

# Variation of pre-ovipositional period in the brown planthopper, *Nilaparvata lugens*, collected in tropical, subtropical and temperate Asia

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*Ms. received: November 29, 2006; accepted: March 9, 2007*

**Abstract:** We investigated the pre-ovipositional period of *Nilaparvata lugens* originating from tropical, subtropical and temperate regions of East and Southeast Asia using laboratory experiments to compare the migration capability of the populations. Macropter females collected in 1992 from Japan and subtropical North Vietnam had a longer immature period than those from tropical Indochina Peninsula, i.e. the day of the first oviposition after eclosion was about 3 days later in the former populations. Populations collected in 1993 and 1994 from Japan, Central and South China, and North Vietnam also had a longer immature period than that of the tropical Malaysian population. Thus, a general trend was demonstrated that macropters originating in temperate and subtropical East Asia had a longer pre-ovipositional period, which is presumably beneficial for pre-reproductive long-distance migration. This finding supports a current hypothesis for the migration system of *N. lugens* existing in East Asia, which has maintained the capability of long-distance migration throughout years in spite of the disadvantage of prolonged oviposition for multiplication.

**Key words:** Delphacidae, macropters, migration, ovarian development, oviposition, rice insect pest

## 1 Introduction

The brown planthopper, *Nilaparvata lugens* Stål, is one of the most serious insect pests of rice in tropical and temperate paddy fields in Asian countries. It does not hibernate in temperate zones of East Asia including Japan and North and Central China (Mochida and Okada 1979; Chen et al. 1982). It temporarily expands from the south into temperate China and Japan during the crop seasons with the assistance of the monsoon winds (Kisimoto 1976; Cheng et al. 1979; Sogawa and Watanabe 1992). Sogawa (1992) suggested that the source areas of Japanese *N. lugens* are North Vietnam and South China and the literatures supporting this hypothesis have been sometimes reported (Kisimoto and Sogawa 1995; Bao et al. 2000; Otuka et al. 2005a). After a series of northward expansions from the source through a few generations, *N. lugens* invade East Asia (Cheng et al. 1979; Sogawa and Watanabe 1992; Zhou et al. 1995). Weather associated with these spring and summer migrations of *N. lugens* are often analysed by many workers (Watanabe and Seino 1991; Kisimoto and Sogawa 1995; Mills et al. 1996; Turner et al. 1999; Otuka et al. 2005b). A hypothesis of autumn return migration from temperate China to hibernating areas was also proposed by Cheng et al. (1979). In fact,

southwestward mass movement of the planthopper has been detected 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 (Wada et al. 1987). Many details of the return migration of *N. lugens*, however, remain still unknown, including whether it actually occurs and its significance in natural selection to maintain long-distance movement.

Compared with the accumulated information on long-distance movement of *N. lugens* in temperate areas, there are very few data about its migration in tropical areas. Using radar, Riley et al. (1987) observed that flight activity is restricted to a short period at dusk and dawn, and that migration distance is generally less than a few tens of kilometers. Additionally, in rearing tests with various insect densities, tropical *N. lugens* produces generally fewer macropters than *N. lugens* collected in Japan (Nagata and Masuda 1980; Iwanaga et al. 1987). These facts indicate that tropical *N. lugens* is less mobile at the population level.

Many studies on insect migration by flight indicate that migration by females occurs when they are sexually immature adults (Johnson 1969). Thus, the pre-ovipositional period, the duration of the interval between adult emergence and reproductive maturity,

determines the time during which the insect can express its migratory potential (Hill and Gatehouse 1993; Wilson and Gatehouse 1993). Macropters of *N. lugens* also migrate pre-reproductively because most immigrants caught in net traps in Kyushu, Japan, were unmated individuals with immature ovaries (Kisimoto 1976). Thus, the macropterous female pre-ovipositional period seems to be a good index of individual migration capability.

In the present study, we compared the pre-ovipositional periods of *N. lugens* macropterous females originating from tropical, subtropical and temperate paddy fields and discuss the ecological significance of the difference in female maturation found among the populations.

