Life-Table Analysis of the Performance of *Nilaparvata lugens* (Hemiptera: Delphacidae) on Two Wild Rice Species

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ABSTRACT Life tables of the planthopper *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) on two wild rice species, *Oryza officinalis* Wall. ex Watt. and *Oryza rufipogon* Griff., and on 'Taichung Native 1' (*O. sativa indica* TN1) were studied at 27°C in the laboratory. The raw data were analyzed based on the age-stage, two-sex life table to take both sexes and the variable developmental rate among individuals and between sexes into consideration. The intrinsic rate of increase (r), the finite rate (λ), the net reproduction rate (R_0) and the mean generation time (T) of *N. lugens* on *O. officinalis* were -0.0616 d^{-1}, 0.9402 d^{-1}, 0.10 offspring, and 36.7 d, respectively, showing that the species is resistant to *N. lugens*. The resistance of *O. officinalis* is expressed in the long developmental time from first to fifth instar of *N. lugens*, the reduced preadult survival rate, the short adult longevity, and low fecundity. However, the population parameters of the *N. lugens* on *O. rufipogon* and TN1 were 0.1096 d^{-1}, 1.1158 d^{-1}, 67.82 offspring, and 38.6 d and 0.1340 d^{-1}, 1.1434 d^{-1}, 144.77 offspring, and 37.2 d, respectively. These population parameters showed that *N. lugens* can successfully survive and reproduce on both *O. rufipogon* and TN1.

KEY WORDS *Nilaparvata lugens*, *O. officinalis*, *O. rufipogon*, life table

The planthopper *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae) is a monophagous pest causing enormous and serious yield loss to the rice, *Oryza sativa* L., crop in Asia (Mochida and Okada 1979, Sogawa 1982). In eastern Asia, *N. lugens* is known to migrate long distances every year, often extending its range in just a few generations from northern Vietnam into China, Korea, and Japan during the rainy early summer (Otuka 2009). Due to the fast development and high fecundity, the population can increase to high density quickly and causes characteristic "hopperburn" (Wu et al. 2004, Catindig et al. 2009). In recent years, *N. lugens* outbreaks have been more common in Asian countries because the species has developed high levels of resistance to major insecticides (Wang et al. 2008).

Wilson and Huffaker (1976) pointed out that plant resistance and biological control are the two core strategies of integrated pest management. A possible alternative to overcome pesticide resistance of insects may be in planting resistant cultivar varieties and integrated this with other tactics. Cultivar resistance has been increasingly recognized as the most desirable and economic control tactic in the management of *N.*

lugens (Velusamy et al.1995, Myint et al. 2009). Rice researchers have begun investigation wild rice species to furnish genes for breeding purposes (Vaughan et al. 2003).

Oryza officinalis Wall. ex Watt. and *Oryza rufipogon* Griff. are two important wild rice species. *O. officinalis*, a species with a diploid CC genome, occurs naturally in tropical and subtropical regions (Vaughan 1994). In China, *O. officinalis* was found previously in southern and southwestern regions, including Guangxi, Guangdong, Hainan, and Yunnan provinces (National Exploration Group of Wild Rices 1984). This species possesses potentially useful gene sources for high biomass production and resistance to insects (Jena and Khush 1990). Molecular approaches have been applied to study important genes of *O. officinalis*, including resistance to *N. lugens* for use in improvement of cultivated rice (Yang et al. 1999, Tan et al. 2004, Sundaramoorthi et al. 2009). *Oryza rufipogon* Griff. is a perennial and widely distributed wild rice species in tropical and subtropical regions of monsoon-susceptible Asia, including southern China (Vaughan 1994). The great genetic diversity of *O. rufipogon* has been documented previously by Ge et al. (1999), Gao et al. (2000b), and Song et al. (2003). The *O. rufipogon* population in Dongxiang of Jiangxi Province in China is the residual population of *O. rufipogon* (Gao et al. 2000a). As the progenitor of Asian cultivated rice (*O. sativa*), *O. rufipogon* has proven to be a valuable gene pool for rice genetic improvement and will play a critical role in future rice breeding (Khush 1997, Zhou et al. 2003, Xia et al. 2009). Most research

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to date has focused on the genetic characteristics of wild rice. On the contrary, the effects of ecological characteristics of wild rice on rice-feeding insects, especially major agricultural pests such as *N. lugens*, has largely been ignored and only limited studies are available.

