

# Starvation tolerance of macropter brown planthopper, *Nilaparvata lugens*, from temperate, subtropical, and tropical populations in East and South-East Asia

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## Abstract

We compared the starvation tolerance of macropter brown planthopper, *Nilaparvata lugens* Stål (Homoptera: Delphacidae), a characteristic favoring long-distance migration, among populations collected from subtropical and temperate East Asia, tropical Indochina, and the Malay Peninsula. Starvation tolerance of planthoppers was significantly affected by climatic zone in which the planthoppers had been collected and by feeding duration after adult eclosion. After 24 h feeding on rice, newly emerged macropters originating from East Asia lived longer without feeding (starvation tolerance) than macropters from the tropical populations. The difference in longevity between the two groups of populations became more conspicuous when macropters fed on rice for 48 or 72 h, indicating that post-eclosion feeding markedly increased starvation tolerance in East Asian populations relative to the tropical populations. These facts provide evidence that *N. lugens* populations that are adapted for long-distance migration are distributed in subtropical and temperate East Asia. From the data on post-eclosion feeding together with starvation tolerance, we discuss the timing of planthopper takeoff from paddies and the difference in resource allocation (vitellogenesis or stored resources) between East Asian and tropical populations.

## Introduction

The brown planthopper, *Nilaparvata lugens* Stål (Homoptera: Delphacidae), is a notorious insect pest of rice in tropical and temperate paddy fields in Asia. This species shows wing polymorphism, producing brachypters and macropters depending on larval density and food quality (Kisimoto, 1965). The brown planthopper does not hibernate in the temperate zones of East Asia, including Japan and northern and central China (Mochida & Okada, 1979; Chen et al., 1982). Instead, during the cropping season, it temporarily expands its distribution from the south into temperate China and Japan with the assistance of the monsoon winds (Kisimoto, 1976; Cheng et al., 1979; Sogawa & Watanabe, 1992). Northern Vietnam is one possible source of Japanese and temperate Chinese *N.*

*lugens* (Sogawa, 1992; Kisimoto & Sogawa, 1995; Bao et al., 2000). After a series of northward expansions over a few generations, *N. lugens* invades as far as temperate East Asia (Cheng et al., 1979; Sogawa & Watanabe, 1992; Zhou et al., 1995). There have been many reports on the association between weather and spring and summer migrations of *N. lugens* (Watanabe et al., 1991; Kisimoto & Sogawa, 1995; Mills et al., 1996; Turner et al., 1999; Otuka et al., 2005, 2006). Cheng et al. (1979) proposed an autumn return migration from temperate China to hibernating areas, which has been supported by the detection of the southwestward mass movement of the planthopper by radar observations (Riley et al., 1991, 1994) and weather analysis (Rutter et al., 1998). There is also evidence of non-adaptive eastward migration in autumn from China to Kyushu, Japan, because immigrants and their progenies are soon killed by cold winter (Wada et al., 1987).

In contrast to the long-distance movement of *N. lugens* in temperate areas, there is little information on migration in tropical areas. Using radar, Riley et al. (1987) showed

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that flight activity is restricted to short periods at dusk and dawn, and that migration distance is generally less than a few tens of kilometers. Additionally, in rearing tests at various insect densities, tropical *N. lugens* produced fewer macropters than *N. lugens* collected in temperate Japan (Nagata & Masuda, 1980; Iwanaga et al., 1987). These facts suggest that tropical *N. lugens* is less migratory.

Genetic and physiological differences between tropical and temperate *N. lugens* populations have been reported. Mitochondrial DNA analysis revealed that three different haplotypes were found in populations of East Asia (Korea and subtropical and temperate China), whereas only one haplotype constituted populations of tropical Indochina and the Malay Peninsula (Mun et al., 1999). The biotype composition of the *N. lugens* populations (proportions of individuals showing virulence on different rice cultivars) in Japan, China, and northern Vietnam are similar, and show a clear discordance from those of tropical populations (Takahashi et al., 1994; Wada et al., 1994; Tanaka & Matsumura, 2000). Higher proportions of macropters generally appear in temperate populations compared to tropical populations in density-controlled rearing experiments (Nagata & Masuda, 1980; Iwanaga et al., 1985, 1987). In addition, Wada et al. (2007) demonstrated that macropter females originating from temperate and subtropical East Asia had a longer pre-ovipositional period than those of tropical populations. This character is presumably beneficial for pre-reproductive long-distance migration by *N. lugens* in East Asia.

