

Life Tables and Development of *Bemisia argentifolii* (Homoptera: Aleyrodidae) at Different Temperatures

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J. Econ. Entomol. 99(3): 691–698 (2006)

ABSTRACT The life history of *Bemisia argentifolii* Bellows & Perring (Homoptera: Aleyrodidae) on tomato (*Lycopersicon* spp.) was studied based on the age-stage, two-sex life table at 15, 20, 25, 28, 30, and 35°C. The intrinsic rate of increase (r) at these temperatures is -0.0176 , 0.0667 , 0.1469 , 0.1611 , 0.1745 , and 0.0989 d⁻¹, respectively. The relationship among the gross reproductive rate (GRR), the net reproductive rate (R_0), and the preadult survivorship (l_a) is consistent with $GRR > l_a \cdot GRR > R_0$ for all results at different temperatures. The mean generation time is 81.9, 48.6, 28.4, 25.3, 22.1, and 18.2 d, respectively. The developmental rate of the egg stage at different temperatures fit a linear equation with a thermal summation 89.2 degree-days and a developmental threshold of 11.4°C. The developmental rates of the nymphal stage fit the model of Stinner et al. and the parameters of C , R_{max} , k_1 , and k_2 were 0.085, 0.0833, 5.298, and -0.263 , respectively.

KEY WORDS life table, *Bemisia argentifolii*, temperature

The silverleaf whitefly, *Bemisia argentifolii* Bellows & Perring (Homoptera: Aleyrodidae), is a cosmopolitan pest (Perring 2001) and a vector of virus diseases (Rubinstein et al. 1999). In Taiwan, *B. argentifolii* is not only a major pest of many Cruciferae, Solanaceae, Leguminosae, and Passifloraceae crops but also an important vector of plant viruses, such as tomato yellow leaf curl virus (TND AIS 2004). In addition to economic crops, *B. argentifolii* can complete its life history on several weed species (Lai and Chen 2002). In Taiwan, the control of *B. argentifolii* has been a major problem in enclosed screen houses and agricultural fields for many years. To be able to predict the population growth of a pest and time control strategies in integrated pest management, it is crucial to understand the survival rate and fecundity of the target pest under different environmental conditions. Life table studies provide the most comprehensive portrayal of the survival, development, and reproduction capabilities of a population under varying conditions. Most traditional female-based, age-specific life tables (Lewis 1942, Leslie 1945, Birch 1948), however, deal with only the female population and ignore the stage differentiation in insect and mite populations. Chi and Liu (1985) developed an age-stage, two-sex life table to take into account the male population and the variable developmental rate occurring among individuals. Chi (1988) gave a detailed description on the data

analysis in two-sex life table. To incorporate predation by the male population and the stage-specific predation rate, Chi and Yang (2003) studied the predation rate of *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) based on the age-stage, two-sex life table. Yu et al. (2005) proved the theoretical relationship among gross reproductive rate, net reproductive rate, and preadult survivorship. They pointed out that an erroneous relationship is obtained when an age-specific female life table is applied to a two-sex population. For a comprehensive understanding of the development and reproduction of *B. argentifolii* on tomato, *Lycopersicon esculentum* Mill., we collected its life history data at different temperatures and analyzed them based on the age-stage, two-sex life table theory (Chi and Liu 1985, Chi 1988).

Materials and Methods

Life Table Study. The stock population of *B. argentifolii* was reared on potted tomato kept in screened cages in a screenhouse at Hualien District Agricultural Research and Extension Station, Hualien, Taiwan. Before conducting the life table study, whitefly cultures were maintained on tomato plants at constant temperatures (15, 20, 25, 28, 30, and 35°C) for a generation in growth chambers. For the life table study, rearing containers made of plastic pots (9 cm in top diameter, 6 cm in bottom diameter, and 7 cm in height) containing tomato seedlings (five-leaf stage) were used. Reversed plastic cups (9.5 cm in top diameter, 6 cm in bottom diameter, and 13 cm in height) were used as

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Table 1. Means and standard errors (in parentheses) of the developmental time, longevity, fecundity, adult preoviposition period and total preoviposition period of *B. argentifolii* at different temperatures

Statistics	Temp (°C)					
	15	20	25	28	30	35
Egg duration (d)	19.4 (0.7)	12.6 (0.2)	6.5 (0.1)	5.4 (0.1)	4.6 (0.1)	3.8 (0.1)
Nymph duration (d)	55.9 (1.2)	26.0 (0.4)	14.1 (0.2)	13.6 (0.1)	12.6 (0.2)	12.0 (0.3)
Total preadult duration (d)	75.4 (2.1)	38.5 (0.5)	20.5 (0.2)	19.0 (0.2)	17.2 (0.2)	15.7 (0.3)
APOP (d)	6.5 (0.5)	1.8 (0.4)	0.4 (0.1)	0.5 (0.1)	0.3 (0.1)	0.5 (0.3)
TPOP (d)	84 (6.0)	39.7 (0.6)	20.8 (0.3)	19.2 (0.2)	17.0 (0.4)	16.0 (0.4)
Adult longevity (d)	5.5 (0.8)	15.8 (1.6)	14.5 (1.2)	15.4 (0.7)	13.3 (0.9)	6.3 (0.6)
Fecundity (eggs/female)	2.0 (1.2)	54 (9.3)	114 (0.8)	109 (6.1)	93.1 (7.4)	16.7 (4.6)