Life-table studies are fundamental to population ecology. A life table gives the most complete description of the survivorship, development, stage differentiation, and reproduction of a population and provides basic data on population growth parameters. Traditional female age-specific life tables, e.g., Lewis–Leslie matrix (Lewis 1942, Leslie 1945, Birch 1948), deal only with female populations and ignore the variable developmental rates among individuals and stage differentiation. However, most economic insect pests are bisexual, and both sexes may cause economical loss. Moreover, developmental rates often differ between the sexes and among individuals (Istock 1981). To consider both sexes and variable developmental rates among individuals, Chi and Liu (1985) and Chi (1988) developed the age-stage, two-sex life table. To compare the ecological characteristics of wild rice and their possible application in breeding insect resistant cultivars, we studied the life table of *N. lugens* reared on two wild species, *O. officinalis, O. rufipogon*, and a susceptive cultivar, 'Taichung Native 1' (*O. sativa indica* TN1). We then analyzed the life history raw data by using the age-stage, two-sex life table.

Materials and Methods

Plants. The medical wild rice *O. officinalis* is indigenous to Huatang County, Guangxi Province, China, whereas the common wild rice, *O. rufipogon*, is indigenous to Dongxiang County, Jiangxi Province, China. Both species were originally collected and planted in the Wild Rice Core Collection Nursery affiliated with the South China Agricultural University (Guangzhou, China). In this study, samples of the two wild rice species were donated by the South China Agricultural University and transplanted to cement troughs (600 cm in width, 1,000 cm in length, 200 cm in depth) in greenhouses on the Experimental Base at the State Key Laboratory for Biocontrol and Institute of Entomology, Sun Yat-sen University (Guangzhou, China). Cement troughs were covered with gauze webbing and wild rice plants were fertilized biweekly (K_2SO_4 compound fertilizer, N–P–K: 15:15:15, product of Norsk Hydro Group, Oslo, Norway). The highly susceptible rice species TN1 (no resistance gene) was provided by the Plant Protection Research Institute of Zhejiang Academy of Agricultural Sciences (Hangzhou, China). TN1 rice seeds were sown every 15 d in identical cement troughs by using similar soil and fertilization. Rice plants at the tillering stage were used in all experiments.

Insect Culture. The *N. lugens* were originally obtained from the Plant Protection Research Institute of Guangdong Academy of Agricultural Sciences (Guangzhou, China). The colony of *N. lugens* was identified as Biotype II and was maintained successively on nonresistant TN1 rice plants in the State Key Laboratory for Biocontrol and Institue of Entomology, Sun Yat-sen University.