In the present study, we compare starvation tolerance after eclosion among macropters originating from temperate, subtropical, and tropical paddy fields in East

and South-East Asia. Difference in starvation tolerance suggests not only differences in migration capability but also timing of migration take-off.

## Materials and methods

### Insects used

Samples from 12 populations of *N. lugens* were collected in 1992–1994 from tropical, subtropical, and temperate paddy fields in Indochina, the Malay Peninsula, China, and Japan. In each collection site, at least 60 samples of adults and aged nymphs were collected from a few paddy fields. The insects collected and their progeny were kept in plastic containers (30 × 26 cm, 28 cm height) and reared on rice seedlings (cv. Reiho or Kinuhikari) until their use in experiments. Collection sites and details including climatic zones are shown in Table 1. The definitions of climatic zones are complicated and differ greatly in the literature. Therefore, we simply classified the collection sites into temperate, subtropical, or tropical, and defined the subtropical region as the area from 20°N to the Tropic of Cancer (23.3°N). *Nilaparvata lugens* can overwinter to the south of the Tropic of Cancer (Cheng et al., 1979).

To obtain newly emerged *N. lugens*, we introduced about 30 females and 30 males into a plastic container (30 × 26 cm, 29 cm height) in which ca. 50 g (wet weight) of sprouting rice seedlings in ca. 800 g artificial soil (Hinokuni-tokotuchi; JA Kumamoto, Kumamoto, Japan) in a plastic case (14.5 × 25 cm, 3 cm height) was provided as food. Ten days later, another case of seedlings was added. Nymphs (progeny of the adults) gradually moved from the old to the new seedlings. A week later, another case of new

**Table 1** *Nilaparvata lugens* populations used for the experiments

Population	Collection			Climate	Time	Generation used after the collection
	Locality	(Latitude, longitude; °N, °E)				
Populations collected in 1992						
Malaysia-92	Muda, Malaysia	(6.1, 100.2)		Tropical	January, 1992	ca.10
Southern Vietnam-92A	Tien Giang Prov., Vietnam	(10.5, 106.5)		Tropical	April, 1992	Several
Southern Vietnam-92B	Hau Giang Prov., Vietnam	(10.0, 105.5)		Tropical	March, 1992	Several
Thailand-92	Suphan Buri Prov., Thailand	(14.1, 100.1)		Tropical	April, 1992	Several
Northern Vietnam-92A	Hai Hung Prov., Vietnam	(21.0, 106.5)		Subtropical	March, 1992	Several
Northern Vietnam-92B	Hanoi, Vietnam	(21.0, 105.5)		Subtropical	March, 1992	Several
Kyushu-92	Kagoshima Pref., Japan	(31.4, 130.3)		Temperate	July, 1992	4
Populations collected in 1993–1994						
Northern Vietnam-93	Hai Duong Prov., Vietnam	(21.0, 106.3)		Subtropical	April, 1993	4
Zhejiang-93	Fuyang, Zhejiang, China	(30.0, 120.0)		Temperate	July, 1993	5
Kyushu-93	Kumamoto Pref., Japan	(32.5, 130.4)		Temperate	July, 1993	2
Malaysia-94	Kota Bharu, Malaysia	(6.1, 102.2)		Tropical	March, 1994	3
Kyushu-94	Kumamoto Pref., Japan	(32.5, 130.4)		Temperate	September, 1994	2

seedlings was exchanged for the old seedlings. When many adults began to emerge, all adults were removed. The next day, we collected new adults within 24 h of eclosion (0-day adults) and used them in the experiments that are described below. Although we could not control nymphal densities strictly, the densities were very high for all cultured populations. Thus, most adults that emerged were macropters in all populations except Malaysia-92, in which a considerable proportion of brachypters emerged.

