights into the response of rice plants to the *N. lugens* infestation.

Rice roots not only play a major 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 that affect physiological activities, such as cytokinins, zeatin, and zeatin riboside (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

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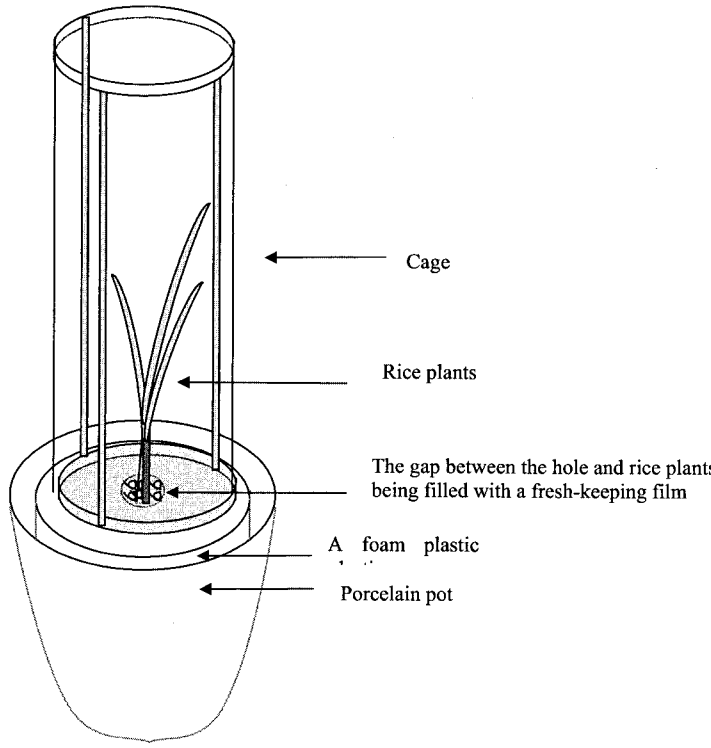

Fig. 1. Schematic illustration of rice plants cultured in a hydroponics solution.

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 and development of rice plants are mainly affected by the function of nutrient uptake, in particular nitrogen (N), phosphorus (P), and potassium (K), in root systems. Thus, if the *N. lugens* feeding influences the uptake capacity of rice roots, it will result in a holistic effect on rice plants. The objective of the current study was to examine the N, P, and K uptake of rice roots in relation to the *N. lugens* infestation density and the duration of *N. lugens* feeding on rice plants.

Materials and Methods

Rice Varieties and Insects. Two rice varieties were used in the experiment. They were 'Xuishui 63' (japonica rice), previously identified as moderately tolerant and susceptible to environmental stresses including pest infestation, and a susceptible variety 'Zhendao 2' (japonics rice) (Luo et al. 2002). Rice seeds were sown on batches in cement tanks (60 by 100 by 200 cm). After washing off soil with tap water, the seedlings bearing six leaves but without tillers were immediately transplanted to porcelain pots (height 13 cm and diameter 13 cm) containing an Espino hydroponics culture solution. Ten seedlings with a similar size were penetrated as a hill through a hole on a foamed plastic plate fixed on a pot with plastic wrap, with rice roots immersed in 1,000 ml of the solution in the pot, and the hill was covered in a nylon cylindrical cage (Fig. 1). The hydroponics solution was changed once a week, and its pH value was adjusted daily to 5.0. N, P, and K concentrations of the standard hydroponics solution (full strength) were measured as 19.667, 7.745, and 9.744 ppm, respectively.

Experimental insects were derived from a stock population of *N. lugens* maintained in the Chinese National Rice Institute (Hangzhou, China). Before the experiment started, the *N. lugens* colony was reproduced for two generations in an insectary at 28 ± 4°C and 14:10 (L:D).

Experiments. To investigate the effect of *N. lugens* densities on N, P, and K uptake, rice plants were subjected to the *N. lugens* infestation at five densities: 15, 30, 60, 90, and 120 fifth instar nymphs per rice hill. Nymphs were released onto each hill 7 d after the transplant of seedlings. The rice hill without any *N. lugens* infestation was used as a control. Six days after infestation, samples of the hydroponics solution were taken from experimental pots, and the remaining N, P, and K concentrations were analyzed.