Life-Table Study. To collect eggs for the life-table study on *O. officinalis*, 10 pots with single rice plants of the tillering stage were prepared. Five gravid *N. lugens* females from the colony were transferred to each pot for oviposition. For the life-table study on *O. rufipogon* and TN1, five pots with a single rice plant of the tillering stage, and two gravid *N. lugens* females were used for both rice species. After 24 h, females were removed. Rice plants with eggs were covered with nylon mesh and placed in an artificial climate box (volume of 950 by 850 by 1, 850 mm; made by Shanghai Permanent Science and Technology Co., Ltd., Shanghai, China). The climate condition was set as $27 \pm 1°C$, 75% RH, and a photoperiod 14:10 (L:D) h. After hatching, first instars were individually transferred to a new rice plant, and the old plants were then examined and the number of hatched and unhatched eggs counted. The total number of eggs used for the life-table study was 195, 89, and 95 eggs for *O. officinalis*, *O. rufipogon*, and TN1, respectively. *N. lugens* were reared individually on plants of the same species of tillering stage, and the survival was recorded daily. As adults emerged, one male and one female reared on the same species of rice were paired and moved to a new rice plant. The rice plants were changed daily until the death of all individuals. Rice plants with *N. lugens* eggs were preserved in a refrigerator at 4°C and later examined to record the number of eggs using a binocular stereomicroscope (model BX50, Olympus Optical Co., Ltd., Tokyo, Japan) The raw life-history data of all individuals of *N. lugens* were analyzed according to the age-stage, two-sex life table (Chi and Liu 1985) and the method described by Chi (1988). The means and SEs of the population parameters were estimated using the jackknife method (Sokal and Rohlf 1995). To facilitate raw data analysis, life-table analysis, and the jackknife method, a user-friendly computer program, TWOSEX-MSChart, was used to estimate parameters (Chi 2008). The age-stage specific survival rate (s_{xj}) (where x is the age and j is the stage), age-stage specific fecundity (f_{xj}), age-specific survival rate (l_x), age-specific fecundity (m_x), and population parameters (r, intrinsic rate of increase; λ, finite rate of increase; R_0, net reproduction rate; and T, the mean generation time) are calculated accordingly. Intrinsic rate of increase was estimated by using the iterative bisection method from the Euler–Lotka formula:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1,$$

with age indexed from 0 (Goodman 1982). We used the Tukey–Kramer procedure (Dunnett 1980) to compare the difference among treatments following the description of Sokal and Rohlf (1995).

Table 1. Life-history statistics (mean ± SE) (*n*) of *N. lugens* reared on *O. officinalis*, *O. rufipogon*, and TN1 at 27°C and 70–80% RH

Statistics	Host species					
	O. officinalis		*O. rufipogon*		TN1	
	Mean ± SE	(*n*)	Mean ± SE	(*n*)	Mean ± SE	(*n*)
Developmental time						
Egg	8.95 ± 0.05a	(152)	7.38 ± 0.09b	(86)	7.48 ± 0.07b	(94)
First instar	3.53 ± 0.06a	(128)	3.30 ± 0.05a	(84)	2.93 ± 0.04b	(92)
Second instar	3.18 ± 0.09a	(95)	2.61 ± 0.07b	(83)	2.61 ± 0.06b	(92)
Third instar	3.34 ± 0.11a	(76)	2.89 ± 0.08b	(79)	2.35 ± 0.07c	(91)
Fourth instar	3.64 ± 0.11a	(53)	3.19 ± 0.09b	(75)	2.74 ± 0.06c	(90)
Fifth instar	4.86 ± 0.11a	(42)	4.62 ± 0.139a	(71)	3.80 ± 0.11b	(88)
Female total preadult	28.17 ± 0.47a	(18)	24.83 ± 0.34b	(36)	22.83 ± 0.26b	(46)
Male total preadult	27.33 ± 0.46a	(24)	22.91 ± 0.32b	(35)	20.86 ± 0.21b	(42)
Female longevity	5.44 ± 0.72a	(18)	18.56 ± 0.94b	(36)	22.61 ± 1.07b	(46)
Male longevity	8.12 ± 1.04a	(24)	14.23 ± 0.79b	(35)	19.52 ± 1.02c	(42)
APOP (d)	5.89 ± 0.26a	(9)	4.59 ± 0.10b	(34)	4.38 ± 0.09b	(45)
TPOP (d)	34.67 ± 0.47a	(9)	29.50 ± 0.39b	(34)	27.22 ± 0.27c	(45)
Fecundity (eggs/female)	1.06 ± 0.30a	(9)	167.67 ± 16.69b	(36)	298.98 ± 22.24c	(46)

Means within a row sharing the same letter are not significantly different at 5% level by using Tukey–Kramer test.