#### **Starvation tolerance (eight populations; experiment I)**

Starvation tolerance of adult brown planthoppers was assayed for eight populations (two originating from subtropical and temperate East Asia, respectively, and four from tropical Indochina and the Malay Peninsula) in experiment I. Approximately 15 female and 15 male macropters that had emerged within 24 h in a population were confined in a single glass container (ca. 2-l) with plenty of rice seedlings as food (two containers/population). The planthoppers were kept for 24 or 48 h in the container and allowed to feed. Planthoppers were then removed and confined individually in test tubes (1.8 cm in diameter, 6 cm height) with tap water (ca. 2 ml). A small filter paper (4 × 1 cm) that facilitated sucking water by the planthopper was placed at the bottom of the tube. Test tubes were checked daily and length of survival without food was used as an index of starvation tolerance.

#### **Starvation tolerance (two populations; experiment II)**

A more detailed experiment to study the relationship between the duration of feeding after eclosion and starvation tolerance was carried out, using the tropical Malaysia-94 and temperate Kyushu-94 populations. Some of the newly emerged planthoppers in experiment I had already begun feeding within 24 h. To obtain adults that had not fed and to determine the exact feeding time after eclosion, we took out new planthoppers within 12 h after eclosion from the rearing containers in experiment II. The planthoppers were confined in a glass container with rice seedlings for either 0, 24, 48, or 72 h. The subsequent procedure was the same as in experiment I. In addition, we supplied newly emerged planthoppers with mature rice plants (cv. Reiho) for 24 h as food after eclosion instead of seedlings to imitate the field condition in which planthoppers take off. A potted rice plant at the milk-ripe stage was placed in a nylon-net cage (25 cm in diameter, 110 cm height), and approximately 30 new adults (half males, half females) that had emerged within 12 h were released (two plants/population). The planthoppers were kept in the cage for 24 h and allowed to feed. The subsequent procedure was the same as in experiment I.

#### **Honeydew excretion measurement (experiment III)**

To estimate the feeding activity of planthoppers after eclosion, we measured honeydew excretion by planthoppers from five populations (two from the tropics and three from subtropical and temperate East Asia). As honeydew excretion by planthoppers reflects feeding activity (Paguia et al., 1980; Park & Song, 1988), honeydew excretion can be used as an index of feeding quantity (Wada et al., 1994; Tanaka, 1999). We used the parafilm sachet method (Heinrichs et al., 1985; Sogawa, 1992) to quantify individual honeydew excretion. A parafilm sachet (ca. 30 × 25 mm) was set on a sheath of a rice plant (cv. Reiho, 30–50 days old). A newly emerged female macropter (within 24 h) was confined within the sachet and kept at 25 °C for 24 h, when it was removed from the sachet and again confined in a new sachet. After removal of the insect, the weight of honeydew in the sachet was measured. In this way, honeydew excreted each day by a planthopper was collected for 5 days after eclosion. After the measurement of honeydew excretion, the 5-day-old planthopper was dissected to check for the presence of mature eggs. We assayed 15 female macropters from each population. Experiments I, II, and III were conducted in a rearing room at 25 ± 1.0 °C.

#### **Statistical analysis**

Because of an accident, we failed to obtain the second half of the survival data for the Southern Vietnam-92B population, and additionally, we did not follow survivorship until the final planthopper died in two populations (Northern Vietnam-93 and Malaysia-94) in experiment I (24 h feeding). Therefore, simple arithmetic means of survival durations are not appropriate to compare starvation tolerance among populations. Instead, we calculated the period (days) required for 50% of planthoppers to die, using regression. Assuming that longevity of planthoppers follows a normal distribution, we can expect a linear relationship between the time after eclosion and the probit of survival rate (Southwood, 1978). Thus, we converted survivorship (%) into probits and calculated the regression between those and the number of days after eclosion. From this, we obtained the time required for 50% of planthoppers to die (LT<sub>50</sub>). We used survivorship data ranging from 10 to 90% for the regression calculations, omitting the data close to 0 or 100% because of their comparatively low reliability. In every population, the relationship between probit of survivorship and time after eclosion was linear (see Table 2), and thus, the initial assumption of normally distributed survivorship appears correct. We used analysis of variance (ANOVA) to compare means of LT<sub>50</sub> or excretions among populations. All tests were conducted using the JMP version 5.01J (software SAS Institute, Cary, NC, USA).