To examine the effect of *N. lugens* feeding duration on the nutrient uptake, two *N. lugens* infestation densities (60 and 120 fifth instar nymphs per hill) were used in the experiment. Nymphs were released onto rice hills in the same way as described above. Samples of the hydroponics solution were taken from experimental pots after 2, 4, 6, 8, and 10 d of *N. lugens*

infestation, and the remaining N, P, and K concentrations were analyzed.

To check the recovery rate of nutrient uptake by rice roots after *N. lugens* infestation, rice plants were subjected to two densities of infestation (i.e., 60 and 120 fifth instar nymphs per hill) for 3 and 6 d, respectively, and then all *N. lugens* were removed from the plants. Samples of the hydroponics solution were taken from experimental pots on different days after *N. lugens* were removed for the analysis of N, P, and K concentrations. As in the above experiments, rice plants without *N. lugens* infestation were used as controls.

Generally, N, P, and K concentrations in the hydroponics solution were higher after the *N. lugens* infestation than those in control, indicating that nutrient uptake of rice roots was negatively affected. The higher the N, P, and K concentrations were in the culture solution, the greater the impact of *N. lugens* infestation on the nutrient uptake of rice roots. Thus, the percentage of reduction in nutrient uptake of rice roots (i.e., N, P, and K concentrations in the culture solution after *N. lugens* infestation minus those in the control, divided by those in the control) was measured as a relative index of the impact of *N. lugens* feeding on the nutrient uptake of rice roots.

These experiments were carried out in greenhouse under natural photoperiod and temperature, using a randomized complete block design. Each experiment was replicated four times, in which each experimental pot was sampled only once, so that all samples were independent.

Quantification of N, P, and K Contents in the Hydroponics Solution. The UV spectrophotometric method with alkaline potassium persulfate digestion was used to determine total N. The alkaline potassium persulfate solution was obtained by dissolving 40 g $K_2S_2O_8$ and 15 g NaOH in 1,000 ml distilled water. A standard solution was prepared by dissolving 0.7218 g KNO_3 in 1,000 ml distilled water. For a standard curve, 0, 1, 3, 5, 7, and 10 ml of the standard solution were diluted to 10 ml in a flask with distilled water, and then 5 ml alkaline potassium persulfate solution was added to each flask, which was heated for 30 min at 120–124°C. After cooling down, 1 ml HCl solution (ratio HCl to water = 1:9) was added to each flask and diluted to 25 ml in volume with distilled water. Absorbance at 220 and 275 nm was recorded by the multipurpose recording spectrophotometer (MPS-2000, Shimadzu, Japan), and adjusted absorbance (A; $a_{220} - 2 \times a_{275}$) was calculated. A standard curve was established with concentrations of the standard solution as ordinate and the absorbance as abscissa. Ten milliliters of sample solution was used to record its absorbance, and the concentration was calculated based on the standard curve.

Total P was determined using the 754 UV spectrometer (Precision Instrument, Shanghai, China). An ammonium molybdate reagent was prepared by dissolving 40 g $(NH_4)_2MoO_4 \cdot 4\ H_2O$ in 400 ml distilled water. Two grams NH_4VO_3 was dissolved in 250 ml distilled water, and added with 450 ml $HClO_4$ to get a desirable NH_4VO_3 solution. Then the ammonium molybolate solution was mixed with the NH_4VO_3 solution and diluted to a volume of 2,000 ml with distilled water. A standard phosphorus solution was obtained by dissolving 0.4394 g KH_2PO_4 in 1,000 ml distilled water. To establish a standard curve, 0, 1, 2, 3, 4, and 5 ml of the standard phosphorus solution was placed in a 100-ml measuring flask, and 20 ml ammonium molybdate reagent was added to each flask and diluted to a volume of 100 ml with distilled water. Absorbance at 400 nm was recorded, and a standard curve was established. To quantify the P concentration in a sample solution, a 50-ml sample solution was taken and added with 20 ml ammonium molybdate reagent and 100 ml distilled water. Ten minutes later, absorbance of the sample solution at 400 nm was recorded, and the P concentration was calculated based on the standard curve.

K was determined using the Atomic Absorption Spectrometer 2100 (Perkin Elmer, Norwalk, CT). A standard solution was prepared by diluting 0.1907 g KCl in 1,000 ml distilled water, and 1 and 2 ppm solutions were further prepared. A standard curve was established based on the solutions containing 1 and 2 ppm K. The absorbance of each sample solution was recorded, and the K concentration was calculated based on the standard curve.