## 2 Materials and Methods

### 2.1 Insects used

Fifteen local populations of *N. lugens* were collected in 1992–1994 from tropical, subtropical and temperate paddy fields in the Indochina Peninsula, China and Japan. The insects collected and their progeny were kept in plastic containers (30 × 25 cm, 28 cm height) and reared on rice seedling (variety: Reiho or Kinuhikari). For Chinese populations, the insects were reared in cages with young rice plants (variety: TN1) for the first few or several generations after collection. Thereafter, the insects were reared in plastic containers with rice seedlings as described above. Collection sites and details of the tested insects are shown in table 1.

In the tested colony, about 30 females and approximately same number of males of the previous generation were introduced into a plastic container (30 × 26 cm, 29 cm height) in which ca. 50 g (wet weight) sprouting rice seedlings with ca. 800 g artificial soils (Hinokuni-tokotuchi; JA Kumamoto, Kumamoto, Japan) in a plastic case (14.5 × 25 cm, 3 cm height) were provided for food plants.

In 10 days later, another case of seedlings was added in the empty space of the container. Nymphs of planthoppers gradually moved to the new seedlings from the old ones. In the next week, another case of new seedlings was exchanged for the old seedlings. When many adults began to emerge, all the adults were removed from the container. In the next day, we collected new adults (0-day adult) and used them for experiments. Although we could not control nymphal densities strictly, the densities were basically very high and adults emerged were mostly macropters in any population.

### 2.2 Measurement of pre-ovipositional period

The pre-ovipositional period, or the period required for ovary maturity, was tested using the following three methods. We conducted experiment I to compare the pre-ovipositional periods among the populations using a criterion of the periods for 50% of the females to begin oviposition. We examined the proportions of females having mature eggs in experiment II as an index of pre-ovipositional periods of the females, to find a simpler method than experiment I. As a good correlation was obtained between these proportions and pre-ovipositional periods, we estimated the pre-ovipositional periods of the populations collected in 1993 and 1994 by simply observing the mature eggs of females in experiment III. All experiments were performed in an insect-rearing room at 25°C (±1°C) under a 14 : 10 h (Light : Dark) photocycle. The variety of the rice seedlings used was Reiho.

#### 2.2.1 Experiment I

Adults within 24 h after eclosion (0-day adult) were paired in a glass test tube (10 cm depth) with one or two rice seedlings. On 3rd or 4th day after eclosion the rice seedlings were taken out and checked for the presence of eggs under a binocular microscope. Thereafter, rice seedlings were changed every day and checked for eggs on them. About 30 pairs were used for each population and the proportions of females which had begun oviposition in relation to adult age were examined.

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

Population	Collection				Generation used after the collection
	Place	(Latitude, longitude; °N, °E)	Climate*	Time	
Populations collected in 1992					
Kyushu 92A	Kagoshima Pref., Japan	(31.4, 130.3)	Temperate	July, 1992	3
Kyushu 92B	Kumamoto Pref., Japan	(32.5, 130.4)	Temperate	July, 1992	3
North Vietnam 92A	Hai Hung Prov., Vietnam	(21.0, 106.0)	Subtropical	April, 1992	Several
North Vietnam 92B	Hanoi, Vietnam	(21.0, 105.5)	Subtropical	March, 1992	Several
South Vietnam 92A	Tien Giang Prov., Vietnam	(10.5, 106.5)	Tropical	April, 1992	Several
South 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
Malaysia 92	Muda Area, Malaysia	(6.1, 100.2)	Tropical	January, 1992	ca. 10
Populations collected in 1993–1994					
Kyushu 93	Kumamoto Pref., Japan	(32.5, 130.4)	Temperate	July, 1993	1 (next)
Kyushu 94	Kumamoto Pref., Japan	(32.5, 130.4)	Temperate	September, 1994	1 (next)
Zhejiang 93	Fuyang, Zhejiang, China	(30.0, 120.0)	Temperate	July, 1993	4
Guangxi 93	Nanning, Guangxi, China	(22.8, 108.1)	Subtropical	April, 1993	Several
Hainan 93	Hainan, China	(19.5, 110.5)	Subtropical	March, 1993	Several
North Vietnam 93	Hai Duong Prov., Vietnam	(21.0, 106.3)	Subtropical	April, 1993	3
Malaysia 94	Kota Bharu, Malaysia	(6.1, 102.2)	Tropical	March, 1994	2

\*The definitions of climatic classification are complicated and greatly different among literatures. Therefore, we simply classify the planthopper-collection sites into three climatic zones (temperate, subtropical and tropical) and define subtropical regions as the areas approximately from 20°N to tropic of Cancer (23.3°N) (including Hainan Island at 19.5°N), which are located between temperate and tropical zones. *Nilaparvata lugens* can overwinter to the south of tropic of Cancer (Cheng et al. 1979).

