

# THE DIFFERENTIATION OF AMINO ACID REQUIREMENTS IN THREE HOST-RELATED POPULATIONS OF THE BROWN PLANTHOPPER, *NILAPARVATA LUGENS* (STÅL) \*

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**Abstract** In order to understand the differentiation of amino acid requirements in host-related populations of the brown planthopper (BPH), *Nilaparvata lugens* (Stål), we established three BPH populations by separately maintaining them on three rice varieties, i. e. TN1 (common susceptible control), Mudgo (containing resistant gene *Bph1*) and ASD7 (containing resistant gene *bph2*) for over 30 generations, and then reared them on 20 holidic diets, each with distinct overall amino acids and ratio of essential amino acid (EAA) to nonessential amino acid (NEAA). The emergence rate, brachypter rate, nymphal duration and weight of newly molted adults were evaluated and compared. The results showed significant difference among the three populations in the effect of amino acid variation on BPH performance, ascending in an order of Mudgo population > ASD7 population > TN1 population. The results also indicated that the required optimum concentrations of overall amino acids by BPH populations on Mudgo and ASD7 were 4.0% - 4.8% and 4.0%, respectively, higher than that of TN1 population (2.4% - 3.2%). In addition, it was found that Mudgo and ASD7 populations were more sensitive to the concentration of EAAs than TN1 population. We propose that there is substantial differentiation in responses to dietary amino acid conditions among different host-associated BPH populations and that such differentiation may be closely related to the induced virulence shift on resistant rice varieties.

**Key words** *Nilaparvata lugens*, host-related population, amino acids, differentiation in nutritional requirement

## 1 INTRODUCTION

The brown planthopper (BPH), *Nilaparvata lugens* (Stål), is one of the most destructive pests of rice throughout the tropical, subtropical and temperate rice-growing areas in Asia (Sogawa 1982, Gallagher *et al.* 1994, Ketipearachchi *et al.* 1998). It has become a key pest in China since the end of 1960s, when the rice agroecosystem changed drastically due to the introduction of high-yielding cultivars and extensive application of various agrochemicals, especially nitrogenous fertilizers and insecticides (Li *et al.* 1996). The severe damage and frequent outbreaks of BPH, along with the hazardous effects of insecticides, prompted researchers to look for the possibility of using variety resistance to control the insect (Sogawa 1982, Ketipearachchi *et al.* 1998).

In Asia, three BPH resistance genes, *Bph1*, *bph2* and *Bph3*, have been widely used to improve the resistance of commercial rice varieties (Cohen *et al.* 1997). In 1973, the International Rice Research Institute (IRRI) located in the Philippines released the first BPH resistant cultivar,

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IR26, which contains a resistant gene *Bph1*, for commercial cultivation (IRRI 1976). This variety was then extensively cultivated and initial result supported this practice being highly successful in controlling BPH. But it was soon realized that, by the end of 1975, IR26 had become susceptible to BPH populations in many areas (Stapley *et al.* 1979). Subsequently, another resistant variety IR36 (with *bph 2*) was also found to show succumbed to virulent BPH population (Panda *et al.* 1995). It has become well-known that, due to the occurrence of new virulent populations (generally referred to as new "biotypes"), resistant rice varieties have to be replaced after several cycles of cultivations (Rombach *et al.* 1994). Therefore, the incidence of virulence shift of BPH has become a major challenge in using variety resistance to control the insect.

It seems that host-associated performance existing within BPH is of genetic control (Hollander *et al.* 1981, Sogawa 1981, Pathak *et al.* 1982, Zhang *et al.* 1997). Many reports have indicated the presence of different "biotypes" in both sympatric and allopatric BPH populations (Sogawa 1982, Takahashi *et al.* 1994). It was also reported that virulence shift of BPH population would be evident if reared for several generations on a rice cultivar carrying resistant gene (Pathak *et al.* 1982, Rombach *et al.* 1994, Zhang *et al.* 1997, Ketipearachchi *et al.* 1998). This implies that virulence shift of BPH is induced by the resistant rice varieties and related to two important aspects: the adaptation mechanism of BPH to resistant rice and the resistant mechanism of rice to the insect. Some chemicals in rice plants, including nutrients and allelochemicals, may play an important role in both mechanisms.

