

## Demography and Consumption of *Spodoptera litura* (Lepidoptera: Noctuidae) Reared on Cabbage and Taro

Shu-Jen Tuan,<sup>1</sup> Chih-Chun Yeh,<sup>1</sup> Remzi Atlihan,<sup>2</sup> Hsin Chi,<sup>1</sup> and Li-Cheng Tang<sup>1,3</sup>

<sup>1</sup>Department of Entomology, National Chung Hsing University, Taichung, Taiwan, Republic of China (sjtuan@dragon.nchu.edu.tw; yehsnake@yahoo.com.tw; hsinchi@dragon.nchu.edu.tw; lctang@dragon.nchu.edu.tw), <sup>2</sup>Department of Plant Protection, Faculty of Agriculture, University of Yuzuncu Yil, 65080 Van, Turkey (ratlihan@yyu.edu.tr), and <sup>3</sup>Corresponding author, e-mail: lctang@dragon.nchu.edu.tw

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### Abstract

*Spodoptera litura* (F.) causes considerable economic damage to multiple agro-crops annually in many countries. In this study, the demography of *S. litura* reared on cabbage and taro was investigated using the age-stage, two-sex life table at  $25 \pm 1^\circ\text{C}$ ,  $60 \pm 10\%$  relative humidity, and a photoperiod of 12:12 (L:D) h. Our results showed that the net reproductive rate, intrinsic rate, and finite rate of population increase on cabbage (1893.1 offspring,  $0.2374\text{ d}^{-1}$ , and  $1.2679\text{ d}^{-1}$ ) were all not significantly different from those on taro (1361.0 offspring,  $0.2298\text{ d}^{-1}$ , and  $1.2584\text{ d}^{-1}$ ). The net consumption rate on cabbage ( $439.1\text{ cm}^2$ ) was, however, three times higher than that on taro ( $141.7\text{ cm}^2$ ). According to the population parameters, both cabbage and taro are suitable host plants for *S. litura*. When both the population growth rate and the consumption rate were taken into consideration, the finite consumption rate on cabbage ( $\omega = 3.8054$ ) was significantly higher than that on taro ( $\omega = 1.3184$ ). In Taiwan, taro and cabbage are commonly planted in adjacent farm plots, with taro being grown from March to November and cabbage from October to April. Because of the overlapping growth periods of the two crops, *S. litura* can easily propagate throughout the year by switching between the adjacent crops during the overlap periods. Pest management strategies for controlling *S. litura* must be thoroughly reevaluated based on ecological characteristics, including its life table and consumption rate on its major host plants.

**Key words:** *Spodoptera litura* (F.), food consumption, life table, cabbage, taro

The tobacco cutworm, *Spodoptera litura* (F.) (Lepidoptera: Noctuidae), is a generalist herbivore and one of the most important economical pests feeding on some 300 species of host plants, including vegetables, fruits, tea, floricultural plants as well as green manures and weeds, in many parts of the world including Asia, Pacific islands, Oceania, North Africa, etc. (Chen and Hsiao 1984, Ramana et al. 1988, Xie and Hu 1999, Ahmad et al. 2007, 2013, Tojo et al. 2008, Xue et al. 2010, Tuan et al. 2014a, b, 2015). Although the Taiwan government and many of its researchers have devoted considerable effort and funds in controlling this pest, it remains a serious problem with major outbreaks occurring biyearly, from May to June and again in October to December (Jiang et al. 2010). Because *S. litura* can feed on a number of economic crops, green manures, and weeds (Jiang et al. 2010, Ahmad et al. 2013, Tuan et al. 2014a, b), it can successfully survive in cultivated and wild habitats. Cabbage (*Brassica oleracea* L.) and taro (*Colocasia esculenta* Schott) are two crops that are widely grown in suitable areas of Taiwan, and they serve as common resources for growth and reproduction of *S. litura* throughout the year.

The fitness of a pest population represents its damage capacity to a host plant. That fitness can only be properly ascertained through

the use of a life table, because it can provide an integrated and comprehensive description of the survival, development, and reproduction of a population. Life tables are also one of the essential tools for implementing ecology-based integrated pest management programs (Jha et al. 2012, Tuan et al. 2014a). The life history data of *S. litura* reared on different host plants and under varying laboratory conditions have been reported previously by several researchers (Garad et al. 1984, Chen and Hsiao 1984, Xue et al. 2010, Shahout et al. 2011). Several of these studies (Ou-Yang 1994, Xue et al. 2010, Shahout et al. 2011) covered only basic biological traits without including a life table analysis, and therefore, were not usable for evaluating the population growth potential of *S. litura*. A few of the life table papers (e.g., Chen and Hsiao 1984) were based on the traditional female age-specific life tables (Lotka 1907, Lewis 1942, Leslie 1945, Birch 1948, Carey 1993) that ignored the male population, stage differentiation, as well as the variable developmental rates among individuals. As Huang and Chi (2012b) pointed out, omitting these critical measures ultimately results in calculating erroneous demographic parameters. To take into account the two sexes, stage differentiation, and the variable developmental rates that occur among individuals, Chi and Liu (1985) and Chi (1988)

developed the age-stage, two-sex life table that results in a comprehensive and mathematically correct description of the development, stage differentiation, and reproduction of an insect population. It is currently being widely used in life table studies of many insect and mite species (Simpson 1991, Yang et al. 1997, Mo and Liu 2006, Huang and Zhang 2015).