### 2.2.2 Experiment II

About twelve 0-day adults of each sex were confined in a glass container (ca. 2 l) with plenty of rice seedlings. Three days later, the females (3-day adults) were removed from the container and transferred individually to a test tube (10 cm depth) containing a rice seedling. The next day, oviposition on the seedling was examined, and the 4-day females were dissected to check for the presence of mature (fully grown) eggs. Two replications were made.

### 2.2.3 Experiment III

Twelve to 18 pairs of 0-day females and males were confined in a glass container (2 l) with plenty of rice seedlings. They were kept in a rearing room for 2, 4, 6 or 8 days, after which, females (2-, 4-, 6- and 8-day adults) were dissected to check for the presence of mature eggs. Basically two replications were made.

## 2.3 Statistical analysis

To obtain the period required for 50% of the females to begin oviposition in experiment I, we used the regression of the accumulated percentage of females that oviposited against the period (day) after eclosion. The percentage data were transferred to probits before regression calculation. If we assumed that the first oviposition days of females follow the normal distribution, we can expect the linear relationship between the period after eclosion and the probit of the accumulated percentages (Southwood 1978). As the variations of data among replications were generally small in experiment II and III, we pooled the data to calculate the net proportion in each treatment of the population. Then, we carried out a method of multiple comparisons for proportions described in Zar (1996).

## 3 Results

### 3.1 Experiment I

The pre-ovipositional periods of *N. lugens* populations collected in 1992 in tropical (South Vietnam, Thailand and Malaysia), subtropical (North Vietnam) and temperate (Kyushu) paddy fields were compared by the pair-rearing method. The day of the first oviposition by the females varied depending on the population (fig. 1). The females of tropical populations started oviposition

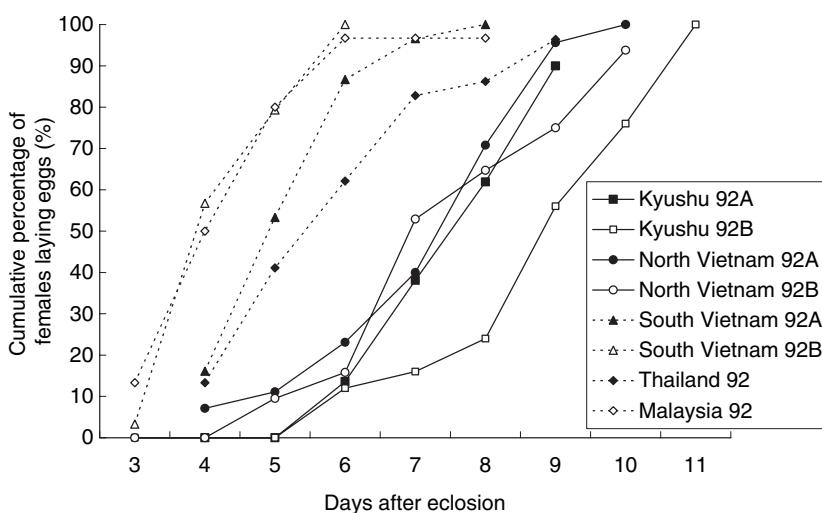
much earlier than those of the other populations. According to regression analysis, the periods required for 50% of the females to begin oviposition were 5.0, 4.2, 5.6 and 4.1 days after eclosion in the tropical populations of South Vietnam 92A, South Vietnam 92B, Thailand 92 and Malaysia 92 respectively. The corresponding periods were 7.4, 8.8, 6.9 and 7.4 days in the temperate and subtropical populations of Kyushu 92A, Kyushu 92B, North Vietnam 92A and North Vietnam 92B respectively. The mean period (4.7 days) in the tropical populations was shorter by about 3 days than that (7.6 days) in the temperate and subtropical populations and the difference was highly significant (*t*-test: *t* = 5.3, *f* = 6 and *P* < 0.01).

