

Chapter 4

Rice Planthoppers in Tropics and Temperate East Asia: Difference in Their Biology

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Abstract Differences in population growth and physiological characters of *Nilaparvata lugens* between the populations of the tropics and of temperate East Asia are discussed. Fundamental differences in population dynamics seem to be related to the origin of initial immigrants and activity of natural enemies. In tropical fields, initial immigrants originate from nearby paddy fields, resulting usually in high immigrant densities. On the other hand, few immigrants after seasonal long-distance migration initiate population in temperate paddy fields. In the tropics, *N. lugens* exhibit various population growth patterns depending on the interaction with the natural enemies. While in the temperate areas, populations tend to increase gradually due to paucity of natural enemies probably due to collapse of natural enemies during cold winter. *N. lugens* in subtropical and temperate East Asia, compared to tropical Asia, produce more macropters, and have longer pre-ovipositional period and more starvation tolerance. Thus, the East Asian population of *N. lugens* is more adapted to migration, while tropical populations in southeast Asia are adapted to multiplication. Biotypic compositions and insecticide resistance in *N. lugens* populations in time and space are quite similar within East Asia (subtropical and temperate areas), while they tended to slightly differ depending on locations in the tropics. It is considered that these characters in East Asian *N. lugens* population are genetically maintained by a migration system mediated by seasonal monsoon wind. Strong population suppression by natural enemies in the tropics implies the possibility that escape from natural enemies was a driving force for evolution of migration in *N. lugens*.

Keywords Brown planthopper • Initial immigrants • Population dynamic • Natural enemy • Evolution of migration

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4.1 Introduction

Status of planthoppers as rice pests have changed depending on time in the tropics. Before the Green Revolution, the brown planthopper (BPH), *Nilaparvata lugens*, was one of the minor insect pests in the tropical paddy fields (Dyck and Thomas 1979; Heinrichs and Mochida 1984). International Rice Research Institute (IRRI) was founded in the Philippines in 1960. In fact, little description of *N. lugens* was found in IRRI Reports published in early 1960s (Kisimoto 1981). The first outbreak of BPH was observed at IRRI fields in 1964 (Iida 1972). In 1966, IR8, a miracle rice, was released, and the green revolution began. In early 1970s, BPH outbreaks frequently occurred in the Southeast Asian countries where high-yielding rice varieties originated from IRRI were introduced (Dyck and Thomas 1979; Kisimoto 1981). IRRI released the varieties such as IR26 and IR32, which were resistant to BPH. However, the BPH overcome the resistance soon by the appearances of new biotypes (Saxena and Barrion 1985). Repeating events of releasing resistant varieties and overcoming their resistance by the appearances of new BPH biotypes have continued until now. Another problem with the BPH management is the development of insecticide resistance in BPH populations. Reduction of susceptibility to organophosphorus or carbamate insecticides appeared in late 1970s (Nagata et al. 1979; Kilin et al. 1981). Recently, the BPH populations showing high resistance to chloronicotinyl insecticides is a serious problem in Asian paddy fields (Matsumura et al. 2008).

The causes for BPH outbreaks in tropical paddy fields after the late 1960s are generally considered to be: (i) introduction of nitrogen responsive high-yielding varieties, which favors BPH multiplication through increased fecundity and low mortality; (ii) improvement of irrigation system, which facilitated intensive and successive rice planting throughout the year favored generation continuity of *N. lugens*; (iii) resurgence induced by abuse of insecticide applications: non-selective insecticide sprays destroy natural enemy fauna and possibly also increase *N. lugens* fecundity to a certain extent.

On the other hand, rice planthoppers, *N. lugens* and *Sogatella furcifera*, were serious pests of rice in East Asia from long time. The oldest record of planthopper outbreak was in 697 AD in Japan (Mochida and Okada 1979). Korean records show planthopper outbreaks since eighteenth century. During the early modern period of Edo era (1600–1867) in Japan, many records are found describing serious famines caused by planthopper damage together with cool and longtime rainy summer (Nagata 1982; Miyashita 1961). One of the great famines occurred in West Japan in 1732, when rice yields were decreased to only 10 % of normal yields. Recent advancements in understanding of wind-assisted long-distance planthopper migration into West Japan (Kisimoto 1976; Seino et al. 1987) explain why serious outbreaks occurred in cool rainy summers. There were many guardian deities of children (jizo), which console dead people on great famines of Edo era in all over Japan (Fig. 4.1a). In Amakusa, Kyushu, West Japan, where planthopper immigrant density is usually higher, farmers have performed an annual festival since Edo era in mid-July (“mushi-oi sai” that means driving away insects) in which they imagine control