In addition to life table data, determining an insect's consumption rate is essential in order to quantify the damage level of the pest and to refine timing of the appropriate control measures (Chi 1990, Tuan et al. 2014a). Life table studies incorporating consumption rate will produce a much more complete description of the growth and damage of the pest population on target host plants (Chi 1990, 2015a). In this study, we collected the life table data, and calculated the demographic parameters to measure the consumption rate of *S. litura* fed on cabbage and taro by using the age-stage, two-sex life table (Chi and Liu 1985, Chi 1988). These data will be invaluable in aiding researchers in constructing a useful pest management program for effective control of *S. litura*.

## Materials and Methods

### Rearing of *S. litura*

The colony of *S. litura* was originally collected from different taro and cabbage fields in Wufeng District, Taichung, Taiwan, and maintained in the Agricultural Pest Management Laboratory, Department of Entomology, National Chung Hsing University, Taichung, Taiwan (R.O.C). Insects were reared on an artificial diet (Tuan et al. 2014b) at  $25 \pm 1^\circ\text{C}$ ,  $60 \pm 10\%$  relative humidity (RH), and a photoperiod of 12:12 (L:D) h in a walk-in growth chamber. The first to third instars were reared in groups of ~100–150 larvae per plastic cup (9.5 cm in diameter and 5.5 cm in height) and provided with filter paper to absorb water condensation. Beginning with the fourth instar, larvae were removed and placed in individual wells of 30-well plastic plates until pupation (Tuan et al. 2014b). Pupae of 4–5 d old were removed and disinfected in 1.2% sodium hypochlorite solution for 15 min and then rinsed with running water for 15 min. Pupae were then sexed and kept in separated plastic containers. Following adult emergence, groups of 10–12 pairs of newly emerged adults were transferred into an oviposition container (13.5 cm in diameter and 18.5 cm in height, and lined with paper towel) and supplied with cotton balls soaked in a 20% honey–water solution. Egg masses were collected daily, and adults were transferred to a new oviposition container.

### Plant Culture

Two host plants species were used in this study: cabbage (*Brassica oleracea* L. cv. Summer-228) and taro (*Colocasia esculenta* Schott cv. Betel nut heart). Host plants were grown in a greenhouse at National Chung Hsing University, Taichung, Taiwan. After 25 d, cabbage seedlings were transplanted individually to plastic pots (14.7 cm in diameter and 12.6 cm in height). Taro bulb roots obtained from a taro field in Tajia District, Taichung, Taiwan, were planted in plastic pots (18 cm diameter and 15 cm height). All host plants were planted in equal-volume well-mixed soils of sandy soil (C098, Sinon Co. Ltd., Taiwan), loam (collected from a vegetable field, Wufeng, Taichung, Taiwan), and organic cultivated soil (Potgrond H, Klasmann-Deilmann GmbH, Germany). During the experimental periods, the fertilizer Compound-Fer 43 (N: P: K: Mg = 15: 15: 15: 4, Taiwan Agricultural Biotechnology Co., Ltd.) was applied at the 3rd wk posttransplanting. Fully expanded young leaves were collected for use in experiments.

### Life Table Study

Life table studies on insects reared on both cabbage and taro were conducted in a walk-in growth chamber at  $25 \pm 1^\circ\text{C}$ ,  $60 \pm 10\%$  RH, and a photoperiod of 12:12 (L:D) h. Ten pairs of newly emerged adults collected from the mass-rearing colony (artificial diet) were placed in an oviposition cylinder (diameter: 13.5 cm, height: 18.5 cm) with leaves of cabbage or taro and provided with a cotton ball soaked with 20% honey solution as adult food. In total, 10 oviposition containers were set up for each host plant treatment. Ten egg masses (each with 300–1,200 eggs) laid on the same day were collected from 10 different containers. The egg masses were then placed on the leaves of either cabbage or taro and kept in rearing containers (diameter: 7 cm, height: 15 cm for cabbage; diameter: 13.5 cm, height: 18.5 cm for taro) covered with a fine mesh on the top and a paper towel on the bottom. To maintain leaf turgidity, the leaf petioles were inserted into water filled 50-ml glass flasks. The eggs were monitored daily for hatching, and the hatch rates of the eggs were calculated. Because the hatch rate of the eggs varied with the age of the female, only hatched neonates were used in the life table study (Tuan et al. 2014b, Mou et al. 2015). The number of individuals (neonates) used for experiments was 73 and 74 on cabbage and taro, respectively. The newly hatched larvae were transferred using a fine brush to rearing containers provided with a single leaf of one of the host plants. The first to third instars were reared in a group of 6–10 individuals. Fourth-instar larvae were transferred individually to rearing containers each containing a fresh leaf. Leaves were replaced or added as needed (approximately every 1 to 3 d, depending on the freshness of leaves and consumption by the larvae). When a larva developed into the sixth instar, peat soil (~5–6 g) was provided for pupation. Newly emerged males and females were paired and placed in individual rearing containers lined with a tissue paper towel and supplied with either a cabbage or taro leaf for oviposition. The adults were provided with fresh 20% honey solution. If there were insufficient individuals of one sex or if a moth of a test cohort lost its mate, another young adult of the opposite sex was supplied from the mass-rearing colony for mating. In this way, all insects were offered a chance to mate before death. The data for the individuals supplied from the mass-rearing colony were excluded from the life table analysis. The egg masses produced by each female were collected daily and kept separately to record the age-specific hatch rates. The development, survival, and fecundity were recorded daily until all individuals died.

