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Effects of nitrogen on the tolerance of brown planthopper, *Nilaparvata Lugens*, to adverse environmental factors

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Abstract The effect of nitrogen content in rice plants on the tolerance of brown planthopper (BPH), *Nilaparvata lugens* Stål to high temperature, starvation and insecticide, was studied in the laboratory at International Rice Research Institute (IRRI), Philippines. Survival of nymphs and adults, fecundity and egg hatchability were significantly increased by the increase of nitrogen content in host plants at 38℃. Moreover, the survival of nymphs, fecundity and egg hatchability were significantly higher in BPH populations on rice plants with a high nitrogen regimen than those on rice plants with a low nitrogen regimen. Meanwhile, the tolerance of female adults to starvation and nymphs to growth regulator buprofezin on rice plants with a high nitrogen regimen were slightly increased. This indicates that the tolerances of BPH to adverse environmental stresses were positively increased by the application of nitrogenous fertilizer. The outbreak potential of BPH induced by the excessive application of fertilizer in rice fields was also discussed.

Key words Brown planthopper, *Nilaparvata lugens* Stål, nitrogen, high temperature, tolerance, insecticide, starvation
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Introduction

The brown planthopper (BPH), *Nilaparvata lugens* Stål, characterized by its monsoon migration, morphological diversity and r-strategy life pattern (Sogawa, 1995), is one of the most economically important insect pests in Asian rice-growing areas. It has been widely emphasized as one of the main species of planthopper group for ecological study and effective pest management (Denno & Perfect, 1994). Its significance was also attributed to its positive or negative ecological and physiological adaptation to environmental factors, as well as its direct and indirect impact on massive rice yield losses (Li *et al*., 1996). Its rapid adaptation to adverse environmental factors had been recognized in virulent changes and biotypes shift, with insecticide-resistant populations developing, macropterous adults emerging, and long-distance immigration occurring (Denno & Perfect, 1994; Hemngway *et al*., 1999; Liu & Gu, 1996; Liu *et al*., 2003; Nagata, 2002; Saxena & Barrion, 1985; Wu *et al*., 1997).

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Rice ecosystems are expected to respond to global warming changes in several fundamental ways. The comprehensive review on the global warming and rice arthropod communities showed that arthropods can evolve in diverse ways in order to adapt the global warming (Heong *et al*., 1995). The tolerance to high temperature indicates differences in BPH adults and nymphs from various countries and from different geographical populations in China. It may imply the ecological adaptation of BPH (Heong *et al*., 1995; Lu *et al*., 2000). In the meanwhile, high temperature can significantly destroy or inhabit the activities of symbiotes, intracellular yeast-like microorganisms that exist in some delphacids related to nutrition, metabolism and reproduction of BPH, which may indicate the physiological adaptation in this insect (Heong *et al*., 1995).

The effects of "green revolution", which promoted intensive rice monocultures with high fertilizer and pesticide applications on the agricultural system has been emphasized (Conway & Barbier, 1990). Chemical components of host plants play a major role in the population biology of BPH. They influence host plant selection and performance and fitness of planthoppers (Cook & Denno, 1994). In nitrogen-rich host plants BPH survives better (Cheng, 1971) and is more fecund (Sogawa, 1971). In choice tests, BPH adults would select nitrogen-rich over nitrogen-poor plants on which to feed and oviposit (Lu *et al*., 2004). The combined effects of increased colonization and improved performance may result in rapid population growth and high densities in nitrogen enriched crops (Kanno *et al*., 1977; Heinrichs & Medrano, 1985; Hu *et al*., 1986). Thus nitrogen fertilization has been implicated as a cause of BPH outbreaks and was perceived as a threat to the rice industry in the 1970s and 1980s (Dyck *et al*., 1979; Heinrichs & Mochida, 1984).

The purpose of this paper is to determine the effects of nitrogen on the tolerance and resistance of BPH to common adverse environmental factors, high temperature, application of insecticide and starvation, in order to clarify the role of nitrogen nutrient in BPH population dynamics and to determine the role of ecological mechanisms in the potential outbreak of BPH populations.