**Table 2**  $LT_{50}$  (time until 50% of the planthoppers died) obtained from the regression of survival rate (probit) against days after eclosion in relation to post-eclosion feeding (n = sample size)

Population	Sex	Feeding duration		Regression			$LT_{50}$ days	Increase of longevity <sup>1</sup>
		After eclosion	n	Slope	Intercept	$r^2$		
Malaysia-94	Female	0 h	30	-0.86	4.74	1.00	5.5	1.00
	Female	24 h	30	-0.42	3.15	0.98	7.6	1.38
	Female	48 h	30	-0.30	2.60	0.98	8.7	1.57
	Female	72 h	30	-0.34	2.99	0.99	8.7	1.58
	Female	24 h (plant) <sup>2</sup>	30	-0.36	2.94	0.96	8.2	1.49
	Male	0 h	29	-0.95	4.63	1.00	4.9	1.00
	Male	24 h	30	-0.35	2.73	0.96	7.8	1.60
	Male	48 h	30	-0.26	2.41	0.98	9.3	1.91
	Male	72 h	28	-0.24	2.06	0.94	8.5	1.75
	Male	24 h (plant) <sup>2</sup>	30	-0.30	2.09	0.96	6.9	1.41
Kyushu-94	Female	0 h	30	-0.98	5.74	1.00	5.9	1.00
	Female	24 h	30	-0.48	4.09	0.99	8.5	1.45
	Female	48 h	30	-0.33	4.26	0.97	12.8	2.17
	Female	72 h	30	-0.37	5.33	0.98	14.4	2.45
	Female	24 h (plant) <sup>2</sup>	30	-0.25	3.40	0.82	13.8	2.35
	Male	0 h	30	-0.90	4.59	1.00	5.1	1.00
	Male	24 h	29	-0.38	3.41	0.95	8.9	1.76
	Male	48 h	29	-0.25	3.51	0.83	14.2	2.81
	Male	72 h	30	-0.33	4.30	0.93	13.1	2.58
	Male	24 h (plant) <sup>2</sup>	29	-0.42	5.63	0.93	13.4	2.65

<sup>1</sup>Increase of  $LT_{50}$  relative to that of the same population without feeding (set at 1.0).

<sup>2</sup>Planthoppers fed on a rice plant at milk-ripe stage for 24 h after their eclosion. In other treatments, planthoppers fed on young seedlings.