### Leaf Consumption Study

The consumption rate of the first three instar larvae that were group-reared with a small quantity of food, was measured by using graph paper (1 mm<sup>2</sup> per lattice), and then divided by the number of surviving larvae in that container. From the fourth instar to pupation, the consumption rate was recorded individually. The leaf area was measured by using a portable leaf area meter (Li-3100A, Li-Cor, Inc. Lincoln, NE, USA). The daily consumption rate was calculated as the differences of leaf areas before and after feeding.

### Data Analysis

The raw life history data of developmental duration and daily fecundity of *S. litura* reared on cabbage and taro were analyzed using the age-stage, two-sex life table in order to take both sexes and the variable developmental rate among individuals into consideration (Chi and Liu 1985, Chi 1988). To facilitate the raw data analysis, a computer program, TWISEX-MSChart (Chi 2015c), was used for the life table analysis.

The age-stage-specific survival rate ( $s_{xj}$ ; where  $x$  = age and  $j$  = stage), the age-specific survival rate ( $l_x$ ), and the age-specific fecundity ( $m_x$ ) were calculated from the survival and fecundity of all cohort results in the daily records. The calculated population parameters were the intrinsic rate of increase ( $r$ ), the finite rate of increase ( $\lambda$ ), the net reproductive rate ( $R_0$ ), and the mean generation time ( $T$ ).

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (1)$$

The intrinsic rate of increase was estimated by using the iterative bisection method from the Euler–Lotka formula:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (2)$$

with the age indexed from zero (Goodman 1982), i.e., zero being the age of the newly laid egg. The finite rate is calculated as

$$\lambda = e^r \quad (3)$$

The mean generation time is defined as the period that a population needs to increase to  $R_0$ -fold of its size when time approaches infinity and the population reaches a stable age-stage distribution. The mean generation time is calculated as

$$T = \frac{\ln R_0}{r} \quad (4)$$

To properly describe the variability of the consumption rate with age and stage, the daily consumption rate of individual *S. litura* was analyzed according to the age-stage, two-sex life table by using the computer program CONSUME-MSChart (Chi 2015a). The age-stage-specific consumption rate ( $c_{xj}$ ; where  $x$  = age and  $j$  = stage) is the mean consumption rate of an individual of age  $x$  at stage  $j$ . The age-specific consumption rate ( $k_x$ ) is the mean areas of leaves consumed by *S. litura* larvae at age  $x$  and is calculated as

$$k_x = \frac{\sum_{j=1}^{\beta} s_{xj} c_{xj}}{\sum_{j=1}^{\beta} s_{xj}} \quad (5)$$

where  $\beta$  is the number of life stages, and  $s_{xj}$  is the age-stage-specific survival rate of the cohort (Chi and Yang 2003). When taking the survival rate into consideration, the age-specific net consumption rate  $q_x$  represents the amount of leaf area consumed by *S. litura* larvae of age  $x$  and is calculated as

$$q_x = k_x l_x \quad (6)$$

The net consumption rate ( $C_0$ ) is the mean total leaf areas consumed by an individual during its life span and is calculated as

$$C_0 = \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} s_{xj} c_{xj} = \sum_{x=0}^{\infty} k_x l_x \quad (7)$$

It also represents the consumption capacity of a pest population including all individuals of both sexes and those that died prior to reaching the adult stage (Chi and Yang 2003). The transformation rate is the ratio of the net predation rate to the net reproductive rate and it is calculated as:

$$Q_p = \frac{C_0}{R_0} \quad (8)$$

It determines the leaf area that *S. litura* requires for the production of one viable egg. The finite consumption rate ( $\omega$ ) is calculated as

$$\omega = \lambda \sum_{x=0}^{\infty} \sum_{j=1}^{\beta} a_{xj} c_{xj} \quad (9)$$

where  $a_{xj}$  is the proportion of individuals belonging to age  $x$  and stage  $j$  in the stable age-stage distribution (Chi et al. 2011, Yu et al. 2013).