Results

The egg duration of *N. lugens* in *O. officinalis* was significantly longer than those in *O. rufipogon* and TN1. No significant difference was found between egg duration in *O. rufipogon* and that in TN1 (Table 1). In general, the developmental time of the nymph stage of *N. lugens* on *O. officinalis* were significantly longer than on *O. rufipogon* and on TN1. The total developmental time of preadult stages of females and males on *O. officinalis* was significantly longer than that on *O. rufipogon* and TN1. It demonstrated that the total developmental rate of *N. lugens* on *O. officinalis* was slower than those reared on *O. rufipogon* and TN1. Both female and male adults survived longer on *O. rufipogon* and TN1 than those reared on *O. officinalis.*

The total preadult mortality of *N. lugens* reared on *O. officinalis* was 78.5%, with only 18 of 195 eggs developing to female adults and 24 to male adults. Among the 195 eggs, 22.1% died in the egg stage and 56.4% in the nymphal stage. Out of 89 eggs on *O. rufipogon*, 36 emerged as female adults and 35 emerged as male adults. The preadult mortality was 20.2%, with 3.4% in the egg stage and 16.9% in the nymphal stage. In contrast to *O. officinalis* and *O. rufipogon*, the preadult mortality was only 7.4% when *N. lugens* was reared on TN1.

The mean total preoviposition period (TPOP) of *N. lugens* was 34.67 d on *O. officinalis,* 29.50 d on *O. rufipogon*, and 27.22 d on TN1. There were significant differences in TPOP of *N. lugens* reared on different hosts. The adult preoviposition period (APOP) on *O. officinalis* was significantly longer than that on *O. rufipogon* and TN1. There was, however, no difference between *O. rufipogon* and TN1. Most entomologists calculate only the APOP. In determining the effect of the preoviposition period on population growth, calculating the TPOP offers more meaningful statistics than does APOP, because it more accurately defines the time length from birth to the beginning of reproduction of the next generation. Mean lifetime fecundities of *N. lugens* were 1.06 eggs per female when

reared on *O. officinalis.* This value was significantly lower than the 167.67 and 298.98 eggs per female found on *O. rufipogon* and TN1, respectively. The high fecundity of *N. lugens* on TN1 shows that *N. lugens* is well adapted to this cultivar.