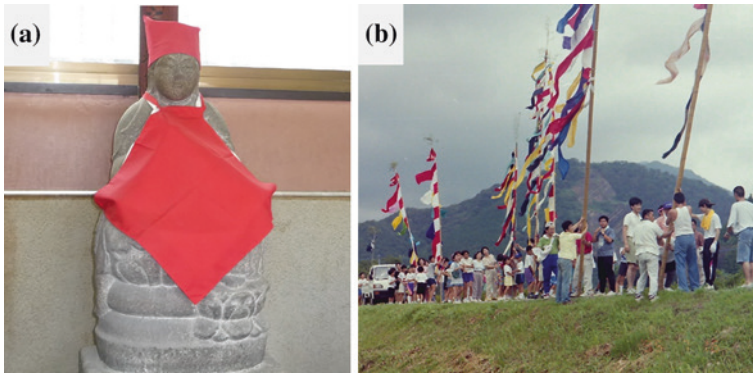


Fig. 4.1 **a** A guardian deity of children (Uenin-Jizo) at downtown of Fukuoka, Japan, which console dead people on great famines in Edo era. **b** Yearly festival of “Mushi-oi sai” in Amakusa, Kumamoto, which is to drive away of rice insect pests

of rice insect pests (Fig. 4.1b). These outbreak events of planthoppers in Japan happened in the periods much before creations of modern high-yielding varieties and synthetic insecticides. In Edo era, farmers sometimes used whale oil or rape seed oil to control planthoppers (Nagata 1982; Tateishi 1981). They tapped or immersed plants and dropped planthoppers onto oil-spread water surface. Planthoppers died from drowning or asphyxiation. Unlike in the tropics, *N. lugens* have been a serious insect pest of rice since history in the temperate regions.

Historically, why is there difference in pest status of *N. lugens* between tropical Asia and temperate East Asia? In order to understand the reason, differences in biology of *N. lugens* between the tropics and temperate East Asia are focused on in this chapter.

4.2 Population Dynamic

Several reports (Kuno and Dyck 1985; Perfect and Cook 1994; Sawada et al. 1993; Wada and Nik 1992) focused on the difference in population dynamic of *N. lugens* between tropical regions and temperate East Asia. Detailed population study was first done in temperate paddy fields in South Japan by Kuno (1968), and Kuno and Hokyo (1970), followed by Watanabe (1996). In temperate Japan, where *N. lugens* cannot overwinter, population dynamics are generally characterized by low initial immigrant population which invades from overseas with the assist of monsoon wind, and high-population growth rate throughout the crop season, resulting in rather monotonous increase through three consecutive generations. Populations of the initial densities finally reach 1,500 times on average (Kuno 1968). The populations in tropical fields, however, show entirely different features. Populations in tropical paddy fields are generally characterized by (i) high initial immigrant density, (ii) low population growth rate, (iii) earlier population peak: The peak occurs in the 2nd

Table 4.1 Differences in general population growth features between tropical and temperate *N. lugens* populations

	Tropical population ^a	Temperate population ^a
<i>Population growth in field</i>		
Initial immigrant density	(High)	Low
Seasonality of immigration	None	Rainy season
Population growth rate	(Low)	high
Population peak in a crop season	(2nd generation)	(3rd generation)
Population predictivity from initial density	(No)	Yes
Population growth pattern	Various patterns	(monotonous increase)
<i>Physiological characters</i>		
Wing form	More brachypters	More macropters
Pre-ovipositional period	Short	Long
Starvation tolerance of macropter	Weak	Strong

^aA parenthesis indicates that there are many exceptions

generation as compared to the 3rd in temperate Japan, (iv) difficult to predict latter population density from the initial population. General feature of the both temperate and the tropical populations is summarized in Table 4.1.

However, the situations are rather complicated in the tropical fields. For examples, as for initial immigrants, the densities were low in the fields of the specific conditions such as rain-fed fields in the Philippine, where rice were planted more synchronously (Cook and Perfect 1989), the first crop of the wet season after the fallow period in Indonesia (Sawada et al. 1993), and the fields just after the fallow period, which was settled in the dry season in Malaysia (Wada and Nik 1992). Additionally, in these fields, populations tended to increase gradually with high-population growth rates, showing rather “temperate type.” Thus, various population growth patterns seem to exist in the tropical fields (Cook and Perfect 1989; Wada and Nik 1992).