## Results

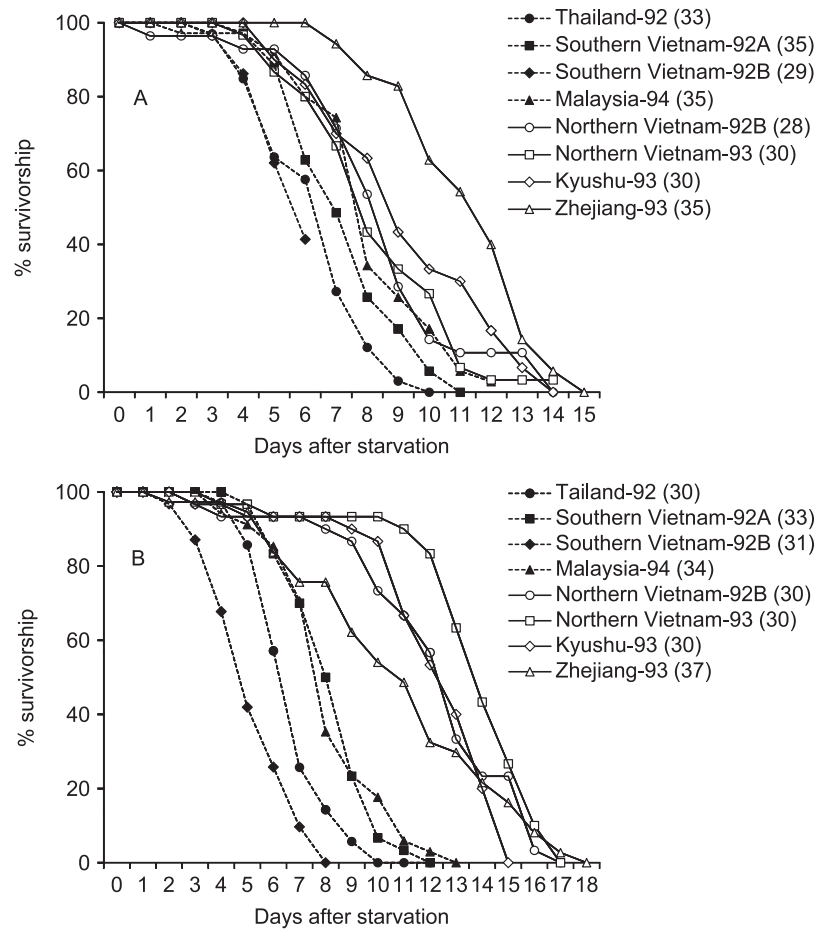
### Experiment I

Survivorship of newly emerged female macropters after 24 h feeding is shown in Figure 1A and that of macropters after 48 h feeding in Figure 1B. Three-way ANOVA (factors: climatic zone, sex, and feeding time) showed that  $LT_{50}$  were significantly affected by climatic zone ( $F = 31.1$ , d.f. = 1,  $P < 0.0001$ ) and feeding time ( $F = 17.1$ , d.f. = 1,  $P = 0.0005$ ). Sex did not affect  $LT_{50}$  significantly ( $F = 0.9$ , d.f. = 1,  $P = 0.4$ ), the average  $LT_{50}$  being 8.6 and 8.3 days after starvation for females and males, respectively. The two-way interaction between climatic zone and feeding time was significant ( $F = 3.7$ , d.f. = 2,  $P = 0.04$ ). The average  $LT_{50}$  of the tropical populations (6.7 days; Thailand-92, Southern Vietnam-92A and Vietnam-92B, and Malaysia-94) were significantly shorter than those of the subtropical population (10.1 days; Northern Vietnam-92B and Vietnam-93) and of the temperate populations (10.4 days; Zhejiang-93 and Kyushu-93) according to the Tukey honestly significant difference (HSD)-test. Thus, *N. lugens* populations were divided into two groups: tropical vs. subtropical and temperate populations. Prolongation of

the  $LT_{50}$  caused by increasing the feeding time after eclosion was also conspicuous, the averages being 7.6 and 9.3 days for populations of planthoppers feeding for 24 and 48 h, respectively.

### Experiment II

Survivorship of females from the tropical Malaysia-94 and temperate Kyushu-94 populations is illustrated in Figure 2, and the regressions used to estimate the  $LT_{50}$  are presented in Table 2. Three-way ANOVA (factors: population, sex, and feeding time) showed that  $LT_{50}$  were significantly affected by populations ( $F = 15.9$ , d.f. = 1,  $P = 0.004$ ) and feeding time ( $F = 44.8$ , d.f. = 1,  $P = 0.0002$ ). There was no significant difference of  $LT_{50}$  between the sexes ( $F = 0.002$ , d.f. = 1,  $P = 0.97$ ). The interaction between population and feeding time was again significant ( $F = 8.71$ , d.f. = 1,  $P = 0.02$ ). This indicates that the effect of feeding time on the increase of  $LD_{50}$  differed between populations. In other words, the longevity of planthoppers from the Kyushu-94 population increased more markedly with increasing feeding duration after eclosion than from Malaysia-94. For example, female macropters that fed on rice seedlings for 72 h had an  $LT_{50}$  of 14.4 days, that is, 2.5 times the

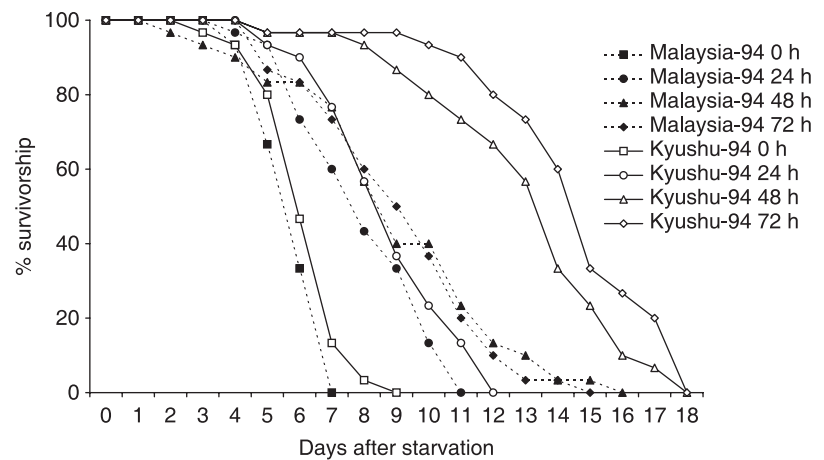


**Figure 1** Longevity of newly emerged macropterous females in eight populations of *Nilaparvata lugens* that fed on young rice seedlings for (A) 24 h or (B) 48 h after eclosion. The numbers in parentheses in the legend indicate the total numbers of females monitored.

longevity of macropters without feeding. In contrast, the increase in longevity of the Malaysia-94 macropters caused by feeding was relatively small: only 1.6 times attained by 72-h feeding females. Males showed the same tendency: 2.8 times for the Kyushu-94 macropters, and 1.9 times for

the Malaysia-94 macropters, although the maximum  $LT_{50}$  was reached at 48 h in both male populations.