Materials and methods

Preparation of host plants

In our research, all BPH cultures and experiments were maintained on standardized host plant materials. Three to four ten-day-old rice seedlings of rice (var: TN1 and IR64) were transplanted into clay pots filled with garden soil fertilized with ammonium nitrate in which 30% was applied at 7 days after transplanting, 30% in tillering and 40% at the reproductive stage. Plants with 4 nitrogen regimens of 200, 100, 50 and 0 kg/ha, labeled as 200N, 100N, 50N and 0N, respectively, were used. The exact amounts of fertilizer input applied to each pot were calculated based on the amount of soil in each pot. To obtain constant host-plant materials for each BPH culture and experiment, seedlings were transplanted at 15-day intervals.

Culture of brown planthopper

Brown planthopper adults were collected from rice fields in Laguna, Philippines and placed in an oviposition cage with the plants of a susceptible rice variety (TN1). On each Monday and Thursday, 45–60-day-old potted plants were placed into this cage and removed 24 hours later. The potted plants with BPH eggs were then placed in another cage with TN1 plants. The adults from this cage were introduced into the cages contained 45–60-day-old IR64 rice plants. Successive cultures of BPH populations in different nitrogen regimens were subsequently maintained on IR64 plants. The populations were named 0NG1, 0NG2 and 0NG3, representing BPH populations successively fed on rice plants applied with 0 kg/ha nitrogen fertilizer for 1, 2 and 3 generation, respectively, and 200NG1, 200NG2 and 200NG3, represented BPH populations successively fed on rice plants applied with 200 kg/ha nitrogen fertilizer for 1, 2 and 3 generation, respectively.

Calibration of chlorophyll meter readings with tissue nitrogen

An electronic chlorophyll meter (SPAD-502, Minolta camera Co., Osaka, Japan) was used for the assessment of tissue nitrogen. At different rice growth stages, eight uppermost fully expanded leaves were selected at random from each nitrogen regimen and the SPAD readings recorded. The tillers bearing these leaves were removed and placed separately in brown paper bags. The samples were placed immediately in an oven at 110℃ for 30 min and dried at 80℃ for 48 h until constant weight. Nitrogen content was determined by micro-Kjeldahl digestion and distillation. A regression of tissue nitrogen content (%) as the dependent variable and SPAD meter reading as the independent variable was established and used to convert SPAD readings. Pooling data from all plant growth stages, the relationship between leaf nitrogen content and leaf SPAD readings was found to be

$N\% = 0.1151\ SPAD - 1.2772$, ($F = 162$, $P < 0.001$),

where N% is the nitrogen content and SPAD is the chlorophyll meter reading. This linear model was used to predict the nitrogen content of plants in all the experiments.

Tolerance of BPH to high temperature

Six 45-day-old potted rice plants in each rate of nitrogen fertilization, trimmed to 2 tillers and recorded SPAD readings, were covered with mylar cages and placed in phytotron cabinet with the temperature of 38 ± 1℃, L12: D12. After 12 h of the adaptation of plants to high temperature, ten 3rd instar nymphs and ten female adults molted in 12 h maintained on TN1 plants introduced into each cage. The survival insects were recorded in every 12 hours. Similar experiments were set up for measuring the tolerance to high temperature of different BPH populations continuously fed on IR64 rice plants with different nitrogen regimens, and were replicated five times in every BPH population.

To quantify the effects of high temperature on the fecundity and egg hatchability of BPH populations, 45-day-old rice plants, trimmed to 4 tillers, recorded SPAD readings and covered by mylar cages, were introduced to one pair of BPH adults and placed in the phytotron cabinet at 38±1℃ and L12: D12. Each BPH population was replicated 10 times, while 20 replications were established for those BPH populations fed on rice plants with low nitrogen fertilizer in order to obtain adequate data, due to their high sensitivity to temperature. The control treatments were kept in the phytotron cabinet at 28±1℃. The adults were checked in every 12 h for 3 days after infestation and replenished with fresh ones when the dead adults were found. Newly hatched nymphs were counted and eliminated in 12 h intervals until no more nymphs were observed for two successive days. The unhatched eggs were recorded by dissecting host plants. Fecundity was calculated as the sum of the number of nymphs and unhatched eggs.

Tolerance of BPH adults to starvation

Ten female adults, molted in 12 h, from BPH populations reared continuously on rice plants with low or high nitrogen fertilizer for three generations, were introduced into a test tube (diameter 2.5 cm, height 20 cm) with a wet cotton ball in airconditioned laboratory at 26±2℃. The survival rates were recorded in 6-hourly intervals. Each population was replicated five times.