The s_{xj} value of *N. lugens* (Fig. 1) gives the probability that a newly laid egg will survive to age x and
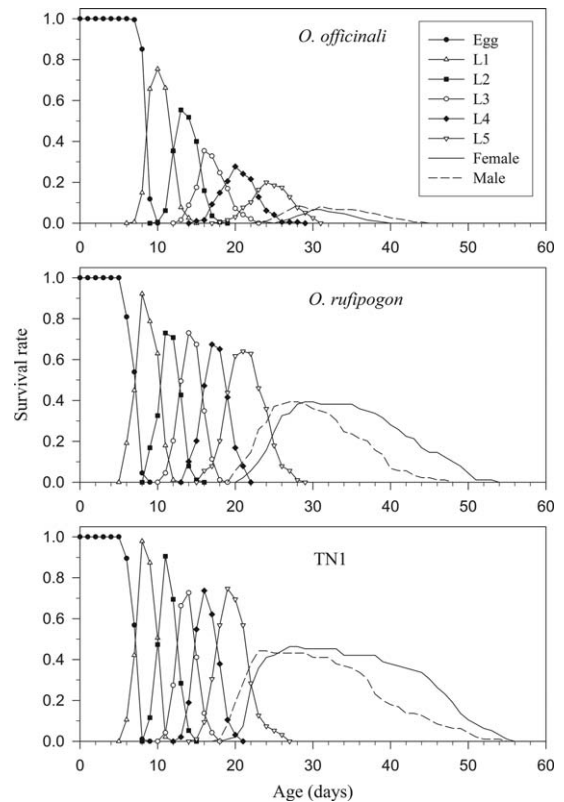
Fig. 1. Age-stage specific survival rate (s_{xj}) of *N. lugens* reared on *O. officinalis*, *O. rufipogon*, and TN1 at 27°C and 70–80% RH.
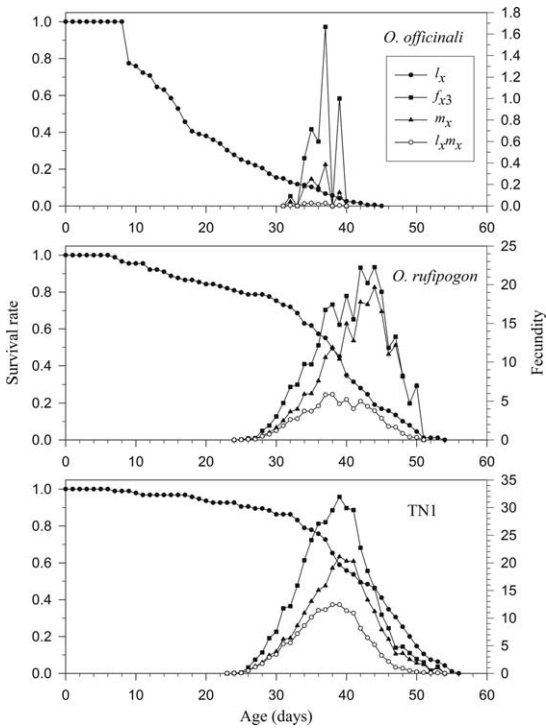
Fig. 2. Age-specific survival rate (l_x), female age-stage-specific fecundity (f_{x7}), age-specific fecundity (m_x), and age-specific maternity $(l_x m_x)$ of *N. lugens* reared on *O. officinalis*, *O. rufipogon*, and TN1 at 27°C and 70–80% RH.

stage *j*. These curves also show the survivorship and stage differentiation. Overlapping between stages shows the variable developmental rate among individuals. In Fig. 1, the s_{xj} values of *N. lugens* on *O. officinalis* dramatically declined compared with those on *O. rufipogon* and TN1. On *O. rufipogo* and TN1, the male adults emerged earlier but were shorter lived than the females. On the contrary, the male adults emerged earlier and survived longer than the females on *O. officinalis*.

Figure 2 illustrates l_x, f_{x7} (the female is the seventh life stage), m_x, and age-specific maternity $(l_x m_x)$ of *N. lugens*. The l_x is the probability that a new egg will survive to age *x* and is calculated by pooling all surviving individuals of both sexes and those that died during the preadult stages. The curve of l_x is a simplified version of the curves in Fig. 1.

The life expectancy (e_{xj}) of each age-stage group of *N. lugens* is plotted in Fig. 3. It gives the expected time that an individual of age *x* and stage *j* will live. The life expectancy of a new born egg (e_{01}) is exactly the same of the mean longevity, e.g., the life expectancy of a new egg was 19.44 d on *O. officinalis*, 35.30 d on *O. rufipogon*, and 40.97 d on TN1.