Statistical Analysis. Data from the experiment on the effect of *N. lugens* infestation density on nutrient uptake were analyzed using an analysis of variance (ANOVA) procedure (SAS Institute 1989). Means were compared using Tukey's honest significant differences test ($P = 0.05$) for the effect of *N. lugens* density on N, P, and K uptake of rice roots. The effect of *N. lugens* infestation duration on the root function and the recovery rate of rice roots after the release of *N. lugens* feeding were analyzed with a *t*-test and compared with the control. To analyze the effect of different levels of *N. lugens* infestation on the uptake of N, P, and K of rice roots, linear regressions were established for the functional reduction of P and K uptake of rice roots and *N. lugens* density.

Results

Effects of *N. lugens* Infestation Densities on N, P, and K Uptake. The ANOVA showed that there were significant differences in N uptake between the two rice varieties ($F = 206.2$; df = 1, 36; $P = 0.0076$) and among *N. lugens* densities ($F = 3.09$; df = 5, 26; $P = 0.0202$), and there were significant interactions between rice variety and infestation density ($F = 4.67$; df = 5, 36; $P = 0.0089$). In the variety 'Xiushui 63', infestation by 15 nymphs per hill did not affect N uptake, but infestation at higher densities significantly reduced N uptake compared with control (without infestation; Table 1). In the variety 'Zhendao 2', however, the *N. lugens* infestation did not significantly influence N uptake, regardless of the *N. lugens* densities (Table 1). These results suggest that the response of the two rice varieties to *N. lugens* infestation is not the same in terms of N uptake.

Table 1. Mean ± SE concentrations of N, P, and K in hydroponics culture solution at different levels of *N. lugens* infestation

Rice variety	*N. lugens* density	N (ppm)	P (ppm)	K (ppm)
'Xiushui 63'	0	6.415 ± 0.409a[a]	0.825 ± 0.207c	1.185 ± 0.081c
	15	6.215 ± 0.120a	1.958 ± 0.906c	4.196 ± 2.694b
	30	8.441 ± 0.434b	1.615 ± 0.467c	2.548 ± 0.744c
	60	7.177 ± 0.563b	4.875 ± 2.534a	6.444 ± 1.691a
	90	7.426 ± 0.515b	4.233 ± 0.769ab	7.872 ± 0.786a
	120	7.589 ± 0.358b	3.214 ± 0.106b	7.314 ± 0.861a
'Zhendao 2'	0	9.586 ± 0.695a	0.449 ± 0.070d	0.760 ± 0.136b
	15	10.318 ± 1.808a	2.304 ± 0.961bc	0.975 ± 0.097b
	30	10.796 ± 1.556a	1.825 ± 0.279c	1.522 ± 0.426b
	60	10.556 ± 1.654a	3.151 ± 0.547ab	4.886 ± 0.757a
	90	9.905 ± 0.901a	2.986 ± 0.267ab	5.544 ± 0.965a
	120	8.575 ± 0.778a	3.551 ± 0.236a	4.952 ± 0.575a

[a] Means were compared using Tukey's honest significant differences test ($P = 0.05$). Means of same rice variety with the same letter within a column were not significantly different as compared to the control (no *N. lugens* infestation).

The *N. lugens* infestation showed a significant impact on the P uptake of rice roots, as indicated by significant differences among *N. lugens* densities ($F = 24.0$; df = 5, 36; $P = 0.0071$) and interaction between variety and *N. lugens* density ($F = 2.48$, df = 5, 36; $P = 0.046$), although there was no significant difference between the two varieties ($F = 2.48$; df = 1,36; $P = 0.067$). In 'Xiushui 63', infestation by 60, 90, and 120 nymphs significantly influenced P uptake as compared with infestation by 15 and 30 nymphs and control (Table 1). In 'Zhendao 2', there were significant differences among *N. lugens* densities, and there was also a positive correlation between the functional reduction (Y) of rice roots and *N. lugens* density (X): $Y = 319.10 + 3.096X$ ($r = 0.8653$, $P < 0.05$), showing that the P uptake function of rice roots decreased with an increase in the *N. lugens* infestation.