### 3.2 Experiment II

Planthoppers from the same populations as those in experiment I were reared in groups after eclosion. About half or more of 4-day females in the tropical populations had laid eggs on rice seedlings (table 2). Among the tropical populations, the Malaysia 92 attained higher proportions of oviposited females than the Thailand 92 and South Vietnam 92A populations. None or very few females from subtropical and temperate populations had started oviposition, and the variations among the proportions of females that had oviposited were not significantly different. Thus, the difference in the pre-ovipositional period between the tropical population and the other populations was again confirmed. Macropters (4-day females) were dissected to check for ovarian development in this experiment. The proportion of females with mature eggs in each population revealed slightly higher values than the figures for oviposition, but the trend paralleled that of oviposition. Therefore, ovarian development could be a good index of the pre-ovipositional period.

### 3.3 Experiment III

Subtropical and temperate Chinese populations in addition to Indochina and Kyushu populations collected in 1993 and 1994 were used in this experiment. The females of the tropical Malaysia 94 population showed much earlier maturity than the other



**Fig. 1.** Cumulative percentage of macropterous females that started oviposition after eclosion. Origins of the *Nilaparvata lugens* populations are given in table 1. Dotted lines indicate tropical populations and solid lines indicate subtropical or temperate populations

**Table 2.** Oviposition and ovarian development of females 4 days after eclosion in *Nilaparvata lugens* populations collected in various locations (experiment II)

Population	Climate of collection site	Insects used	Females oviposited		Females with mature eggs	
			Number	Percentage*	Number	Percentage*
Kyushu 92A	Temperate	24	2	8.3 cd	3	12.5 c
Kyushu 92B	Temperate	20	0	0 d	1	5.0 c
North Vietnam 92A	Subtropical	22	2	9.1 cd	4	18.2 c
North Vietnam 92B	Subtropical	24	0	0 d	2	8.3 c
South Vietnam 92A	Tropical	21	9	42.9 bc	14	66.7 b
South Vietnam 92B	Tropical	22	14	63.6 ab	20	90.9 ab
Thailand 92	Tropical	25	13	52.0 b	19	76.0 ab
Malaysia 92	Tropical	24	23	95.8 a	24	100 a

\*Within a column, percentages followed by the same letter are not significantly different at the 5% probability level.

**Table 3.** Ovarian development of females after eclosion in *Nilaparvata lugens* populations collected in various locations (experiment III)

Population	Climate of collection site	Percentage* of females with mature eggs at various days after eclosion (females dissected)			
		2 days	4 days	6 days	8 days
Kyushu 93	Temperate	0 (33)	6.9 c (29)	45.5 bc (33)	84.8 ab (33)
Kyushu 94	Temperate	0 (23)	5.9 bc (17)	25.0 c (28)	45.5 b (22)
Zhejiang93	Temperate	0 (15)	18.5 bc (27)	53.8 bc (26)	92.0 a (25)
Guangxi93	Subtropical	3.7 (27)	38.7 ab (31)	75.0 ab (28)	90.3 a (31)
Hainan 93	Subtropical	0 (30)	25.0 abc (28)	37.0 bc (27)	93.1 a (22)
North Vietnam 93	Subtropical	0 (24)	14.8 bc (54)	46.9 bc (64)	80.6 a (31)
Malaysia 94	Tropical	6.7 (30)	60.0 a (30)	93.0 a (27)	100 a (14)

\*Within a column, percentages followed by the same letter are not significantly different at the 5% probability level.

populations (table 3). More than half and most females attained maturity by 4 and 6 days after eclosion respectively. At 6 days, the proportion of the females with mature eggs differed significantly from those of the females in other populations except for the subtropical Guangxi 93, which showed slightly earlier maturity than the other subtropical and temperate populations. However, the differences in the proportions of mature females of Guangxi 93 were significant only from that of Kyushu 93 at 4 days and from those of Kyushu 94 at 6 and 8 days. The Kyushu 94 population showed the latest maturity. The proportion of mature females differed significantly from the subtropical and temperate Chinese populations at 8 days. It was noteworthy that a few or some females of the subtropical and temperate populations retained immature ovaries even at 8 days after eclosion.