Resistance of BPH nymphs to insecticide

Five serial concentrations of buprofezin, an insect growth regulator with the characteristics of species specificity and high molt-inhibition through chitin biosynthesis inhibition, 0.25, 0.5, 1, 2 and 4 mg/kg (ppm) based on the data of preliminary experiments, were prepared using Applaud® 25% WP and distilled water for determining the susceptibility of 3rd or 4th instar nymphs of BPH populations to buprofezin. Main stems of 45-day-old rice plants were individually separated, cleared with tap water and the inactive fibrous roots removed. The air-dried plants were uniformly sprayed from low to high concentrations of buprofezin with an atomizer attached to a pressure pump and air-dried in room again. The control treatment was sprayed with distilled water only. Two treated plants were installed into a test tube (diameter 2.5 cm, height 20 cm) containing 1-cm-deep water. Each test tube was introduced with ten 3rd or 4th instar nymphs and sealed with cotton. The survival rates were recorded in third and fifth day after treatment. This experiment was replicated three times in each concentration and conducted at 26 ± 2℃.

Data analysis

The tolerances of BPH to high temperature, starvation and insecticide were compared with the median effective doses, median lethal time (LT_{50}) for high temperature and starvation, and median lethal concentration (LC_{50}) for insecticide. They were calculated by probit analysis using the Data Processing System (DPS) developed by Tang and Feng (1997). Values in percentages were transformed by arcsine before analysis. Linear regressions were analyzed in IRRISTAT 4.0 Windows. Analysis of variance (ANOVA) and Duncan's multiple range test were performed using PROC ANOVA or PROC GLM.

Results

Effects of high temperature on BPH

Mortalities of BPH The mortality rates of BPH female adults and nymphs at 38℃ were significant and negatively related to the nitrogen content in host plants (Figs. 1 and 2). The similar linear trends in nymphs and adults were regressed at 2nd, 4th and 6th day after infestation. This implied the same influences of nitrogen content on nymphs and adults at high temperature. However, the tolerances of nymphs of different BPH populations to high temperature could be classed into two groups, on 200N rice plants and 0N rice plants (Table 1), meanwhile the values of LT_{50} of populations on 0N rice plants were obviously lower than those on 200N rice plants. Furthermore, the LT_{50} values slightly increase on 200N rice plants and gradually decreased on 0N rice plants with the extension of BPH generations fed continuously on the host plants.

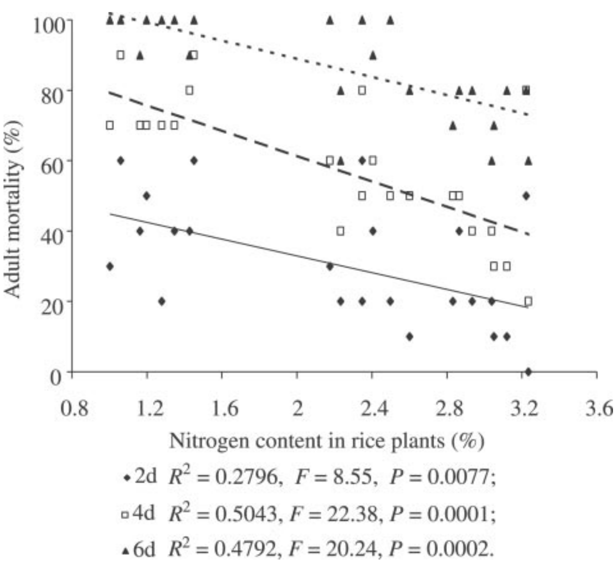

Fig.1 Mortality of BPH female adults on rice plants with different nitrogen content at 38℃.

Table 1 Tolerance of BPH nymphs to high temperatures (LT_{50}) at 38 ℃.

BPH populations	LT_{50} (h)	95% Confidence Limits	Regressive parameter *a*	Slope	χ^2
0NG1	2.03	1.71−2.42	3.9990	3.2550	6.252*
0NG2	1.77	1.49−2.10	4.0879	3.6706	4.583*
0NG3	1.52	1.31−1.78	4.1368	4.7200	4.089*
200NG1	3.64	3.31−4.01	1.9054	5.5021	2.932*
200NG2	4.18	3.87−4.51	0.5705	7.1311	4.163*
200NG3	4.53	4.17−4.62	0.9481	6.1777	3.005*

*$P < 0.05$.