The effect of the *N. lugens* infestation on the K uptake of rice roots varied with nymph densities ($F = 52.62$; df = 5, 36; $P = 0.0032$). There were also significant difference between the two rice varieties ($F = 39.84$; df = 1, 36; $P = 0.0043$) and significant interaction between rice variety and *N. lugens* density ($F = 2.31$; df = 5, 36; $P = 0.046$). K concentrations in the hydroponics culture solution were less reduced as *N. lugens* densities increased (Table 1), as shown in linear regressions: $Y = 2.7028 + 0.0481X$ ($r = 0.9056$, $P < 0.01$) for 'Xiushui 63', and $Y = 0.8376 + 0.04356X$ ($r = 0.9011$, $P < 0.01$) for 'Zhendao 2', where Y is K concentration (ppm) and X is *N. lugens* density. The relationship between *N. lugens* density and percent reduction in K uptake also followed a linear regression: $Y = 142.59 + 3.7378X$ ($r = 0.8463$, $P < 0.05$) for 'Xiushui 63', and $Y = 12.11 + 5.7087X$ ($r = 0.8645$, $P < 0.05$) for 'Zhendao 2', where Y is percent reduction in K uptake and X is *N. lugens* density.

Effects of *N. lugens* Feeding Duration on N, P, and K Uptake. In both rice varieties, there was no clear relationship between *N. lugens* feeding duration and the impact on the N uptake of rice roots, but the effect of different *N. lugens* feeding durations on the P and K uptake of rice roots was significant, although the two rice varieties showed different patterns (Table 2). In 'Zhendao 2', *N. lugens* feeding for 2 d (a short feeding time) increased K uptake in both rice varieties; however, the effect disappeared when *N. lugens* feeding duration was longer than 2 d. In 'Xiushui 63', infestation for 2, 4, 6, and 8 d at a *N. lugens* density of 60 nymphs reduced the P and K uptake significantly.

Recovery Rates of N, P, and K Uptake after *N. lugens* Removal. The recovery rates of N, P, and K uptake after the removal of *N. lugens* were related to the original *N. lugens* density and infestation duration (Table 3). Generally, the recovery rate of N uptake was faster than that of P and K. For example, in the case where rice plants were infested by 60 nymphs for 3 d, N uptake fully recovered on the third day of *N. lugens* removal in 'Xiushui 63' and on the sixth day in 'Zhendao 2'. It took 6 d for 'Xiushui 63' to restore the N uptake to a normal level after being fed by 120 nymphs for 3 d. In the case where rice plants were infested at a *N. lugens* density of either 60 or 120 nymphs for 6 d, N uptake did not fully recover until 6 d after the removal of *N. lugens* from both varieties. However, the recovery rate of P uptake in 'Zhendao 2' was faster than 'Xiushui 63'. For example, in 'Zhendao 2' infested by 120 nymphs for 3 d, P uptake recovered on the sixth day after *N. lugens* removal, but in 'Xiushui 63' subjected to the same infestation level, P uptake was still depressed on that day. On the contrary, the recovery rate of K uptake was faster in 'Xiushui 63' than in 'Zhendao 2'. For example, in 'Zhendao 2', K uptake did not recover on sixth day after *N. lugens* removal in the situation of 120 nymphs infestation for 6 d, but in 'Xiushui 63', K uptake recovered on that day.

Discussion

This study showed that the two rice varieties responded differently to the *N. lugens* infestation in the N uptake of their rice roots. Variation in the *N. lugens* infestation level did not change N uptake in 'Zhendao 2', whereas the N uptake was significantly reduced in 'Xiushui 63' when infested by 30 or more *N. lugens* nymphs, although feeding by 15 nymphs did not exert any significant impact on the N uptake. However, the variety 'Xiushui 63' seemed to have a greater N uptake

Table 2. Effects of *N. lugens* nymph feeding duration on nutrient uptake of rice roots