The reproductive value (v_{xj}) gives the expected contribution of individuals of age *x* and stage *j* (Fig. 4). The major peaks in reproductive values of females reared on *O. officinalis*, *O. rufipogon* and TN1 were at the age of 34 d $(v_{34} = 2.2)$, 36 d $(v_{36} = 89.1)$ and 35 d
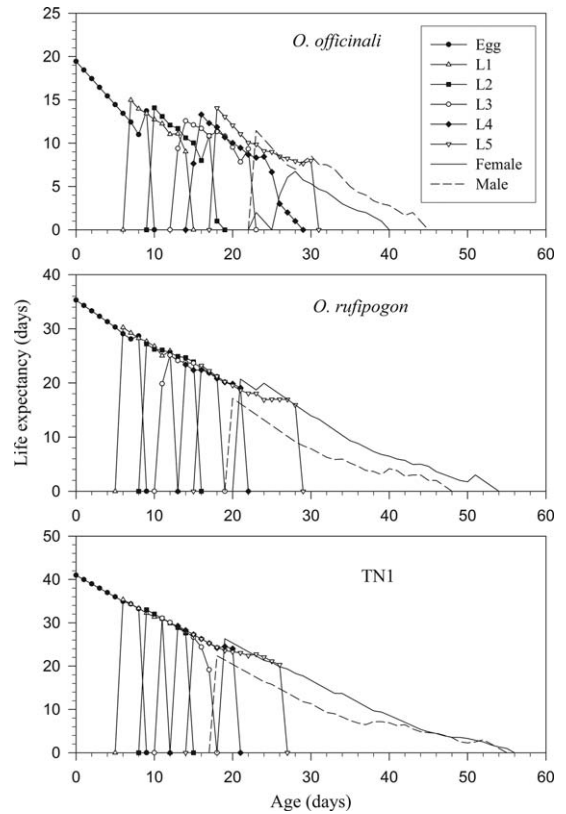

Fig. 3. Age-stage-specific life expectancy (e_{xj}) of *N. lugens* reared on *O. officinalis*, *O. rufipogon*, and TN1 at 27°C and 70–80% RH.

$(v_{35} = 153.6)$. It shows that individuals at the peak reproduction can contribute much more than a newborn egg. For example, a newly laid egg on TN1 has a reproductive value of 1.1, but a female of age 34 has a much higher reproductive value of 153.6.

The means and SEs of *r*, λ, R_0, *GRR*, and *T* were estimated using the jackknife method are shown in Table 2. The intrinsic rate of increase was $-0.0616\,d^{-1}$ on *O. officinalis*, which is significantly much lower than those on *O. rufipogon* $(0.1096\,d^{-1})$ and TN1 $(0.1340\,d^{-1})$. On *O. officinalis*, λ, *GRR*, and R_0 were $0.9402\,d^{-1}$, 1.16 offspring, and 0.10 offspring, respectively, which were significantly different from those on *O. rufipogon* and TN1. On *O. officinalis*, *T* was 36.7d, which was significantly different from that on *O. rufipogon* but not from that on TN1. On *O. rufipogon*, λ, *GRR*, R_0, and *T* were $1.1158\,d^{-1}$, 208.02 offspring, 67.82 offspring, and 38.6 d, respectively, and on TN1, values were $1.1434\,d^{-1}$, 237.49 offspring, 144.77 offspring, and 37.2 d, respectively. *GRR* was not significantly different between *O. rufipogon* and TN1.

Discussion

Traditional age-specific life tables (Lewis 1942, Leslie 1945, Birch 1948, Caswell 1989, Martínez-Villar et al. 2005) focused only on the survival and the fecun-
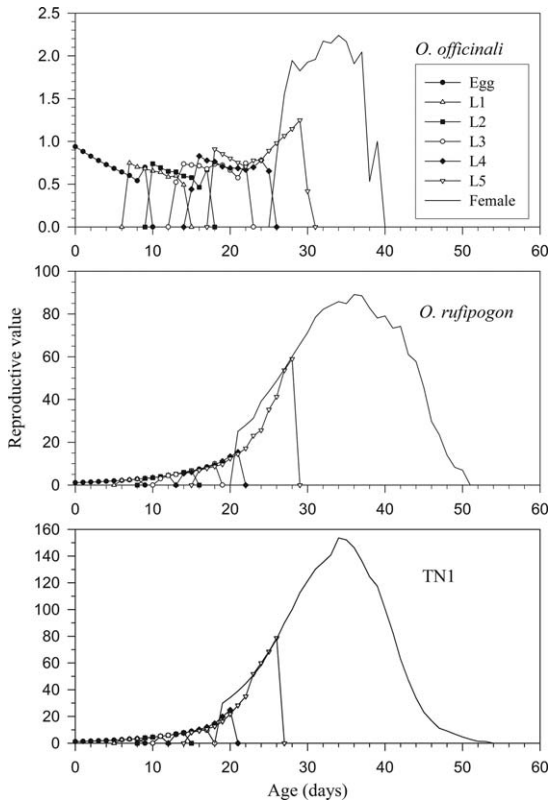
Fig. 4. Age-stage-specific reproductive value (v_{xj}) of *N. lugens* reared on *O. officinalis*, *O. rufipogon*, and TN1 at 27°C and 70–80% RH.