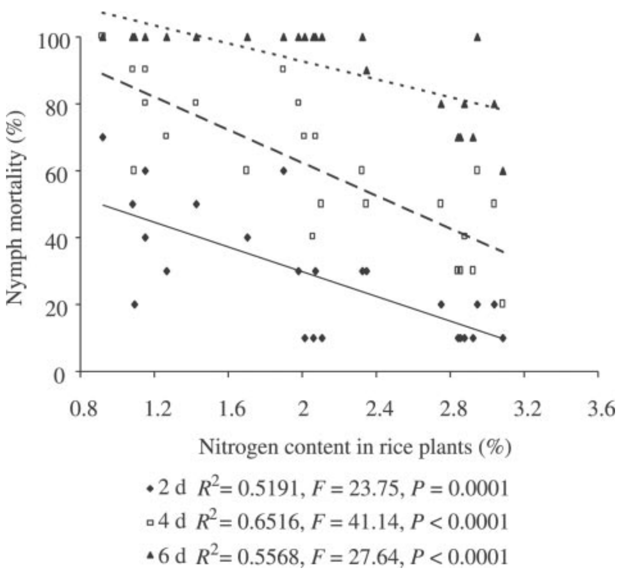

Fig. 2 Mortality of BPH nymphs on rice plants with different nitrogen content at 38℃.

Fecundities of BPH The BPH fecundities strongly increased with the increase of the nitrogen content in host plants both at 38℃ and 28℃ (Fig. 3). Fecundities of BPH populations may be divided into four groups, being attributed to the nitrogen content in host plants and temperatures, though they lightly increased on 200N rice plants and decreased on 0N rice plants with the extension of generations at 28℃, respectively, while relative constant fecundity rates were found both on 0N and 200N rice plants with the extension of generations at 38℃ (Table 2). The percentage changes in 0N rice plants at 38℃ were markedly higher than those on 200N rice plants, indicating that the effects of high temperature on fecundity rates of BPH populations on 0N rice plants were stronger than those on 200N rice plants. However, no significant differences in fecundities among generations from the same host plant were recorded in all four treatments of host plants and temperatures.

Table 2 Effect of high temperature on fecundities (eggs laid/female) of BPH populations successively fed on rice plants with different nitrogen regimes.

Hostplants	Temperature (℃)	Generations fed on the same host plants 0†	1	2	3
0N rice plant	28	178.8*	150.1**	119.4**	91.5*
	38	43.6	36.4	40.2	33.7
	Change (%)	−308.83	−312.36	−197.01	−171.51
200N rice plant	28	465.5**	474.1*	540.7**	559.5*
	38	213.3**	267.1**	271.5**	317.7**
	Change (%)	−118.24	−77.50	−99.15	−76.11

† BPH was collected from the population on TN1 rice plants.
Significant difference in means between temperatures at *0.05 level, **0.01 level.

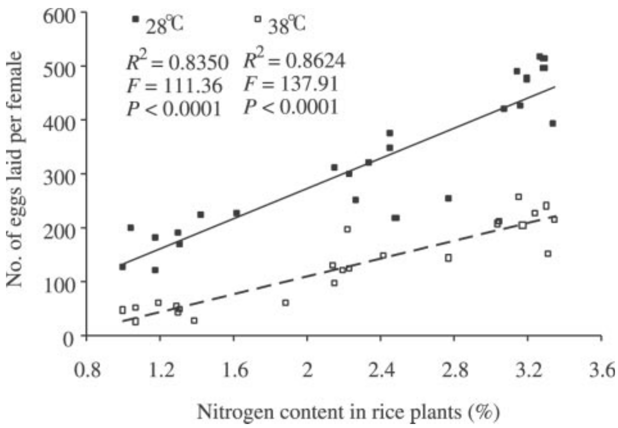

Fig. 3 Effects of high temperature on fecundities of BPH population maintained on TH1 on the rice plants with different nitrogen content.

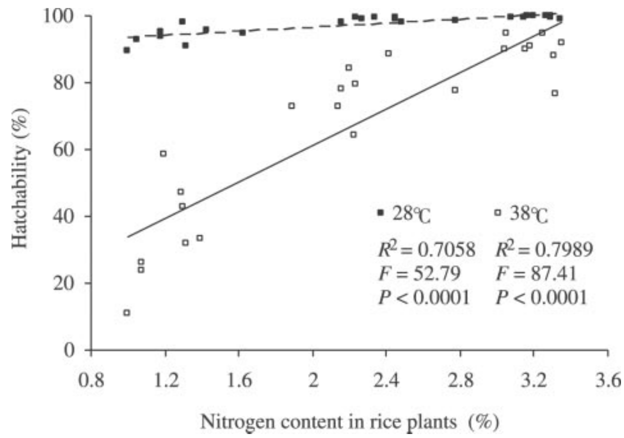

Fig. 4 Effect of high temperature on egg hatchability of BPH population maintained on TN1 on the rice plants with different nitrogen content.