The standard errors of the developmental time, fecundity, longevity, consumption, and population parameters obtained from different cohorts were estimated by using 100,000 bootstraps. The differences between the treatment means were compared by using the paired bootstrap test (Efron and Tibshirani 1993, Huang and Chi 2013, Polat Akköprü et al. 2015).

## Population and Consumption Projection

The life table and consumption rate data from the above studies were used to simulate the population growth and consumption capacity of *S. litura* by using the program TIMING-MSChart (Chi 2015b) and the method described in Chi (1990) and Tuan et al. (2014a). Both TWOSEX-MSChart and TIMING-MSChart are available at <http://140.120.197.173/Ecology/>.

## Results

### Demographic Parameters of *S. litura*

The developmental times, longevity, and fecundity of *S. litura* are listed in Table 1. There were no significant differences in developmental times between cabbage- and taro-reared larvae, except the developmental times of egg, fifth instar, and pupal stage of *S. litura* reared on cabbage were significantly shorter than those reared on taro (Table 1). The survival rate from egg stage to adult female and male was 44 and 34% on cabbage, and 39 and 36% on taro, with a sex ratio ( $\text{♀}:\text{♂}$ ) of 1.28:1 and 1.07:1, respectively. The mean fecundities of *S. litura* on cabbage and taro were 4318.6 and 3472.8

**Table 1.** Developmental time, adult preoviposition period (APOP), total preoviposition period (TPOP), oviposition period, adult longevity, and fecundity (eggs per female) of *S. litura* fed on cabbage and taro

Stage	Developmental time (d) (mean $\pm$ SE) <sup>a</sup>				P
	n	Cabbage	n	Taro	
Egg	73	3.9 $\pm$ 0.0b	74	4.0 $\pm$ 0.0a	0.0006
L1–L3	64	6.8 $\pm$ 0.1a	66	6.7 $\pm$ 0.1a	0.6504
L4	64	2.1 $\pm$ 0.1a	65	2.2 $\pm$ 0.1a	0.7054
L5	63	2.5 $\pm$ 0.1b	65	2.8 $\pm$ 0.1a	0.0002
L6	63	2.9 $\pm$ 0.1a	59	2.8 $\pm$ 0.1a	0.4808
Larval	63	14.3 $\pm$ 0.2a	59	14.2 $\pm$ 0.1a	0.5542
Prepupa	63	2.0 $\pm$ 0.0a	59	2.0 $\pm$ 0.0a	0.5197
Pupa	57	9.0 $\pm$ 0.1b	56	9.4 $\pm$ 0.1a	0.0429
Preadult	57	29.1 $\pm$ 0.2a	56	29.5 $\pm$ 0.2a	0.1726
Adult longevity					
Female	32	11.5 $\pm$ 0.5a	29	11.3 $\pm$ 0.5a	0.7616
Male	25	15.9 $\pm$ 1.3a	27	13.9 $\pm$ 0.7a	0.1769
APOP	32	1.5 $\pm$ 0.3a	29	1.1 $\pm$ 0.3a	0.4267
TPOP	32	30.1 $\pm$ 0.4a	29	30.0 $\pm$ 0.5a	0.7968
Oviposition period	32	7.8 $\pm$ 0.5a	29	7.1 $\pm$ 0.5a	0.2556
Fecundity (all eggs)	32	4769.3 $\pm$ 295.3a	29	4014.5 $\pm$ 323.3a	0.0841
Fecundity (hatched eggs)	32	4318.6 $\pm$ 355.7a	29	3472.8 $\pm$ 389.4a	0.1089

<sup>a</sup> Means followed by different letters in the same row are significantly different between host plants—determined by using the paired bootstrap test ( $B = 100,000$ ).

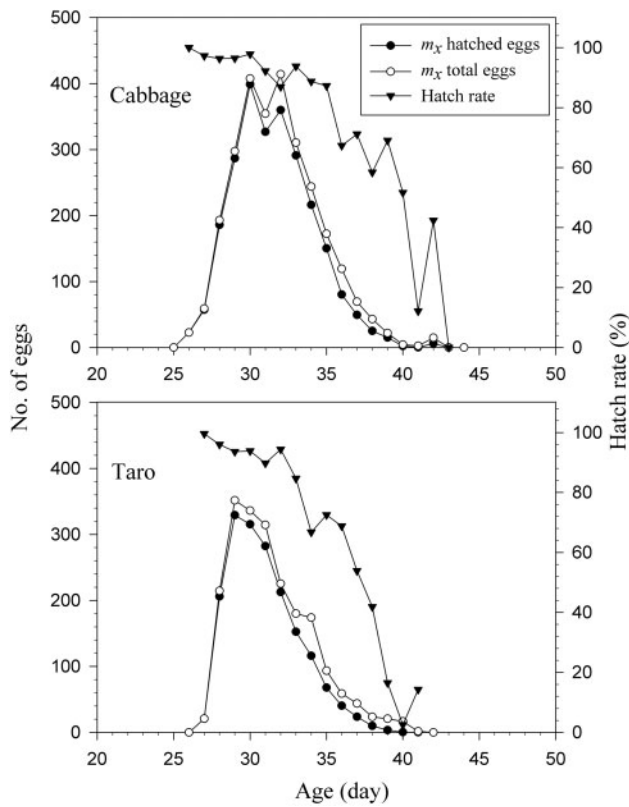


Fig. 1. Number of total eggs, hatched eggs, and hatch rate of *S. litura* fed on cabbage and taro.

hatched eggs, respectively. These figures, however, were not significantly different. No differences were found in adult (both female and male) longevity between individuals of *S. litura* reared on cabbage and taro (Table 1).