APOP, adult preoviposition period; TPOP, total preoviposition period.

covers. At the center of the cup bottom, a 4-cm-diameter hole was cut and covered with fine mesh cloth for ventilation. For the life table study, 10 pairs of adult whiteflies were released into each of a total 10 rearing containers. After 24 h, one egg was left on each leaf and the remaining eggs were removed. In total, 50 eggs were collected and kept in growth chambers at each respective temperature (120 eggs were used for 28°C) and a photoperiod of 12:12 [L:D] h. The developmental stage and survival of *B. argentifolii* were recorded daily. As the whitefly reached the red-eyed nymphal stage (also erroneously referred to as the pupal stage), the leaves were cut from the stem and kept individually in new rearing containers. On the day of adult emergence, males and females were paired and subsequently kept in individual rearing containers. The fecundity and survival were recorded daily until the death of all individuals. Life history data were analyzed according to the age-stage, two-sex life table theory (Chi and Liu 1985) and the method described by Chi (1988). The means and standard errors of the life table parameters were estimated by using the jackknife method (Sokal and Rohlf 1995). The population parameters calculated were intrinsic rate of increase (r), finite rate of increase (λ), gross reproductive rate (GRR), net reproductive rate (R_0), and mean generation time (T). The intrinsic rate of increase is estimated by using iterative bisection method from

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

with age indexed from 0 (Goodman 1982). The mean generation time is defined as the length of time that a population needs to increase to R_0 -fold of its size (i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$) at the stable age-stage distribution. The mean generation time is calculated as $T = (\ln R_0) / r$. To facilitate the tedious process of raw data analysis, a computer program TWOSEX-MSChart for the age-stage, two-sex life table analysis (Chi 2005) in Visual BASIC (version 6, service pack 6) for Windows system is available at <http://140.120.197.173/Ecology/> (Chung Hsing University, Taichung, Taiwan) and <http://nhshbig.inhs.uiuc.edu.tw/www/chi.html> (Illinois Natural History Survey, Champaign, IL). We fit the devel-

opmental rate of the egg stage to the linear equation $y = a + bx$ by using linear regression (Sokal and Rohlf 1995), where y is the developmental rate (1/d) and x is the temperature. The thermal summation (K) then was calculated as $K = 1/b$. The developmental threshold (T_0) was calculated as $T_0 = -Ka$. The developmental rate of the nymphal stage was fitted to the model of Stinner et al. (1974) as

$$R_{\tau} = \frac{C}{1 + e^{k_1 + k_2 \tau}} \quad [1]$$

where R_{τ} is the developmental rate at temperature τ , $C = R_{\max} \times (1 + e^{k_1 + k_2 T_{opt}})$, R_{\max} is the maximum developmental rate, T_{opt} is the temperature at which R_{\max} occurs, k_1 and k_2 are empirical constants ($k_2 < 0$), $\tau' = \tau$ for $\tau \leq T_{opt}$, and $\tau' = 2 \cdot T_{opt} - \tau$ for $\tau > T_{opt}$.

Results and Discussion

In this study, the silverleaf whitefly completed development and produced offspring at all tested temperatures on tomato plants. The mean developmental times decreased with increases of temperature (Table 1). The means of the total preadult developmental

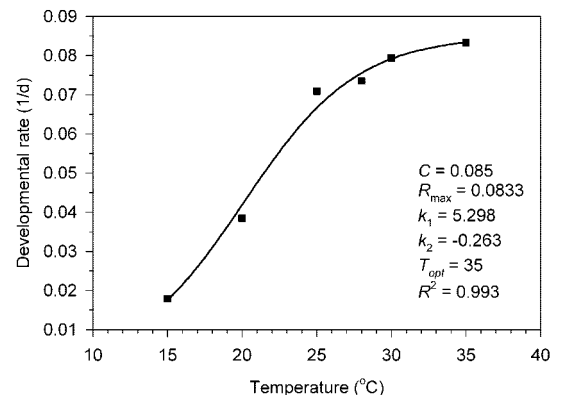


Fig. 1. Developmental rate of the nymphal stage of *B. argentifolii* at different temperatures fitted to the model of Stinner et al. (1974).