Egg hatchability of BPH Egg hatchability was positively related to the nitrogen content in host plants both at 38℃ and 28℃. Rates markedly elevated with the increase of the nitrogen content at 38℃, while they lightly increased at 28℃ (Fig. 4). However, percentage changes were obviously higher on 0N rice plants than on 200N rice plants, and they were markedly increased with the extension of BPH generations fed on 0N rice plants, while no obvious differences were recorded in populations on 200N rice plants (Table 3). Two-way ANOVA results indicated that the tolerances to high temperature of eggs of BPH populations on 200N rice plants were much higher than those on 0N rice plants (host plants $P < 0.0001$, generation $P = 0.0325$).

Tolerance to starvation of BPH female adults

The median effective times (LT_{50}) at 28℃ of BPH populations on 200N rice plants were generally higher than those on 0N rice plants (Table 4). The LT_{50} values of females increased gradually on 200N rice plants and decreased slightly on 0N rice plants with the extension of successive generations on the same host plants. Consequently, LT_{50} of 200NG3 females were significantly higher than those of 0NG2 and 0NG3.

Tolerance of BPH nymphs to insecticide

The LC_{50} values of BPH populations to buprofezin at third day after treatments were higher than those at fifth day in all tested BPH populations (Table 5), even though they fluctuated between generations both on 0N and 200N rice plants at third day due to the heterogeneous nymphs and the different susceptibilities to buprofeszin between various instar nymphs. The LC_{50} values at the fifth day were higher, but not significant, in the populations on 200N rice plants than those on 0N rice plants, implying that the tolerance to buprofezin of BPH populations may be increased on 200N rice plants.

Table 3 Effect of high temperature on egg hatchability (%) of BPH populations successively fed on rice plants with different nitrogen regimes.

Host plants	Temperature (℃)	Generations fed on the same host plants			
		0†	1	2	3
0N	28	93.89*	89.12**	81.10**	78.70**
rice plant	38	34.31	20.87	19.84	14.00
	Changes (%)	−173.65	−327.02	−308.77	−462.14
200N	28	99.72	98.18	98.16	98.51
rice plant	38	89.66	85.43	85.79	81.82
	Changes (%)	−11.22	−14.92	−14.42	−20.40

† BPH was collected from the population on TN1 rice plants.
Significant difference in means between temperatures at *0.05 level, **0.01 level.

Table 4 Tolerance to starvation (LT_{50}) of BPH female adults at 28 ℃.

BPH Populations	LT_{50} (h)	95% Confidence Limits	Regressive parameter *a*	Slope	χ^2
0NG1	51.09 ab	43.67−59.76	−3.8413	5.1753	2.179*
0NG2	38.59 b	30.84−48.28	−0.7033	3.5949	3.584*
0NG3	42.15 b	33.98−52.31	−0.8629	3.6079	5.597*
200NG1	51.89 ab	44.72−60.21	−4.7667	5.6946	2.563*
200NG2	51.38 ab	43.87−60.19	−3.7435	5.7106	2.27*
200NG3	60.25 a	53.39−68.00	−7.6033	7.0807	1.276*

The means of LT_{50} with the same letters indicated no significant difference at $\alpha = 0.05$; $*P < 0.05$.

Table 5 Median lethal concentration (LC_{50}) of Buprofesin to BPH nymphs.

BPH Populations		LC_{50} (ppm)	95% Confidence Limits	Regressive parameter *a*	Slope	χ^2
3d after treatment	0NG1	1.49	1.14−1.95	4.6421	2.0508	1.159*
	0NG2	0.99	0.72−1.35	5.0044	1.6159	2.510*
	0NG3	1.37	1.03−1.83	4.7410	1.8555	1.934*
	200NG1	2.40	1.77−3.26	4.1914	2.1192	3.221*
	200NG2	0.95	0.63−1.45	5.0212	1.1531	3.865*
	200NG3	1.16	0.63−2.16	4.9475	0.7735	1.120*
5d after treatment	0NG1	0.66	0.54−0.80	5.5515	3.0666	5.086*
	0NG2	0.38	0.24−0.60	5.6045	1.4445	2.564*
	0NG3	0.48	0.31−0.73	5.4491	1.4101	3.559*
	200NG1	0.83	0.68−1.02	5.2235	2.9112	2.202*
	200NG2	0.70	0.48−1.04	5.1978	1.3182	2.497*
	200NG3	0.72	0.51−1.02	5.2107	1.4928	4.538*

$*P < 0.05$.