Both the age-specific fecundity and the age-specific hatch rate varied with different host plants and the age of the female (Fig. 1). The total mean number of eggs and hatched egg of *S. litura* reared on cabbage were 4769.3 and 4318.6 eggs, respectively, while those on taro were 4014.5 and 3472.8 eggs per female, respectively. The overall hatch rates were 90.5% on cabbage and 86.5% on taro. In general, the fecundity and hatch rate of *S. litura* reared on cabbage were higher than for those reared on taro. The fecundity of older females was lower than that of young females on both host plants, and decreased significantly after age 32 d (Fig. 1). The age-stage-specific survival rate ( $s_{xj}$ ) of *S. litura* represents the probability that a newborn individual will survive to age  $x$  and stage  $j$  (Fig. 2). Because the developmental rates vary among individuals as well as between sexes, there was obvious overlapping between different stages (Fig. 2). The age-specific survival rate ( $l_x$ ) and the age-specific fecundity ( $m_x$ ) of *S. litura* reared on cabbage and taro are shown in Fig. 3. The curve of  $l_x$  is a simplified version of the curves of  $s_{xj}$ . The highest peaks of  $m_x$  occurred on day 30 with 398.9 offspring on cabbage, and on day 29 with 329.1 offspring on taro. The net reproductive rate, intrinsic rate of increase, finite rate, and mean generation time of *S. litura* reared on cabbage and taro are listed in Table 2. There was no significant difference between them.

Food Consumption Rate of *S. litura*

The age-stage specific consumption rates ( $c_{xj}$ ) of *S. litura* fed on cabbage and taro are plotted in Fig. 4. It shows the mean leaf areas

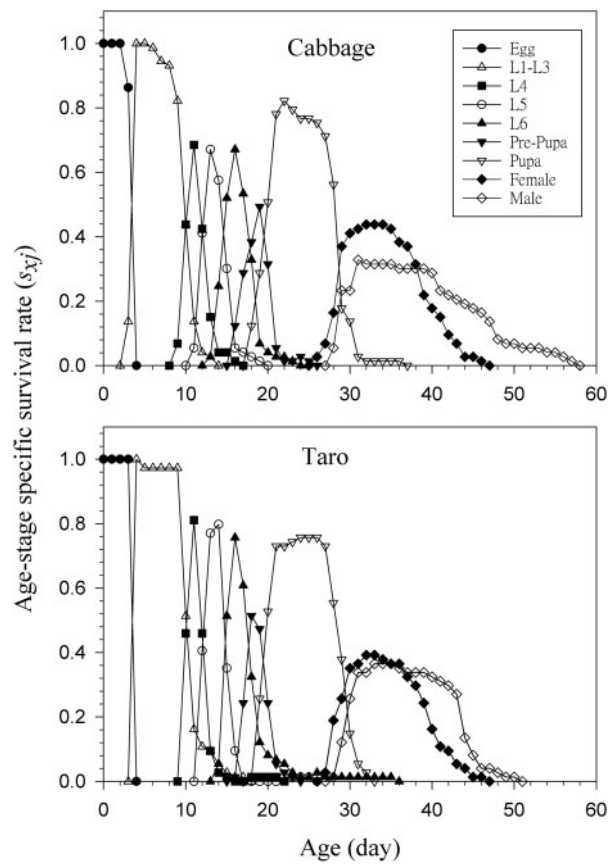


Fig. 2. Age-stage-specific survival rate ( $s_{xj}$ ) of *S. litura* fed on cabbage and taro based on using only hatched eggs.