What are the fundamental differences between temperate and tropics? According to vigorous studies since the 1970s (Kisimoto 1976; Kisimoto and Sogawa 1995; Otuka et al. 2006), the source of immigrants of *N. lugens* and *S. furcifera* in temperate fields is long-distance (over 1,500 km) migrants, thus the densities of initial immigrants are usually very low. However, *N. lugens* in the tropic are considered to be much less mobile (Riley et al. 1987; Perfect and Cook 1987). Origins of initial immigrants were estimated less than from 30 km. Therefore, immigrant densities are usually high in the tropics where rice is more or less staggered planted. But the densities are low even in tropical fields around which there are no or very few paddy fields in the later growth stages from which planthoppers are expected to emigrate (Kisimoto and Rosenberg 1994). In fact, after the fallow period, initial immigrant densities were very low but populations increased gradually as of temperate areas (Wada and Nik 1992; Sawada et al. 1993).

The other fundamental difference seems to lie in the factor, which determines the population growth pattern. In temperate fields, populations basically increase through generations although the situation is not so simple due to variation in the proportions of macropters to brachypters in the population (Suzuki 2002). Thus, the later populations are predictable from initial immigrant densities. On the other hand, tropical *N. lugens* exhibit various population growth patterns. Some determinants, probably within-field factors, regulate population growth. One of the important determinants, which many authors pointed out, is natural enemy activity. Kuno and Dyck (1985) described importance of *Microvelia*, due to the close relationship between population change rates of *N. lugens* and *Microvelia* densities. Cook and Perfect (1989) suggested abundance of natural enemies over the first 20 days after transplant was a critical factor in determining later population size. Kenmore et al. (1984) showed physical exclusion of predators or reduction of predators, in particular, spiders and velliids, caused outbreak of *N. lugens*. Sawada et al. (1993) concluded that high *N. lugens* densities in synchronous planting areas were caused by paucity of natural enemy activity. Wada and Nick (1992) concluded that interaction between planthopper and natural enemies was a major factor, which determines population growth patterns of planthoppers. Thus, natural enemy activity fluctuates by specific situations in the tropics, which seems to cause the variation in population growth patterns. Importance of natural enemy activity as a factor, which regulates *N. lugens* population in the tropics, has been verified by frequent occurrences of hopperburns (resurgence) caused by abuse of insecticides (Heinrichs and Mochida 1984; Heong 2009).

Determinants other than natural enemy interaction, Sawada et al. (1993) pointed out water availability in the field causing big fluctuation of population growth rates in dry season in Indonesia. Kuno and Dyck (1985) suggested climate and rice varieties also influence population growth of *N. lugens*.

4.3 Natural Enemy Abundance

Difference in the *N. lugens* population growth in fields between temperate and tropics is mainly attributed to natural enemy activities. Since *N. lugens* are not able to overwinter in temperate regions, specific natural enemies hardly exist. In addition, cold winter is thought to significantly destroy natural enemy fauna. Immigrants, which invade young paddy fields, are able to increase their populations through a few generations with advantage of paucity of natural enemies. Although some predators (*Cyrtorhinus*) and parasitoids (Drynids) invade fields, accompanying planthopper migration (Kisimoto and Rosenberg 1994; Kitamura and Nishikata 1987), there is likely to be an establishment time lag that often precludes their effectiveness (Perfect and Cook 1994). In other word, *N. lugens* succeed to escape from natural enemies by long-distance migration and explode their population in temperate habitats.

On the other hand, natural enemy activities in the tropics without winter seem to be maintained, more or less, continuously throughout the year. Before the green