Rice-induced populations of BPH are considered to be the genetic variants, showing different gustatory responses to the phloem chemicals that are responsible for varietal resistance (Sogawa 1982). Amino acids are the dominant nitrogen nutrients in rice phloem (Fukumorita *et al.* 1982). They are not only the basic nutrients for insect's survival and development (Blum 1985), but also gustatory factors stimulating their feeding behavior (Sogawa 1972). It was reported that three BPH biotypes maintained in IRRI showed substantial differentiation in their gustatory responses to some amino acids, such as asparagine, aspartic acid, and valine (Sogawa 1978, Saxena *et al.* 1985). However, little information is available to answer if different rice-induced BPH populations differentiate in their survival and development responses to amino acid composition. In the present study, we attempted to clear this uncertainty by comparing the performance of three host-related BPH populations on chemically defined diets varying in overall amino acids and ratio of essential amino acids (EAAs) to nonessential amino acids (non-EAAs).

## 2 MATERIALS AND METHODS

### 2.1 Insects

Previously, Zhang *et al.* (1997) observed obvious virulence shift of two BPH populations after having been cultured for nine and three generations on rice varieties Mudgo and ASD7, respectively. Here we established three host-related populations of BPH by maintaining the paddy field population (in Fuyang County, Zhejiang, China) on three rice varieties, i.e. TN1 (common susceptible control), Mudgo (containing resistant gene *Bph1*) and ASD7 (containing resistant gene *bph2*), respectively, for more than 30 generations. The condition is 26 – 30°C, over 80% of relative humidity (RH), and a photoperiod of 12 – 14 h. We then used the one-day-old

nymphs from the three populations to initiate the present experiments.

## 2.2 Artificial diet

Diet formulae were based on a chemically defined diet D-97 (Fu *et al.* 2001). A total of 20 chemically defined diets were designed, representing all combinations of four different total amino acids (2.4%, 3.2%, 4.0% and 4.8%, W/V) and five ratios of essential amino acids (EAAs) to nonessential amino acids (NEAAs) (26:74, 34:66, 42:58, 50:50 and 52:48, W:W). Here EAAs include ten kind of amino acids, i.e. arginine, histidine, methionine, isoleucine, leucine, lysine, phenylalanine, threonine, tryptophane, and valine. NEAAs include alanine, asparagine, aspartic acid, cysteine, cystine,  $\gamma$ -amino butyric acid, glutamic acid, glutamine, glycine, proline, serine, and tyrosine. All of the amino acids were from the Sino-american Biotechnology Company. Compositions except amino acids of the 20 diets were maintained as the same as those of D-97.

Diets prepared were filter-sterilized through a Millipore disposable filter (0.45  $\mu\text{m}$ ), and stored at  $-20^{\circ}\text{C}$  until used.

## 2.3 Rearing procedure

BPH was raised on above diets from one-day-old nymphs to adult stage under the condition of  $(27.0 \pm 0.5)^{\circ}\text{C}$ , over 90% RH, and 12–14 h photoperiod. Rearing method was referred to Fu *et al.* (2001). Glass cylinders, 15.0 cm in length and 2.5 cm in diameter, were used as feeding chambers. The artificial diets were held between two layers of stretched Parafilm M (about four times of the original area) which were located at one open end of the chamber and renewed every two days. The opposite end of the chamber was enclosed with a piece of nylon mesh after test insects had been introduced. The chambers were covered with a sheet of wet black cotton cloth, but the end with the artificial diet was exposed to light.

Twenty-five one-day-old nymphs were infested into each chamber and four replicates were used. The emergence rate and brachypter rate were obtained by counting the number of newly emerged adults every day and recording the wingmorphs of them. Nymphal duration was determined from the period from the day hatched to the day molted. The weight of adults within 24h after emergence was measured individually on a balance of 0.01mg-sensitivity (Mettler AE240).

## 2.4 Statistical analyses

The results were analyzed using Data Processing System (DPS) (Tang and Feng 1997). The effects of amino acid variation on each BPH performance index were evaluated by analysis of variance for a two-factor design, i.e., a 4 overall amino acids  $\times$  5 EAA:NEAA ratios factorial design. When there was significant effect for an amino acid factor (overall amino acid or EAA:NEAA ratio) on a BPH performance index ( $P < 0.05$ ), the optimum amino acid condition for the performance index was determined by testing the difference between different levels of amino acid factor using Duncan's Multiple Range Test. That is, the optimum amino acid condition for a performance index was determined by the significant difference between the amino acid level corresponding to a good BPH performance (e.g., higher emergence rate, shorter nymphal duration) and other levels. The optimum amino acid condition possibly had two or more levels if there was no significant difference between the performance index for these levels and there existed significant difference between them and other levels. The percentage data were normalized by

square root arcsine transformation before used for analyses.