#### 4 Discussion

Our laboratory rearing tests demonstrated clearly that macropterous females of *N. lugens* collected in Japan, China and North Vietnam have longer pre-ovipositional periods than macropters in tropical populations. This result may have been slightly influenced by unintentional selection after field collections, as the pre-ovipositional period seems to be a characteristic that is easily selected during laboratory rearing. However, pre-ovipositional periods apparently differed between the populations of subtropical North Vietnam

and the populations of tropical South Vietnam and Thailand, in which individuals of the same generation after collection were tested in experiments I and II. In addition, the population of Malaysia 94 tested in the early generation (second) after collection showed very early ovarian maturity in experiment III. Therefore, in *N. lugens*, there is a tendency for macropterous females of subtropical and temperate populations to mature more slowly. This longer immaturity of macropters seems to be important to facilitate long-distance movement for *N. lugens* in this zone, because the insect migrates during the pre-ovipositional period.

The difference of pre-ovipositional periods found among populations seems to be genetically based. The pre-ovipositional period of *N. lugens* is influenced by food quality and probably by nymphal rearing densities. Kisimoto (1965) reported that the pre-ovipositional period of macropterous females of Japanese *N. lugens* ranged mostly from 5 to 12 days after eclosion with great individual variation, being influenced by growth stage and quality of rice. In our experiment, however, food (young rice seedlings) was the same for any of the populations. Nymphal density is probably another factor to influence immature periods of macropters. Iwanaga and Tojo (1986) showed that ovarian development in *N. lugens* is controlled by juvenile hormone (JH), as in many other insects. Rearing densities in *N. lugens* greatly affects its wing dimorphism, which is also controlled under JH titre according to the theory of wing dimorphism in insects proposed by Roff (1986). Thus the nymphal rearing

densities probably influence JH titres of macropters after eclosion, causing variations of pre-ovipositional periods. Unfortunately, we did not control nymphal densities strictly, however, the densities were very high regardless of the populations (almost same at first glance). Therefore, the differences in pre-ovipositional period were probably attributable to the genetic difference among populations, rather than environmental factors including food quality or nymphal density.

If we collected more *N. lugens* populations in East Asia, we would probably find wider variations of pre-ovipositional period. In fact, Iwanaga et al. (1985, 1987) reported great variations of wing polymorphism associated with rearing densities among *N. lugens* populations collected in East Asia, although most populations exhibited higher ratios of macropters, as compared with those collected in South Asian. The populations collected in East Asia were progenies of immigrants and therefore, they attributed this variation to the origins of the immigrants. Equally like wing polymorphism, the pre-ovipositional period of *N. lugens* collected in East Asia depends on the origin of the immigrants. Thus, we could conclude that the immigrants having longer pre-ovipositional period invade East Asia more frequently.

Present study seems to provide further evidences that *N. lugens* populations having similar characteristics are distributed in subtropical and temperate East Asia. The biotype compositions of the *N. lugens* populations (proportions of individuals showing virulence on different rice varieties) in Japan, China and North Vietnam are similar, and show a clear discordance from the biotypes of tropical populations (Takahashi et al. 1994; Wada et al. 1994; Tanaka and Matsumura 2000). Mitochondrial DNA analysis also pointed out the similarity of haplotypes found in the populations of East Asia (Korea and China including subtropical and temperate regions) with different compositions of haplotypes in the populations of tropical Indochina Peninsula (Mun et al. 1999). In addition, in our experiments, macropters of *N. lugens* in temperate and subtropical East Asia generally possessed longer pre-ovipositional periods compared with those in tropical regions, although slight variations of pre-ovipositional periods were found.

These facts suggest comparatively genetically uniform populations existing in these areas. It is considered that the migration system of *N. lugens* in East Asia is mediated by seasonal monsoon winds, allowing northward expansion during spring and summer and southward return movements in autumn. This system probably maintains *N. lugens* having longer immaturity genetically for long years, which enable them to migrate long distances, in spite of the great disadvantage of prolonged oviposition for multiplication.

#### Acknowledgements

We thank Nik Mohd. N., N. K. Ho, B.V. Ich, P. Raywat and H. Inoue for the help with insect collection and M. Matsumura for the help with the statistical analysis. Thanks are also because of M. Dairiki for rearing insects.

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