Variety	*N. lugens* density	Feeding days	N (ppm)	*t* Value	P (ppm)	*t* Value	K (ppm)	*t* Value
'Zhendao 2'	120	2	12.893 ± 1.242	1.97	1.644 ± 0.269	0.25	3.13 ± 0.31	5.90^b
		CK	10.849 ± 1.674		1.579 ± 0.441		4.30 ± 0.25	
		4	9.565 ± 0.348	19.99^b	0.368 ± 0.173	0.29	3.06 ± 0.27	0.85
		CK	3.467 ± 0.521		0.338 ± 0.118		3.19 ± 0.17	
		6	2.616 ± 0.521	0.72	0.154 ± 0.011	2.89^a	3.07 ± 0.17	2.71^a
		CK	2.803 ± 0.467		0.109 ± 0.029		2.76 ± 0.24	
		8	3.722 ± 0.268	6.35^b			3.33 ± 0.21	10.43^b
		CK	2.586 ± 0.237				1.66 ± 0.20	
		10	3.756 ± 0.408	2.53^a			1.56 ± 0.08	9.80^b
		CK	3.110 ± 0.449				1.04 ± 0.14	
'Xiushui 63'	60	2	3.641 ± 1.036	1.67	1.431 ± 0.419	4.59^b	2.786 ± 0.23	4.84^b
		CK	3.538 ± 0.946		0.456 ± 0.096		3.546 ± 0.20	
		4	3.877 ± 1.531	1.67	1.176 ± 0.286	3.59^a	3.166 ± 0.16	5.48^b
		CK	2.619 ± 0.183		0.641 ± 0.115		2.717 ± 0.21	
		6	2.598 ± 0.382	0.40			2.30 ± 0.37	1.64
		CK	2.699 ± 0.349				2.624 ± 0.13	
		8	1.719 ± 0.289	0.55			2.471 ± 0.15	2.78^a
		CK	1.799 ± 0.399				2.908 ± 0.27	

Means ± SE are shown.
^{a} and ^{b} indicate that there are significant differences at $P = 0.05$ and $P = 0.01$ levels in comparison with the CK (no *N. lugens* infestation) (Tukey's Studentized range test).

capacity than did the variety 'Zhendao 2' at all *N. lugens* infestation levels (i.e., feeding nymph densities). The relatively greater capacity of N uptake in the variety 'Xiushui 63' might partially contribute to its tolerance to pest infestation and other environmental stresses compared with the susceptible variety 'Zhendao 2'.

There is empirical evidence that *N. lugens* feeding on rice plants can decrease the contents of nitrogen and photosynthetic products in leaves and hence reduce the growth of main shoot and tillers (Sogawa et al. 1994; Rubia-Sanchez et al. 1999). These physiological responses of rice plants to *N. lugens* infestation may be responsible for changes in the nutrient uptake of their roots, which were demonstrated in the current study, as in general the nutrient uptake of roots depends on the demand of the plant, which is determined by its growth rate and the content of nitrogen in the tissues (Lambers et al. 1998). Results of the current study have further shown that the effect of *N. lugens* infestation on the nutrient uptake of rice roots varies with the nutrient elements concerned. For

Table 3. Recovery rates (means ± SE) of nutrient uptake of rice root after *N. lugens* removal

Variety	*N. lugens* density	*N. lugens* infestation days	Recovery duration (days)	N (ppm)	P (ppm)	K (ppm)
'Xiushui 63'	60	3	3	4.81 ± 0.44	5.14 ± 0.27	1.69 ± 0.23^b
			6	5.37 ± 1.19	3.4 ± 0.61^b	9.3 ± 0.75^b
		6	3	8.1 ± 0.45^b	7.37 ± 0.70^b	2.49 ± 0.15^b
			6	8.59 ± 0.62^b	4.93 ± 0.54^b	1.39 ± 0.30
	CK	3		5.61 ± 0.61	5.01 ± 0.54	3.09 ± 0.32
		6		5.47 ± 0.65	1.84 ± 0.50	1.16 ± 0.26
	120	3	3	8.14 ± 0.45^b	5.27 ± 0.84	1.94 ± 0.54^b
			6	6.23 ± 0.75	4.66 ± 0.40^b	3.08 ± 1.00^b
		6	3	9.71 ± 1.29	8.85 ± 1.28	3.15 ± 0.56
			6	8.74 ± 0.36^b	6.24 ± 0.49^b	1.48 ± 0.34
	CK	3		5.61 ± 0.61	5.01 ± 0.54	3.09 ± 0.32
		6		5.47 ± 0.65	1.84 ± 0.50	1.16 ± 0.26
'Zhendao 2'	60	3	3	9.80 ± 0.50^b	6.79 ± 0.49^b	2.04 ± 0.04^a
			6	5.18 ± 2.22	3.59 ± 0.49	9.06 ± 2.15^b
		6	3	9.99 ± 0.28^b	5.93 ± 0.52	2.18 ± 0.10^b
			6	8.95 ± 0.26^b	4.45 ± 0.94	1.17 ± 0.16^b
	CK	3		8.73 ± 0.47	5.63 ± 0.13	1.75 ± 0.17
		6		3.29 ± 1.04	3.85 ± 0.75	1.54 ± 0.10
	120	3	3	8.42 ± 0.60	6.84 ± 0.71^a	2.78 ± 0.02^a
			6	5.43 ± 1.83	4.34 ± 0.54	9.36 ± 0.34^b
		6	3	10.95 ± 0.28^b	6.48 ± 0.59^a	5.42 ± 0.91^b
			6	9.41 ± 0.34^b	7.51 ± 0.30^b	4.11 ± 0.06^b
	CK	3		8.73 ± 0.47	5.63 ± 0.13	1.75 ± 0.17
		6		3.29 ± 1.04	3.85 ± 0.75	1.54 ± 0.10