revolution, *N. lugens* populations were effectively suppressed into low level by local natural enemies. However, after the green revolution, introduction of high-yielding varieties favored multiplication of *N. lugens* (Lu and Heong 2009) and resulted in an environmental shift. When natural enemy activities are disturbed by some reasons, outbreaks of *N. lugens* quickly occur. Abuse of insecticides is a typical case in which natural enemy activities are disturbed. Insecticide applications disorganize predator–prey interaction and the food web structure, thus favoring *N. lugens*, an r-strategist pest with high fecundity and short life span (Heong 2009). There are factors besides insecticide applications, which disturb natural enemy activities in the tropics. The dry season allowing most insects living in paddy fields to face shortage of hosts seems one of them. The crop-free fallow period is sometimes considered for planthopper management (Nozaki et al. 1984). However, *N. lugens* population levels were ironically higher in the crops after the fallow period than in the other crop season with asynchronous plantings (Wada and Nik 1992; Sawada et al. 1993; Way and Heong 1994). It is quite probable that eradication of *N. lugens* in a certain area by the fallow period destroys residential natural enemies and favors a few new planthopper immigrants from other areas or possibly within the area. The crop-free fallow period in the dry seasons sometimes provided more serious impact on biodiversity. Hopperburn frequencies relative to planting area were extremely high in the paddy fields, which were seeded just after the fallow period in the Muda Area of Malaysia in 1990 (Wada and Nik 1992). Climate and farmer practices profoundly influence predator–prey interactions, and thus, *N. lugens* seem to exhibit various population growth patterns in the tropics.

4.4 Physiological Characters

Nagata and Masuda (1980) first found the genetic difference of the physiological character between tropical and temperate *N. lugens*. They found that Japanese BPH populations produce higher proportion of female macropters compared to tropical population (Thailand and Philippine), which dominates brachypters at same rearing densities. Iwanaga et al. (1985, 1987) reported that majority of the populations collected from various locations of Japan and coastal areas of China produced more female macropters as compared to the populations collected in tropical Philippine, Indonesia, and Malaysia. However, they found that a few populations in Japan exhibited a similar trend of the wing-form production as tropical populations. This was explained by the difference in the sources of immigrants, i.e., Japanese *N. lugens* were originated from South China in most cases, but sometimes also from other tropical countries.

Wada et al. (2007) demonstrated that *N. lugens* populations collected from subtropical and temperate East Asia (Northern Vietnam, Central China, and Kyushu, Japan) had longer adult immature stage before oviposition, compared to tropical populations (Southern Vietnam, Thailand, and Malaysia). The periods required for 50 % female to begin oviposition at 25 °C were 4.7 days for tropical populations

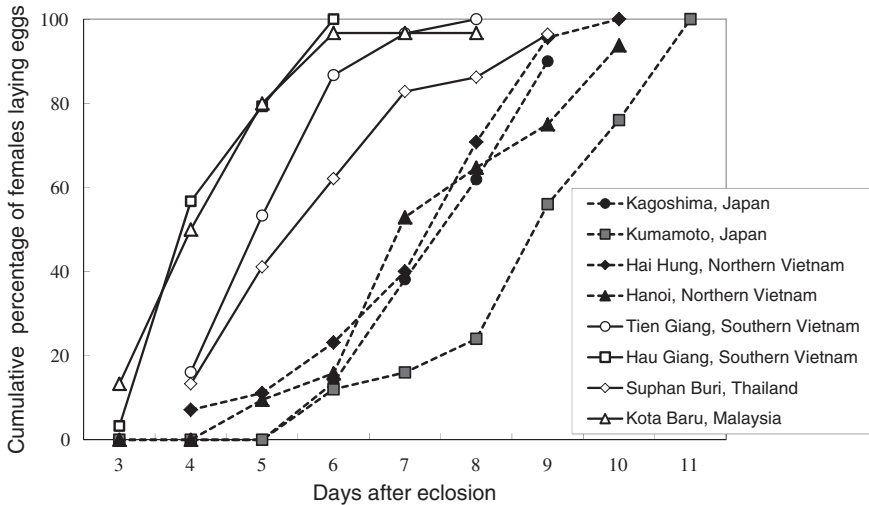


Fig. 4.2 Difference in pre-ovipositional periods among *N. lugens* populations originated from temperate, subtropical, and tropical Asia (*solid lines* indicate populations from tropical Southeast Asia, and *dotted lines* indicate populations from temperate and subtropical East Asia)