In both populations, the effect of feeding duration on increased starvation tolerance was also apparent when macropters fed on plants at the milk-ripe stage, instead of



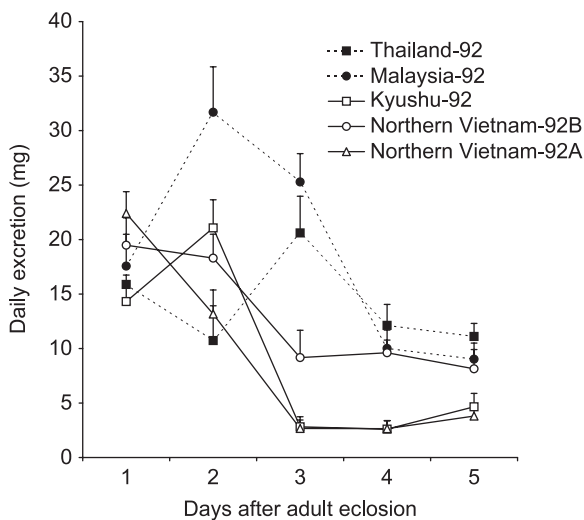
**Figure 2** Longevity of newly emerged macropterous females in a tropical (Malaysia-94) and a temperate (Kyushu-94) population of *Nilaparvata lugens* that fed on young rice seedlings for 0, 24, 48, or 72 h after eclosion.

on young rice seedlings (Table 2). However, there was a difference in responses to rice growth stage between the two populations. Both female and male macropters from Kyushu-94 population increased their longevities more when they fed on plants at the milk-ripe stage for 24 h compared to those that fed on young seedlings for the same duration (Table 2). In contrast, longevities of macropters feeding for 24 h in Malaysia-94 population were almost the same, irrespective of the growth stage of their food plants.

#### Honeydew excretion

Female macropters fed voraciously for the first few days after eclosion (Figure 3). The mean quantities of honeydew excreted by female macropters on the 1st day (1-day-old adults) ranged from 14.3 to 22.4 mg, and were not significantly different among populations (ANOVA:  $F = 2.35$ ,  $d.f. = 4$ ,  $P = 0.06$ ) (Figure 3). However, macropters of the two populations collected in subtropical northern Vietnam (92A, 92B) and of the temperate Kyushu-92 population maintained a high level of excretion until day 2, whereas female macropters of the two tropical populations maintained a high level of excretion until day 3. Excretions by 3-day-old adults were significantly different among populations (ANOVA:  $F = 22.5$ ,  $d.f. = 4$ ,  $P < 0.0001$ ); the populations were divided into two groups, with plant-hoppers from the tropical populations excreting significantly more than those from the subtropical and temperate populations (Tukey HSD test).

Ovary maturation of 5-day-old females differed greatly among populations. The proportions of females possessing



**Figure 3** Daily honeydew excretion (mean + SE) by female macropters of *Nilaparvata lugens* from five local populations originating from East and Southeast Asia.

mature eggs at 5 days after eclosion were 92.9 and 100% in the tropical Thailand-92 and Malaysia-92 populations, but only 29.4, 28.6, and 0% in the subtropical northern Vietnam-92A and Vietnam-92B and the Kyushu-92 populations.

#### Discussion

Results clearly show that *N. lugens* populations originating from subtropical and temperate East Asia are potentially more tolerant to starvation than those from tropical Indochina and the Malay Peninsula. Using exactly the same populations (same original collections), Wada et al. (2007) confirmed that all subtropical and temperate populations had longer pre-ovipositional periods than the tropical populations. A long pre-reproductive period and starvation tolerance are apparently correlated and are beneficial characters for pre-reproductive migration. So we can conclude that the life history of the East Asian populations is more tuned to long-distance migration compared to the tropical populations.