^{a} and ^{b} indicate that there are significant differences at $P = 0.05$ and $P = 0.01$ levels in comparison with the CK (no *N. lugens* infestation) (Tukey's Studentized range test).

example, the N uptake of rice roots was less influenced by *N. lugens* infestation than the P and K uptake; the recovery rate of N uptake by rice roots after the release of *N. lugens* infestation was also faster than that of P and K uptake in 'Zhendao 2'. A possible explanation for this phenomenon is that there is oversupply N in plants or it can be reused in rice plants (Mae and Ohira 1981). The total free amino acid content of chlorotic leaf blades was found to be four times greater than that of healthy ones, and that of brown leaves ≈1.8 times more (Sogawa 1971). Therefore, the impact of *N. lugens* infestation on N uptake was not as obvious compared with that on P and K uptake by rice roots.

The experimental results revealed that *N. lugens* infestation caused a decrease in the P and K uptake of rice roots in both varieties, and the influences became more serious with the increase of *N. lugens* density and the prolongation of infestation duration. P is closely related to many physiological and biochemical process in plants, such as protein biosynthesis and cell division and growth, and P is also important for photosynthesis in green plants. For instance, a deficiency of P will result in plant dwarfing (Wang 2000). However, K plays an essential role in plant growth because it activates over 60 enzymes, promotes protein synthesis, and is involved in sugar synthesis. Plant stems under the condition of K deficiency become delicate and easy to lodge. Thus, we believe that the hopperburn caused by *N. lugens* infestation is attributed, at least partially, to the reduction of P and K uptake by rice roots. However, the reduction is not completely caused by the drain of phloem sap because *N. lugens* feeding promotes the K uptake under certain conditions (e.g., a short time of *N. lugens* feeding). *N. lugens* infestation at higher densities might result in serial impacts on rice plants because of the reduction of P and K uptake. For example, the water contents of rice plants decreased ≈12–14% (Cagampang et al. 1974). As chlorosis increased, the protein content of the leaves decreased steadily; chlorotic and brown leaves had 33 and 73% less protein than did healthy leaves, respectively (Sogawa 1971). Of course, it is also possible that *N. lugens* infestation impairs P and K uptake because of sucking assimilates from the plant, but the decline of root system function was found to cause senescence of rice plants (Wang 2000). Therefore, we hypothesize that *N. lugens* feeding affects the biosynthesis of cytokinins and zeatins, and the latter indirectly affects P and K uptake by root system because these substances regulate growth and development of rice plants (Yang et al. 2000, 2001). Nevertheless, the physiological and biochemical mechanisms underlying the relationship between the reduction of P and K uptake and hopperburn remain to be investigated.

In summary, the effect of *N. lugens* on the nutrient uptake function of rice roots was shown mainly in the P and K uptake and to a lesser extent in the N uptake, although it varied with the *N. lugens* infestation levels and rice varieties. The reduction of P and K uptake by rice roots may be partly responsible for a decrease in the growth of rice plants and the occurrence of hopperburn, caused by the *N. lugens* infestation. Interestingly, our experiments have demonstrated that *N. lugens* infestation at a density of ≤15 nymphs per rice hill does not affect these macronutrient uptake of rice roots significantly. This finding provides empirical evidence supporting the economic thresholds proposed for control measures against the *N. lugens* infestation on rice plants.

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