dity of the female population, ignoring the male population as well as the stage differentiations. Ignoring stage overlapping and male populations results in miscalculations in the survival and fecundity curves as well as other problems (Chi 1988, Chi and Yang 2003, Yu et al. 2005, Chi and Su 2006). Chi and Liu (1985) developed the age-stage, two-sex life table to take into account the male population and the variable developmental rate occurring among individuals. In our study, the overlapping in curves of s_{xj} (Fig. 1) shows the potential of the age-stage, two-sex life table in revealing the stage differentiation of *N. lugens* due to the variable developmental rates among individuals.

Table 2. Mean and standard errors of population parameters of *N. lugens* reared on *O. officinalis*, *O. rufipogon*, and TN1 at 27°C and 70–80% RH

Pop parameter	*O. officinalis*	*O. rufipogon*	TN1
r	−0.0616 ± 0.0107a	0.1096 ± 0.0041b	0.1340 ± 0.0036c
λ	0.9402 ± 0.0100a	1.1158 ± 0.0046b	1.1434 ± 0.0041c
GRR	1.16 ± 0.44a	208.02 ± 21.22b	237.49 ± 24.46b
R_0	0.10 ± 0.03a	67.82 ± 11.03b	144.77 ± 18.77c
T	36.7 ± 0.55a	38.6 ± 0.55b	37.2 ± 0.32ab

Means within a row sharing the same letter are not significantly different at 5% level by using Tukey–Kramer test.

Similarly, the stage differentiation can be observed in curves of e_{xj} and v_{xj} (Figs. 3 and 4). The two-sex life table has been widely applied to insects and mites, such as the aphid *Therioaphis maculate* (Buckton) (Hemiptera: Aphididae) (Silva et al. 2006), the predatory gall midge *Feltiella acarisuga* (Vallot) (Diptera: Cecidomyiidae) (Mo and Liu 2006), *Tetranychus urticae* Koch (Acari: Tetranychidae) (Kavousi et al. 2009), and *Chrysoperla externa* (Hagen) (Neuroptera: Chrysopidae) (Schneider et al. 2009).

In a free-choice seedbox screening test, Velusamy et al. (1995) showed that three wild rice species (*O. officinalis*, *Oryza punctata* Kotschy ex Steud., and *Oryza latifolia* Desv.) are resistant to *N. lugens* nymphs in comparison to cultivated rice species. *N. lugens* caged on resistant wild rice had slow nymphal development, reduced longevity, low fecundity, and low egg hatchability compared with *N. lugens* on cultivated resistant species. Our experiment found similar results. There were, however, more significant differences revealed when using life-table analysis. The demographic parameters (*r*, *GRR*, R_0, and *T*) of *N. lugens* population on *O. officinalis* versus *O. rufipogon* and *O. officinalis* versus TN1 differed significantly (Table 2). For example, the intrinsic rate of increase (*r*) is −0.0616 on *O. officinalis*, 0.1096 on *O. rufipogon*, and 0.1340 on TN1.