Interestingly, the East Asian populations had markedly increased starvation tolerance after feeding. In fact, the tolerance of females of Kyushu-94 increased 2.5-fold after 72 h of feeding compared to unfed females. The increase also occurred when the insects fed on older plants that planthoppers attack in the field before take-off. Feeding after eclosion apparently contributed to starvation tolerance, probably by increasing reserves in the East Asian populations. On the other hand, post-eclosion feeding contributed less to starvation tolerance in the tropical populations. Among Malaysia-94 females, the maximum  $LT_{50}$  was only 1.6 times that of unfed insects. This suggests that nutrition obtained by feeding was allocated not only to reserves but also to something else in the tropical populations. An increase in starvation tolerance after post-eclosion feeding has been reported previously by Kusakabe & Hirao (1976). In their study using a Kyushu population, tolerance reached the maximum when newly emerged insects fed on rice for 3.5 days, with decreasing longevities when insects fed for 6.5 days.

Our study also suggests a difference in response to quality (age) of rice plants between the planthoppers from tropical and East Asian populations. In the tropical Malaysia-94 population, longevities were almost the same between planthoppers that fed on mature plants and on young seedlings for 24 h. On the other hand, planthoppers that fed on mature plants lived much longer than those feeding on young seedlings in the temperate Kyushu-94 population. As emigration of planthoppers is frequently observed in paddy fields at the ripening stage (Cheng et al., 1979), a great increase in longevity of planthoppers feeding on mature plants may be a significant response related to

migration. It would be interesting to clarify the longevities and pre-ovipositional periods of planthoppers feeding on rice plants at various growth stages in the field.

Taken together, available information on post-eclosion feeding, starvation tolerance, and ovary development suggests a difference in the allocation of resources between tropical and East Asian populations. Feeding was maximized 2–3 days after eclosion (Figure 3), as was also reported by Tanaka (1999). The feeding of tropical populations was maximized in the first 3 days. Much of this energy intake was probably invested in ovary development. Otherwise, vitellogenesis would be triggered simply by initiation of post-eclosion feeding. This period approximately coincides with the pre-oviposition period [50% of females started oviposition by 4.1 days after eclosion in the Malaysia-92 population, and 5.6 days in the Thailand-92 population (Wada et al., 2007)]. As some females had already started oviposition before these days, the onset of oviposition may decrease feeding. On the other hand, feeding was maximized at the first 2 days in the East Asian populations, but this energy intake seems to have been invested not in ovary development but in reserves, judging from the immature ovaries at day 5 and the remarkably increased starvation tolerance after feeding. The beginning of feeding reduction on day 3 approximately coincided with the maximization of starvation tolerance. As the number of populations used in our honeydew experiment was limited, more study is necessary to confirm the difference in feeding behaviors between tropical planthoppers vs. temperate and subtropical planthoppers.

Although *N. lugens* is a typical long-distance migrant, timing of planthopper take-off from fields in relation to adult age has been rarely discussed. Kisimoto & Sogawa (1995) described that adult planthoppers take off actively after a teneral period of 1–2 days. Ohkubo (1981) also suggested take-off by young adults without feeding. However, our study emphasizes the importance of post-eclosion feeding before take-off, because starvation tolerance increases more than twice in East Asian planthoppers. Kusakabe & Hirao (1976) also suggested post-eclosion feeding before migration because of increase of longevities after feeding. Ohkubo (1981) reported that the average flight duration of Japanese *N. lugens* tested with a tethered flight technique maximized on day 4 after eclosion. This fact also suggested post-eclosion feeding until macropters develop flight capability. As tolerance is maximized by 2 or 3 days of feeding, the fact that the reduction of feeding occurred on day 3 in East Asian planthoppers may indicate the timing of take-off from the rice fields.

Our results provide further evidence that *N. lugens* populations with similar characteristics are distributed in subtropical and temperate East Asia. These populations are

adapted to migration with their longer pre-ovipositional period and higher starvation tolerance after post-eclosion feeding. These characteristics are apparently maintained by a migration system mediated by seasonal monsoon winds, allowing northward expansion during spring and summer and southward return in autumn for hibernation. It will be interesting to clarify how meteorological mechanisms and adult behavior isolate *N. lugens* populations in East Asia from tropical populations.

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