Discussion

A previous finding indicated that the nymphs survived better and had shorter life spans, the females weighed heavier, laid more eggs and lived longer, as well as egg hatchability being significantly increased on rice plant with high nitrogen regimens, implying that in areas where nitrogen-rich crops are abundant over long periods, ecological fitness of the brown planthoppers are potentially higher (Lu *et al*., 2004). The results of this study indicated that the nitrogen content in rice plants should enhance the tolerance of BPH to adverse environmental factors through the biological and ecological improvement of BPH.

Under high temperature, egg hatchabilities of BPH decreased, egg periods prolonged, adult emergence rates reduced, nymph development period extended, preoviposition period was prolonged, nymph and adult survival and fecundity decreased (Lu *et al*., 1999; Heong *et al*., 1995; Yu & Wu, 1991). Findings show that the application of nitrogen fertilizer could increase the atmosphere temperature through the releasing NO_2 by the N dioxide (Conway & Pretty, 1991). The increasing tolerance to high temperature of BPH in nymph survival, fecundity and hatchability, resulted from the application of nitrogen fertilizer may predict the outbreak potential of BPH populations during global warming. Consequently, the excessive application of nitrogen fertilizer may affect the BPH population in two ways and may establish other vicious cycles around the globe.

Starvation may be the most common adverse environmental factor caused frequently by the agricultural practices, climate shifts, and rice harvests in rice-based ecosystem. In temperate rice growing countries, such as China, Japan and Korea, BPH could not survive through the year due to low temperatures in the winter season (Chen *et al*., 1979). Its monsoon migration *via* air stream from southeast Asian countries, Vietnam and Philippines, to east Asia counties, China, Japan and Korea, takes long time and without food (except water vapor), so the tolerance to starvation becomes a most critical factor to successfully migrate to a new terminal and find a new food resource (Wu *et al*., 1997). The population abundance of BPH in rice fields of East Asian counties depends strongly on the initial BPH immigrants from Indo-China and the virulence of BPH to resistant rice varieties, which are related to the migration abilities and the characteristics of BPH (Sogawa, 1995; Wu *et al*., 1997). According to the results in this study, more immigrants in terminal rice fields may be from those emigration fields with high nitrogen fertilizer, since the female adults which fed on host plants with high nitrogen fertilizer have higher tolerance to starvation. On the other hand, more BPH individuals on rice fields with high nitrogen fertilizer could survive and find their new habitats over long distance, such as neighboring rice fields and newly transplanted fields, resulting in high BPH resources and outbreak potential.

Resistance to insecticide and insecticide-induced resurgence become the serious problems in the management of rice planthoppers (Denno & Perfect, 1994). Host plants can modify the susceptibility of herbivores to pesticides, and the differences in susceptibility of BPH populations on specific host plants have been related to the various levels of metabolizing enzymes presumably induced by the host plants (Tan & Guo, 1996; Yang *et al*., 2001). Buprofezin is one of the insect growth regulators, a new chitin synthesis inhibitor, and has a special active mechanism−the increase of the mixed-function oxidase activity was the major mechanism of the metabolic resistance of buprofezin (Liu *et al*., 1998). In this experiment, the slightly increased tolerance of BPH populations on host plants with high nitrogen fertilizer may be attributed partly to the changes of chemicals in host plants, in addition to the ecological fitness components increased with the extension of the generations of BPH fed continuously on host plants with high nitrogen fertilizer (Lu *et al*., 2004). Therefore, the circle of a long-term excessive application of nitrogen fertilizer, BPH population increase and yield lost may stimulate the increase of spray times, and result in the resurgence of BPH population. Histological observation and ultrastructural inspection showed that the buprofezin takes a longer time to affect the nymph molting. This may be the reason why the LC_{50} values at day 3 after treatment were higher and unstable than those at day 5 in this study.

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