The effects of amino acid variation on BPH performance were also integrated by means of principal component analysis (PAC). The analysis was based on all the performance indices, i. e., emergence rate, brachypter rate, nymphal duration, and weight of newly molted adults.

Relationships between dietary EAA concentration and each BPH performance index were examined with linear regression analysis. The correlation was considered significant when the  $P$  value was  $< 0.05$ .

### 3 RESULTS

#### 3.1 Effects of dietary amino acids on performance of three populations

There were substantial differences among the effects of dietary amino acids on performance of three BPH populations (Table 1, Table 2, Table 3). First, overall amino acid had significant effect only on the emergence rates of TN1 and ASD7 populations, but it affected all the observed indices of the Mudgo population except the emergence rate ( $P < 0.05$ ). Second, the effect of EAA: NEAA ratio on TN1 population was smaller than that on Mudgo and ASD7 populations.

**Table 1** Effects of amino acid variation on the emergence rate and brachypter rate of the three host-related BPH populations.

Amino acid factor	Mean of emergence rate (%)			Mean of brachypter rate(%)			
	TN1 population	Mudgo population	ASD7 population	TN1 population	Mudgo population	ASD7 population	
Overall amino acid	2.4%	54.7 <sup>△</sup> a	39.0	39.8 b	18.1	42.8 <sup>△</sup> a	37.5
	3.2%	57.5 <sup>△</sup> a	46.2	40.3 b	11.7	33.5 ab	44.7
	4.0%	45.5 b	37.6	45.8 <sup>△</sup> a	15.0	28.4 b	36.4
	4.8%	39.0 b	40.2	35.3 b	16.4	28.0 b	42.2
	$P$ value	$< 0.01$	$> 0.05$	$< 0.05$	$> 0.05$	$< 0.05$	$> 0.05$
EAA: NEAA ratio	58:42	48.6	34.4	48.3 <sup>△</sup> a	8.9	34.3	34.1 b
	50:50	55.4	39.3	38.8 bc	15.5	26.4	45.3 <sup>△</sup> a
	42:58	50.2	39.1	40.3 b	20.9	37.8	45.2 <sup>△</sup> a
	34:66	46.4	42.3	42.8 ab	18.9	37.4	50.6 <sup>△</sup> a
	26:74	44.0	49.1	32.6 c	13.2	34.3	24.6 b
$P$ value	$> 0.05$	$> 0.05$	$< 0.01$	$> 0.05$	$> 0.05$	$< 0.05$	
Reciprocal action	$P$ value	$> 0.05$	$< 0.05$	$< 0.01$	$> 0.05$	$> 0.05$	$> 0.05$

Notes: " $P$  value" represented the significant level for the effect of amino acid factor on BPH performance determined by analysis of variance for a two-factor design. Data for a factor within a column followed by a same letter showed no significant difference according to Duncan's Multiple Range Test at the level of 0.05. The optimum overall amino acids or EAA: NEAA ratios were corresponded to the data indicated by " $\Delta$ ".

**Table 2** Effects of amino acid variation on the newly molted adult weight of the three host-related BPH populations.

Amino acid factor	Mean weight of male adult (mg)			Mean weight of male adult (mg)			
	TN1 population	Mudgo population	ASD7 population	TN1 population	Mudgo population	ASD7 population	
Overall amino acid	2.4%	0.998	0.889 b	0.948	1.492	1.463 b	1.421
	3.2%	1.000	0.916 b	0.914	1.512	1.497 b	1.476
	4.0%	1.009	0.997 <sup>△</sup> a	0.937	1.552	1.557 <sup>△</sup> a	1.438
	4.8%	0.987	0.973 <sup>△</sup> a	0.935	1.494	1.576 <sup>△</sup> a	1.387
	<i>P</i> value	> 0.05	< 0.01	> 0.05	> 0.05	< 0.01	> 0.05
EAA: NEAA ratio	58:42	1.032	0.942 b	0.969	1.538	1.498 b	1.430 b
	50:50	1.008	0.990 <sup>△</sup> a	0.928	1.547	1.628 <sup>△</sup> a	1.500 <sup>△</sup> a
	42:58	0.988	0.934 b	0.910	1.491	1.577 <sup>△</sup> a	1.440 ab
	34:66	0.985	0.956 ab	0.927	1.502	1.494 b	1.414 b
	26:74	0.985	0.913 b	0.925	1.472	1.429 b	1.380 b
<i>P</i> value	> 0.05	< 0.05	> 0.05	> 0.05	< 0.01	< 0.05	
Reciprocal action	<i>P</i> value	< 0.01	> 0.05	> 0.05	> 0.05	< 0.01	> 0.05

Notes: See Table 1 for details.