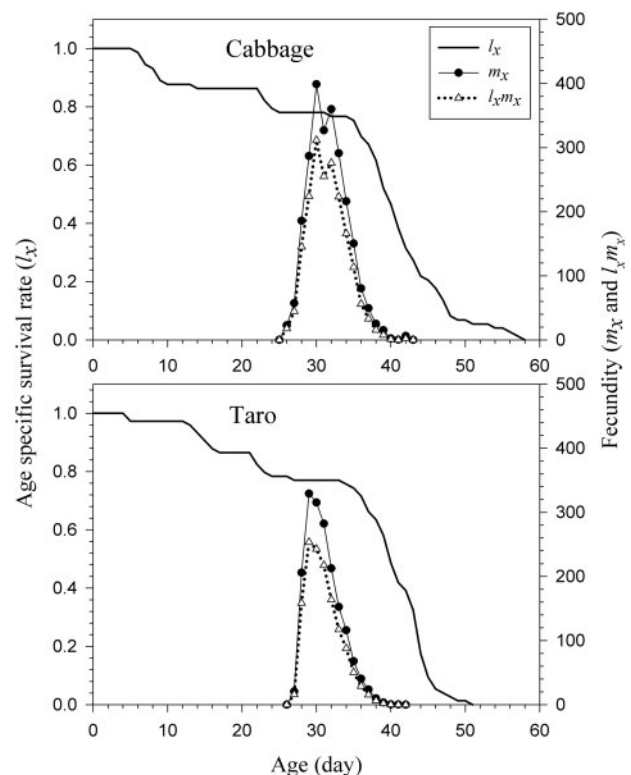
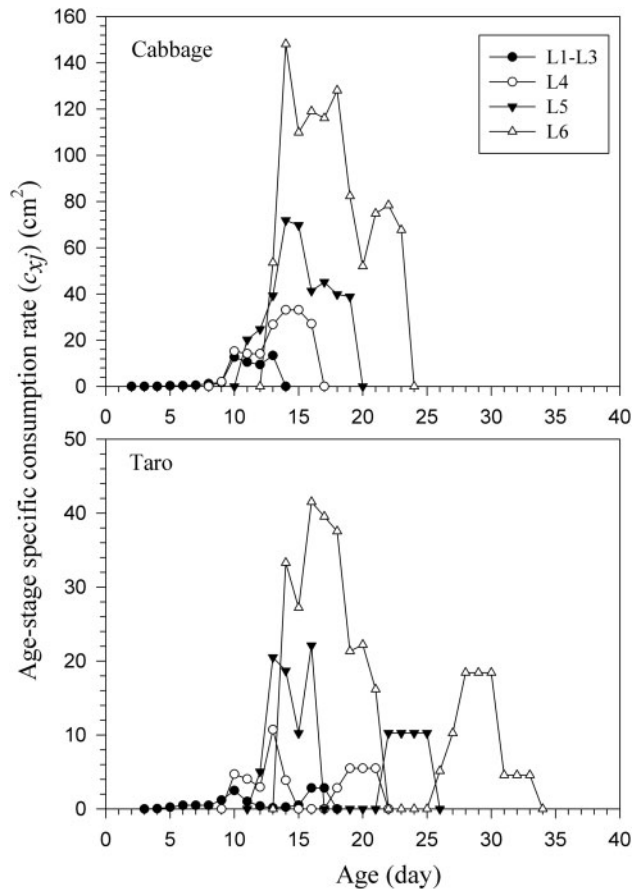


Fig. 3. Age-specific survival rate ( $l_x$ ), fecundity ( $m_x$ ), and net maternity ( $l_x m_x$ ) of *S. litura* fed on cabbage and taro based on using only hatched eggs.

**Table 2.** Population parameters of *S. litura* calculated by Jackknife and Bootstrap methods (mean  $\pm$  SE estimated on cabbage and taro)

Population parameter	Cabbage ( $n = 73$ )	Taro ( $n = 74$ )	<i>P</i>
Intrinsic rate of increase, $r$ ( $d^{-1}$ )	0.2374 $\pm$ 0.0057a	0.2298 $\pm$ 0.0066a <sup>a</sup>	0.3710
Finite rate of increase, $\lambda$ ( $d^{-1}$ )	1.2679 $\pm$ 0.0072a	1.2584 $\pm$ 0.0083a	0.3712
Net reproductive rate, $R_0$ (offspring per individual)	1893.1 $\pm$ 293.7a	1361.0 $\pm$ 247.2a	0.1657
Mean generation time, $T$ (d)	31.8 $\pm$ 0.3a	31.4 $\pm$ 0.3a	0.3484

<sup>a</sup> The means followed by different letters are significantly different between host plants—determined by using the paired bootstrap test ( $B = 100,000$ ). The standard errors were estimated by using 100,000 bootstraps.

**Fig. 4.** Age-stage-specific consumption rate ( $c_{xj}$ ) of *S. litura* fed on cabbage and taro.

consumed by *S. litura* larvae at age  $x$  and stage  $j$ . The overlap of consumption rates of different stages revealed the variability in the developmental rates among individuals as well. In general, the consumption rate increased with the instar (Table 3, Fig. 4). The consumption rate of the entire larval stage of *S. litura* reared on cabbage was significantly higher than for the larvae fed on taro, especially in the later instars. The mean leaf areas consumed by a sixth instar of *S. litura* were 338.5 cm<sup>2</sup> on cabbage and 107.9 cm<sup>2</sup> on taro, respectively. The net consumption rate of 439.1  $\pm$  23.7 cm<sup>2</sup> on cabbage was significantly higher than that on taro (141.71  $\pm$  8.64 cm<sup>2</sup>; Table 3). When feeding on cabbage, the transformation rate ( $Q_p$ ) was 0.2319, which was significantly higher than on taro. When both the population growth rate and the consumption rate were taken into consideration, the finite consumption rate on cabbage ( $\omega = 3.8054$ ) was significantly higher than that on taro ( $\omega = 1.3184$ ).