and 7.6 days for East Asian populations (Fig. 4.2). Further, Wada et al. (2009) reported that macropters originated from East Asia were more tolerant to starvation than those from tropical countries. Macropters feed actively on rice for the first 2 or 3 days after eclosion (Tanaka 1999). Macropters of East Asia populations possess increased starvation tolerance after the post-eclosion feeding (live 2.6 times longer without feeding than newly emerged adults) relative to the tropical populations (1.7 times). Accordingly, the periods required for 50 % macropters to die without feeding after 2-day post-eclosion feeding were 11.5 days for East Asia populations and 7.0 for tropical populations. These results also suggest the timing of takeoff by *N. lugens*: macropters emigrate from a paddy field after two- or three-day post-eclosion feeding when they maximize starvation tolerance. Figure 4.3 illustrates a typical example showing the difference in longevity of macropters between temperate and tropical populations, in relation to post-eclosion feeding. Taken pre-ovipositional periods into consideration, Wada et al. (2009) suggested the difference in resource allocation (vitellogenesis or stored resources) between East Asia and tropical populations: Macropters of East Asia populations invest energy intake from feeding mainly on reserves, which enhance starvation tolerance, while those of tropical populations invest on ovary development as well as stored reserves.

These differences in characters, which are closely related to dispersal or migration, provide the evidence that *N. lugens* populations which are adapted to pre-ovipositional migration are distributed in subtropical and temperate East Asia. On the other hand, *N. lugens* populations in the tropics are adapted to multiplications with higher brachypter production and shorter pre-oviposition period. These differences

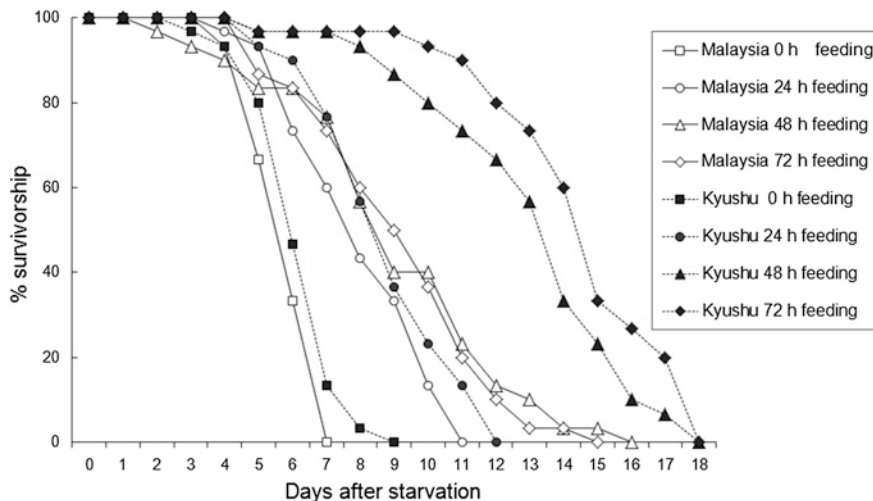


Fig. 4.3 Increase in starvation tolerance after feeding on rice for 0, 24, 47, and 72 h after adult molt in the tropical Malaysia population and the temperate Kyushu population in 1994 (*solid lines* indicate the progenies of Malaysia populations, and *dotted lines* indicate the progenies of Kyushu populations)

influence population dynamic in fields, in particular, numbers of eggs laid relative to adult density. But information on the difference in oviposition performance between populations in tropics and East Asia is not yet available.

Other characters that are not directly related to migration also indicate genetic difference between *N. lugens* populations in East Asia and in the tropics. The study of biotypes (individual or population that shows virulence to different cultivars) was widely carried out in Asia (Saxena and Barrion 1985). Sogawa (1992) suggested that the change from biotype 1 to biotype 2 capable of feeding on rice with Bph 1 resistance gene had simultaneously occurred in Northern Vietnam, China, and South Japan. Due to the capability of feeding on ASD7 with bph2 resistance gene, similarity of the biotype composition in local populations throughout subtropical and temperate East Asia again reported by Wada et al. (1994) and Takahashi et al. (1994). Tanaka and Matsumura (2000) reported that increase of *N. lugens* capable of feeding on ASD7 in Japan occurred after wide spread of varieties with bph2 gene in China and Northern Vietnam. As a whole, biotype compositions in time and space are quite similar within East Asia, while they tended to slightly differ depending on locations in the tropics.

Development of chloronicotinyl insecticide resistance in *N. lugens* which appeared from the mid-2000s in Asian countries has been a serious problem until now. Geographical differences in resistance development against various insecticides also suggest genetic similarity of *N. lugens* in East Asia. *N. lugens* in Northern Vietnam, China, and Japan had high resistance to imidacloprid (Matsumura et al. 2008; Matsumura and Sanada-Morimura 2010). The

populations in Southern Vietnam also exhibited high resistance, but the populations in the Philippines were still susceptible to this chemical. This fact suggests insecticide resistance occurred simultaneously over the countries in East Asia, but the status of resistance depended on the local situations in the tropics.