**Table 3** Effects of amino acid variation on the nymphal duration of the three host-related BPH populations.

Amino acid factor	Mean nymphal duration of male (day)			Mean nymphal duration of female (day)			
	TN1 population	Mudgo population	ASD7 population	TN1 population	Mudgo population	ASD7 population	
Overall amino acid	2.4%	16.9	22.3 a	19.0	18.1	23.7 a	20.6
	3.2%	16.8	20.2 b	19.0	17.8	22.7 b	20.3
	4.0%	16.6	18.5 <sup>△</sup> c	18.8	17.9	20.3 <sup>△</sup> c	21.1
	4.8%	16.8	18.4 <sup>△</sup> c	18.8	17.9	20.4 <sup>△</sup> c	20.9
	<i>P</i> value	> 0.05	< 0.01	> 0.05	> 0.05	< 0.01	> 0.05
EAA: NEAA ratio	58:42	17.4 a	21.5 a	18.1 <sup>△</sup> c	18.2 a	23.3 a	20.2 <sup>△</sup> b
	50:50	16.1 <sup>△</sup> c	18.4 <sup>△</sup> d	18.6 <sup>△</sup> bc	17.3 <sup>△</sup> b	20.4 <sup>△</sup> c	20.1 <sup>△</sup> b
	42:58	16.8 b	19.7 c	19.1 ab	18.1 a	21.0 bc	20.6 ab
	34:66	16.8 b	19.2 c	19.2 ab	18.0 a	21.2 b	21.0 a
	26:74	17.4 a	20.4 b	19.6 a	18.5 a	23.0 a	21.9 a
<i>P</i> value	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	
Reciprocal action	<i>P</i> value	> 0.05	< 0.01	< 0.01	< 0.01	< 0.01	> 0.05

Notes: See Table 1 for details.

Besides having significant effects on nymphal development period of all the three populations, EAA:NEAA ratio had no marked influence on other indices of TN1 population, but had substantial effects on adult weight of Mudgo population, as well as on emergence rate, brachypter

rate and adult weight of ASD7 population ( $P < 0.05$ ). Third, the reciprocal action of overall amino acid and EAA:NEAA ratio had significant effect on female nymphal duration and male adult weight for TN1 population, on emergence rate and male nymphal duration for ASD7 population, while on emergence rate, female adult weight, and nymphal duration of both sexes for Mudgo population ( $P < 0.05$ ).

The effects of amino acid variation were integrated using principal component analysis of all the performance indices. Principal component 1 and 2 explained 57.4% and 14.2% of the total variation, respectively. From the view of the eigenvectors of each principal component (Table 4), principal component 1 integrated all the performance indices and principal component 2 mainly represented emergence rate and adult weight. Based on these two principal components, the performance of each population on every artificial diet could be explained as Fig. 1. The range of distribution area of performance markers for a BPH population is proportional to the effects of amino acid variation on performances of the population. It is obvious that the distribution area of performance markers for Mudgo population is the largest, and that for TN1 population is the smallest (Fig. 1). In other words, the effect of amino acids variation on the three populations appeared to be in an ascending order of Mudgo > ASD7 > TN1. It also suggested diverse responses of different populations to different dietary levels of amino acids. The two populations on resistant rice varieties (especially Mudgo) are more sensitive to the variation in dietary amino acids.