From these life-history and demographic parameters of *N. lugens* on *O. officinalis* (Tables 1 and 2), it is deduced that *O. officinalis* is highly resistant to *N. lugens*. The high mortality of eggs, low survival rate, slow development of nymphal stage, and low reproductive value (Figs. 1 and 4) all indicate that *O. officinalis* is detrimental to the survival of *N. lugens*. These facts show that the resistance of *O. officinalis* to *N. lugens* is due to multiple aspects, including ovicidal and larvicidal activity. Resistance has also been found in *O. officinalis* to planthopper *Sogatella furcifera* (Horvath) and leaffolder *Cnaphalocrocis medinalis* (Guenee) by Jin et al. (2006), Tan et al. (2004), and Zhang et al. (2009). These characteristics of *O. officinalis* have been recognized as valuable gene pool traits for rice genetic improvement and will play a critical role in future rice breeding programs (Jena and Khush 1990). In China, increasing attention has been paid to the high resistance of *O. officinalis* to *N. lugens* in improvement of rice cultivars (Chen et al. 2002, Tan et al. 2004).

Demographic parameters of *N. lugens* revealed that the species can successfully survive, grow, develop, and reproduce on *O. rufipogon* and TN1 (Tables 1 and 2). It also demonstrated that compared with *O. officinalis*, *O. rufipogon* has no or little resistance to *N. lugens*. Fujita et al. (2006), however, reported that *O. rufipogon* was highly resistant to the leafhopper *Nephotettix cincticeps* Uhler. Way and Heong (1994) suggested that rice resistance, including moderate resistance, is fundamental to successful biological control by natural enemy complexes. Cohen et al. (1997) pointed out that high levels of resistance are not necessary for successful *N. lugens* control. It is evident from these studies and others that different wild rice

species are capable of contributing to rice breeding programs in varying degrees and in differing aspects.

Our results demonstrate two major advantages in applying an age-stage, two-sex life table: the stage overlapping can be accurately demonstrated (Figs. 1–4) and the correct relationship between R_0 and F can be obtained. Yu et al. (2005) and Chi and Su (2006) gave a detailed discussion and mathematical proof on the inevitable problems resulting from applying a female age-specific life table to a two-sex population and the problem of l_x and m_x based on adult age.

This study is the first to apply the age-stage, two-sex life table theory to evaluate the demographic characteristics of *N. lugens* on wild rice. Our results provide a comprehensive description of the survival, development, and reproduction of a cohort of individuals. There are, however, still problems that cannot be resolved by life tables alone. In addition, life-table parameters often vary with different environmental variables, host species, and other factors. Kisimoto (1965) demonstrated that the potential fecundity of brachypterous and macropterous females was 250–540 and 300–600 eggs, respectively. In our study, the mean fecundity of *N. lugens* on *O. officinalis, O. rufipogon,* and TN1 was 1.06, 167.67, and 298.98 eggs, respectively. Although TN1 was the cultivar with susceptibility to *N. lugens*, the number of eggs laid by the planthopper decreased compared with the figure reported by Kisimoto (1965). The difference may be due to the daily replacement of rice plants disturbing the feeding and oviposition behavior of female planthoppers. In addition, *N. lugens* adults are dimorphic, having macropterous and brachypterous forms. In this study, adult females with different wing forms were not isolated because determination of the wing forms is complex and dependant on many factors, including crowding and host stage during the nymphal stage (Kisimoto 1965). However, the number of surviving female adults reared on *O. officinalis* was too small for comparison. Moreover, because only a single genotype of each the three rice species were used in this study, it is possible that intraspecific variations in population parameters and in resistance to brown planthopper may occur in other genotypes of the three species and may have been overlooked in this study.

Because life-table studies under different environmental conditions and on different host plants are a tedious and time-consuming process, the application of life tables in pest management programs is far from satisfactory. However, without the basic and solid knowledge of life tables, it is impossible to construct an ecologically sound pest management program. With the increasing awareness on the importance of sustainable agriculture and environmentally friendly pest management, life-table studies on key pests and their practical application in pest control are certainly and urgently worth pursuing.

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