4.5 Some Implications of Evolution for Planthopper Migration

Studies of physiological characters demonstrated that there is a so-called East Asian population of *N. lugens* (Sogawa 1993), which are migratory and are isolated to some extent from tropical populations. Studies of long-distance migration have indicated genetic exchange within East Asia. *N. lugens* overwinter in subtropical East Asia (Northern Vietnam and southern end of China) (Chen et al. 1982; Cheng et al. 1979). In spring, the first northeastward migration occurs from overwintering sites to early crops in South China (Otuka et al. 2008). After population multiplications through one or two generations in South China, another step of northeastward migrations occur, which led to initial immigrants in newly planted rice in Japan, Korea, and Central China (Sogawa and Watanabe 1992; Otuka et al. 2006). Although migration events are not clearly observed compared to early summer migration (Kisimoto and Rosenberg 1994), southwestward return migration from temperate regions toward overwintering sites has been demonstrated (Cheng et al. 1979; Riley et al. 1994; Qi et al. 2010). Destinations of *N. lugens* migration depend entirely on wind directions. Wind-dependent migration simulations can predict long-distance immigrations (Seino et al. 1987; Watanabe et al. 1991; Otuka et al. 2005). So, the migration system of *N. lugens* in East Asia is mediated by seasonal monsoon winds, allowing northeastward expansion during spring and early summer, and southwestward return movement in autumn. This system maintains *N. lugens* having longer adult immaturity genetically for long years in spite of disadvantage of prolonged oviposition for multiplication.

Rice cultivation began about 10,000 years ago in Central China and about 4–8000 years ago in Japan (Sato 2008). Because rice is the only host plant of *N. lugens*, East Asian population must be evolved after northern expansion of rice by mankind in East Asia. In the process of forming East Asian population, yearly seasonal monsoon is considered to favor mobile *N. lugens* and cause differentiation of the East Asian population probably from tropical populations.

The phenomenon of the effective population suppression by natural enemies in the tropics together with successful escape from natural enemies in temperate regions implies significance of migration as one of the strategies for the rice planthoppers. Evolution of migration has often been discussed in relation to heterogeneous or ephemeral environments in time and space (Roff and Fairbairn 2007). Migration is a strategy to avoid impending unfavorable habitat caused by climate or inter- and intraspecific competitions. Seasonal fluctuation and heterogeneous distribution of food resource should be a typical example causing insect migration.

But escape from predators and parasites is also a factor, which may favor evolution of migration (Southwood 1978; Pulido 2007).

In the tropics, planthopper populations usually collapse within a crop period, partially due to predation and parasitism by natural enemies. However, the extinction of the populations in a paddy field does not occur only by the function of natural enemy activities. It is partially caused by the appearance of macropters, which emigrate from the paddy field (Kuno and Hokyo 1970). Appearance of macropters increases with advancement of rice growth (Kisimoto and Rosenberg 1994). In addition, the natural enemy pressure on the planthopper population was also the factor, which increases with the advancement of rice plant growth stages (Wada and Nik 1992): egg mortality due to egg parasitoids (Watanabe et al. 1992) and young nymph mortality caused by predators (Wada and Nik 1992) increases with plant ages and planthopper generations in a crop period. Therefore, staying in a field for a few generations seems to lead the planthopper population to take a risk of the high natural enemy pressure and finally to become extinct. The simplest way to avoid natural enemy pressure for planthoppers seems to take off the field even before deterioration of quality of the host plant. Rice planthoppers migrate from field to field, otherwise they may not be able to survive in the tropics. This idea seems to be probable if we consider *S. furcifera*, which produce high proportions of macropters even in early rice (Kuno 1968; Watanabe 1996). In addition, because *N. lugens* populations were always low in ancient tropical paddy fields, a risk of population decline caused by natural enemies seems to be more critical than deterioration of rice damaged by planthoppers themselves. The similar causal aspect of migratory flight escaping from natural enemy attacks was demonstrated in the other important migratory agricultural pest, *Spodoptera litura* (Tojo et al. 2008). Rice planthoppers migrate from fields to fields to escape from natural enemies, exploring new habitats in the tropics, which may be the preadaptation of long-distance migration of East Asian *N. lugens*.

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