### Population and Consumption Projection

The simulated population growth and leaf consumption of *S. litura* on both cabbage and taro are plotted in Fig. 5. Because the age-stage, two-sex life table can describe the stage differentiation, the emergence of each life stage can be observed in Fig. 5A and C. Moreover, because the egg, pupal, and adult stages do not feed, the curves of population size and leaf consumption showed different fluctuation. In Fig. 5B and D, the arrows show that even though the total population size did not increase, the leaf consumption increased significantly due to the higher consumption rate of older instars.

### Discussion

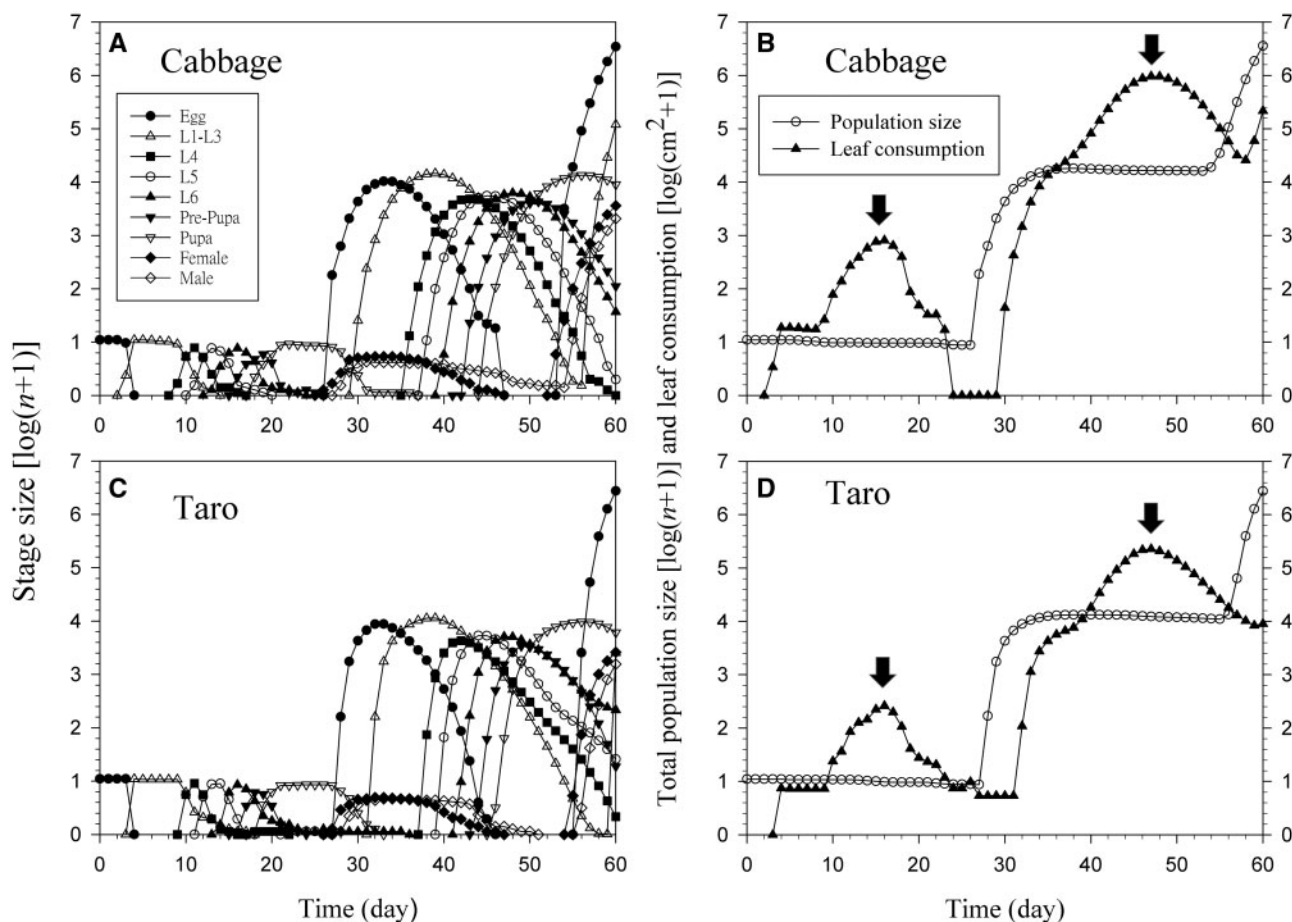
Because life tables obtained from cohorts reared on different host plants under laboratory conditions can reflect the suitability of the host plant, they have been used to assess the biotic potential of an insect (Sánchez and Pereyra 1995, Sánchez et al. 1997, Yang and Chi 2006). The traditional female age-specific life tables are, however, incapable in revealing the stage differentiation and inclusion the data relevant to male individuals and their consumption rate (Huang and Chi 2012a). Our results reinforce the advantages of using the age-stage, two-sex life table to reveal the stage differentiation and to include the male portion of the population.