**Table 4** The eigenvectors of principal component 1 and 2 for BPH performance indices on 20 artificial diets.

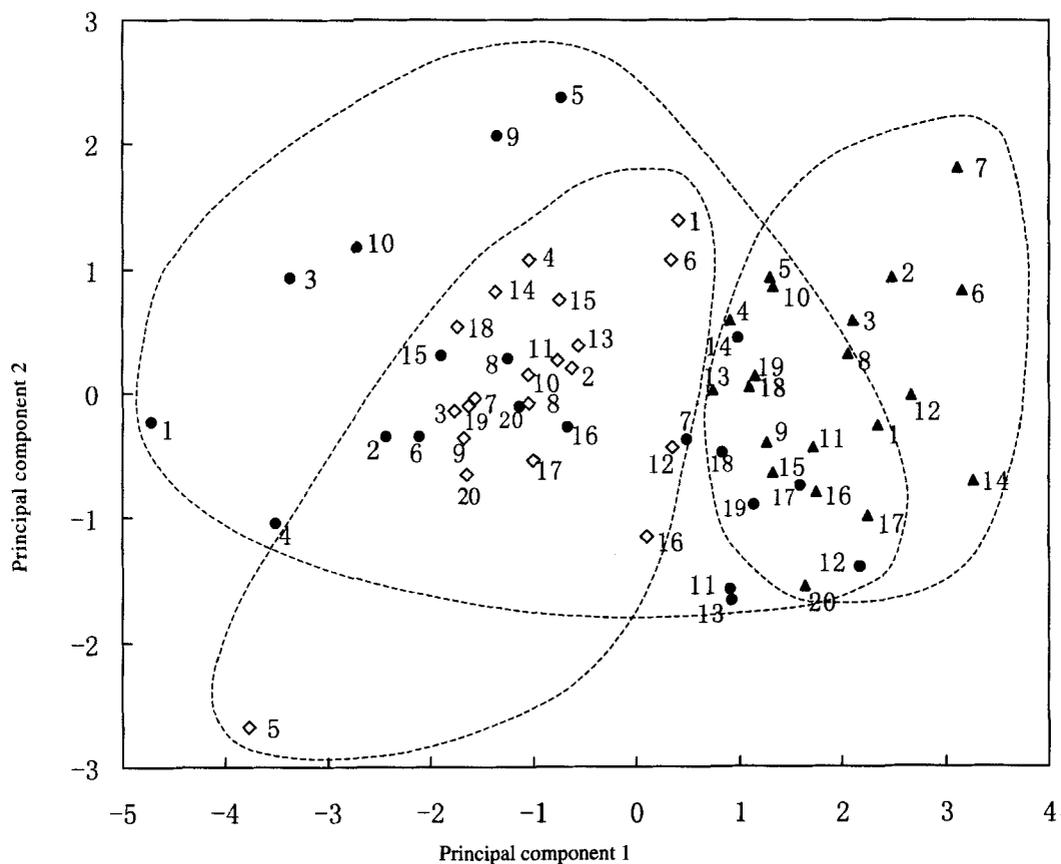
Principal component	Emergence rate	Brachypter rate	Weight of newly molted adult		Nymphal duration	
			Female	Male	Female	Male
Principal component 1	0.245	-0.385	0.464	0.339	-0.475	-0.486
Principal component 2	0.954	0.134	-0.212	-0.157	0.022	0.043

Notes: The significance of each performance index on principal component is in direct proportion to the absolute value of the eigenvector.

### 3.2 The optimum amino acid condition for three populations

The results also indicated that the optimum total amino acid concentrations for each of the three BPH populations were different, although the optimum EAA:NEAA ratio for the three populations was almost the same (i.e. 50:50) (Table 1, Table 2, Table 3). The populations on resistant Mudgo and ASD7 required higher overall amino acids. In view of performance indices influenced significantly by different overall amino acids, the most suitable concentrations for Mudgo population and ASD7 population were 4.0% - 4.8% and 4.0%, respectively, while that of TN1 population was 2.4% - 3.2%.

In addition, difference was still found in the correlation between the dietary EAA concentration and two performance indices (adult weight, nymphal duration) (Table 5). A significant correlation was only found between the dietary EAA concentrations and nymphal duration of ASD7 population while only the correlation between EAA and adult weight of Mudgo population ( $P < 0.05$ ).



▲ TN1 population ● Mudgo population ◇ ASD7 population

**Fig. 1** Principal component analysis based on the performance of the three BPH populations on 20 chemically defined diets.

Notes: The digits from 1 to 20 represented 20 kinds of chemically defined diets varying with overall amino acid and EAA: non-EAA ratio. The dotted circles showed the scattered area of each population on various diets.

**Table 5** Linear correlation between the dietary EAA concentration ( $x$ , %) and the performance indices ( $y$ ) of three host-associated BPH populations.