As would be expected, the food consumption rate of *S. litura* increased with each instar, with the final instar larvae having the highest consumption rate on both host plants (Table 3 and Fig. 4). This phenomenon is associated with a rapid growth in the final instar (Tuan et al. 2015) and possibly to the storage of nutrient reserves for transformation processes that occur during the subsequent pupal phase (Prattisoli et al. 2002). The consumption rates of *S. litura* on cabbage were significantly higher than on taro, which probably reflects the differing nutrient values and water contents of the two plant species. It also means that the amount of defoliation caused by *S. litura* larvae on cabbage is heavier than that occurring on taro. Because the defoliation of cabbage is directly related to the loss of product value, while the defoliation of taro does not directly relate to the taro corm production, *S. litura* is usually viewed as a much more economically important pest on cabbage than it is on taro. Although the higher leaf consumption of *S. litura* on cabbage did not result in significant difference in the immature developmental time, adult longevity, fecundity, or in other population parameters (Tables 1 and 2), it did result in a higher finite consumption rate on cabbage than on taro (Table 3). Our results demonstrate that it is not justifiable to compare the extent of potential damage of a pest species solely based on its population growth rate (i.e., intrinsic rate and finite rate) or consumption rate. Instead, a more accurate prediction should be based on the population increase rate plus the consumption rate, i.e., the finite consumption rate (Yu et al. 2013). Fig. 5 demonstrates the advantages of combining the life table with

**Table 3.** Mean consumption rate of each instar, net consumption rate, transformation rate, and finite consumption rate of *S. litura* fed on cabbage and taro

Instar	Consumption rate (cm <sup>2</sup> /larva) (mean ± SE) <sup>a</sup>				
	<i>n</i>	Cabbage	<i>n</i>	Taro	<i>P</i>
First to third	64	12.9 ± 1.3a	66	4.6 ± 0.3b	<0.0001
Fourth	64	33.8 ± 2.0a	65	9.3 ± 0.8b	<0.0001
Fifth	63	122.6 ± 6.3a	65	44.4 ± 2.6b	<0.0001
Sixth	63	338.5 ± 12.4a	59	107.9 ± 6.3b	<0.0001
Net consumption rate, <i>C</i> <sub>0</sub> (cm <sup>2</sup> /individual)	73	439.1 ± 23.4a	74	141.7 ± 8.6b	<0.0001
Transformation rate, <i>Q</i> <sub><i>p</i></sub>	73	0.2319 ± 0.0364a	74	0.1041 ± 0.0201b	0.0068
Finite consumption rate, <i>ω</i>	73	3.805 ± 0.178a	74	1.318 ± 0.072b	<0.0001

<sup>a</sup> Means followed by different letters in the same row are significantly different between host plants—determined by using the paired bootstrap test. Standard errors were estimated by using 100,000 bootstraps.

**Fig. 5.** (A–D) Population and consumption projection of *S. litura* on cabbage and taro.

consumption rate to reveal the leaf consumption capacity (or damage capacity), which may be not coincide with population dynamics.

Although the nutrient content, i.e., nitrogen, proteins, and carbohydrates, of cabbage was lower than those in taro (Tuan et al. 2015), the consumption rate of *S. litura* on cabbage was higher than on taro (Table 3). The compensatory intake of host plant leaf material may explain the higher fecundity found in the cabbage cohort (Tuan et al. 2015). In Taiwan, cabbage is commonly planted from October to the following April, and taro is widely planted from March through November, resulting in at least a one month overlap in both the beginning and end of these two planting seasons.

Moreover, many other suitable host plants, e.g., cauliflower, peanut, taro, sesbania, sunn hemp, etc., are commonly grown in Taiwan throughout the year (Tuan et al. 2014a, b). The presence of these alternant host plants explains why *S. litura* outbreaks occur annually during the cabbage postharvest period, as well as during the early cropping season of taro in Taiwan (Fei et al. 2010, Jiang et al. 2010, Tuan et al. 2014b).

Understanding the effect of different host plant species on the ecology of insect pests is crucial for their management (Greenberg et al. 2001). The high population growth potential of *S. litura* on cabbage, taro, sunn hemp, sesbania observed in this study and Tuan

et al. (2014b) revealed the complexity and difficulty in management of this pest. As shown in this study, life table studies offer the most comprehensive understanding of the survival, stage differentiation, and reproduction of pest populations. Moreover, the age-stage, two-sex life table can describe the variation in consumption rate due to stage differentiation. Conclusively, a joined study of life table and consumption rate provides necessary data for predicting population growth and pest damage. These information will provide a solid scientific foundation for devising an effective and timely integrated pest management program for controlling *S. litura*.

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