Performance indices( $y$ )		TN1 population				Mudgo population				ASD7 population			
		a	b	r	p	a	b	r	p	a	b	r	p
Nymphal duration (day)	Male	ns	ns	ns	0.40	ns	ns	ns	0.07	22.0	-0.8	0.51	0.02
	Female	ns	ns	ns	0.23	ns	ns	ns	0.07	20.4	-0.9	0.65	0.00
Adult weight (mg)	Male	ns	ns	ns	0.31	0.86	0.06	0.67	0.00	ns	ns	ns	0.06
	Female	ns	ns	ns	0.38	1.39	0.09	0.49	0.03	ns	ns	ns	0.22

Notes: "a" and "b" represented two constants of the equation " $y = a + b \cdot x$ ". "r" and "p" represented the correlation coefficient and its significant level, respectively. Data of "a", "b" and "r" were not shown ("ns" instead) for those with no significant correlation ( $P > 0.05$ ).

#### 4 DISCUSSION

We found that BPH populations on resistant rice varieties (especially Mudgo) showed more sensitive response to variation in dietary amino acids than that on susceptible rice variety. Moreover, the former required higher overall amino acids and had substantial correlation with the concentration of EAAs. This is the first unambiguous evidence showing that the host-associated populations of rice BPH can respond differently to the dietary amino acid composition. It can be concluded that intraspecific variation exists in the ability of BPH to survive and develop on diets with different amino acid conditions. A previous study on BPH revealed that, unlike biotype 1 (TN1 population), the feeding behaviors of BPH biotypes 2 and 3, separately maintained on resistant Mudgo and ASD7 at IRRI, can be significantly stimulated by some amino acids, such as alanine and glutamic acid (Sogawa 1978). It is inferred that the tolerance of Mudgo and ASD7 population under different amino acid conditions is lower than TN1 population. Thus, we suggest that the selection of BPH population on resistant rice variety can cause an excessive requirement for amino acids.

Considering that the host-associated BPH populations were reared on three rice varieties with different resistant genes, it is quite possible that amino acids are biochemically important for the rice varieties to display the resistance to BPH and potentially play an important role in the formation of new host-related insect populations (or biotypes). However, it is still unknown the correlation between the resistant mechanism of rice to BPH and the differentiation of response to amino acid variation in different host-associated populations reared on artificial diets. This is largely due to the lack of information about the amino acid compositions in phloem sap which has been technically difficult to collect from rice varieties (TN1, Mudgo and ASD7 in this case). So far, studies on pea aphid, *Acyrtosiphon pisum*, did not establish a clear correlation between performance on plants and corresponding mimicking diets for the aphid clones (Sanstrom 1994). It is possible that the differentiation of response of BPH to dietary amino acids is also related to some other aspects, such as the effect of artificial diets on symbionts, which are related to host insect's nutritional requirements. Further studies on composition comparison of phloem amino acids of different rice varieties and symbionts in BPH are needed to clarify this uncertainty.

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### 三个褐飞虱寄主种群对氨基酸需求的分化

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取分别在水稻品种 TN1(常用感虫对照)、Mudgo(含 *Bph1*)或 ASD7(含 *bph2*)上连续饲养 30 代以上的 3 个褐飞虱 *Nilaparvata lugens* 寄主种群, 分别饲养于 20 种氨基酸总量与配比不同的全纯人工饲料上, 以羽化率、短翅率、若虫历期以及初羽化成虫体重为指标对不同种群的氨基酸需求进行了比较。发现不同褐飞虱种群随氨基酸营养条件的改变有明显不同的表现, 其中 Mudgo 种群最容易受到氨基酸营养条件的影响, 而 TN1 种群所受影响最小。抗虫品种 ASD7 和 Mudgo 上的两褐飞虱种群所需的最佳氨基酸总浓度(分别为 4.0%~4.8%、4.0%)高于 TN1 种群(2.4%~3.2%), 同时, 前两种群对必需氨基酸浓度的变化较 TN1 种群敏感。这些结果表明, 不同褐飞虱寄主种群对饲料氨基酸的需求存在明显的分化, 推测氨基酸可能是抗虫水稻品种胁迫褐飞虱致害性变异的一种重要机制。

**关键词** 褐飞虱 *Nilaparvata lugens* 寄主种群 氨基酸 营养需求分化