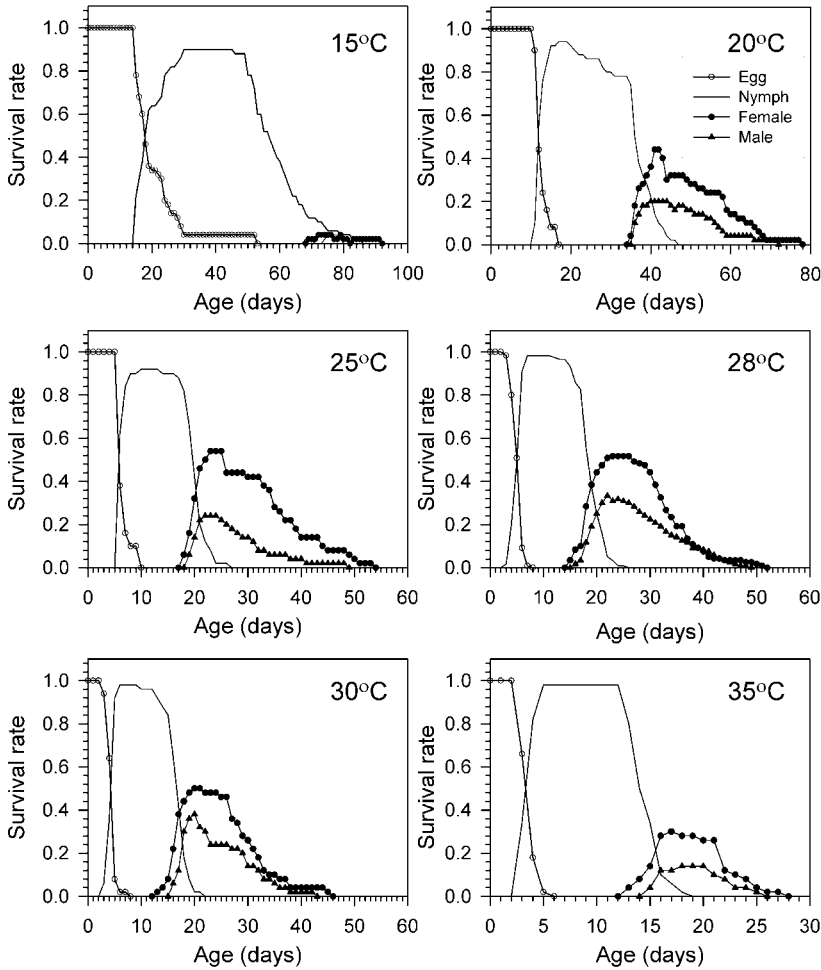


Fig. 2. Age-stage specific survival rate (s_{xj}) of *B. argentifolii* at different temperatures.

time ranged from 15.7 to 75.4 d. Nava-Camberos et al. (2001a) reported that *B. argentifolii* did not develop at 35°C. Wagner (1995), however, reported that the whitefly biotype B (synonymous with *B. argentifolii*) could complete its development at 34.7°C. In our study, *B. argentifolii* completed its life history at 35°C with a total preadult duration time of 15.7 d and an adult longevity of 6.3 d. The developmental rates of the egg stage fit the linear equation: $y = -0.1274 + 0.0112x$ with a coefficient of determination (R^2) of 0.985. The thermal summation (K) for the egg stage is 89.2 degree-days (DD). The estimated developmental threshold for the egg stage is 11.4°C by extrapolating the regression line, which is close to the threshold of 11.0°C for egg to adult reported by Nava-Camberos et al. (2001a). **Because the developmental threshold is estimated by extrapolation, it should be interpreted with caution.** The nymphal duration varied from 12 d at 35°C to 55.9 d at 15°C (Table 1). The developmental rates of the nymphal stage fit the model of Stinner et al. (1974) and the parameters of C , R_{max} , k_1 , and k_2 were 0.085, 0.0833, 5.298, and -0.263 , respectively

(Fig. 1). The coefficient of determination was 0.993. The optimal temperature (T_{opt}) was 35°C, at which the R_{max} occurred. **Some authors have used Duncan multiple range test or other multiple comparisons to compare the mean developmental times obtained at different temperatures (Bayhan et al. 2005). Mead (1988) and many statisticians pointed out the frequent misuse of the multiple comparison.** For the description of the temperature-dependent developmental rate, the linear or nonlinear regression analysis is appropriate to explore the dependence of responses (here, developmental rate) on the increase of independent variable (here, temperature).

The age-stage survival rates (s_{xj}) of *B. argentifolii* at different temperatures are plotted in Fig. 2, showing the probability that a newborn will survive to age x and stage j . Because the age-stage, two-sex life table takes the variable developmental rate among individuals into consideration, significant overlapping between stages can be observed in Fig. 2. If the survival curves were constructed based on the means of each stage

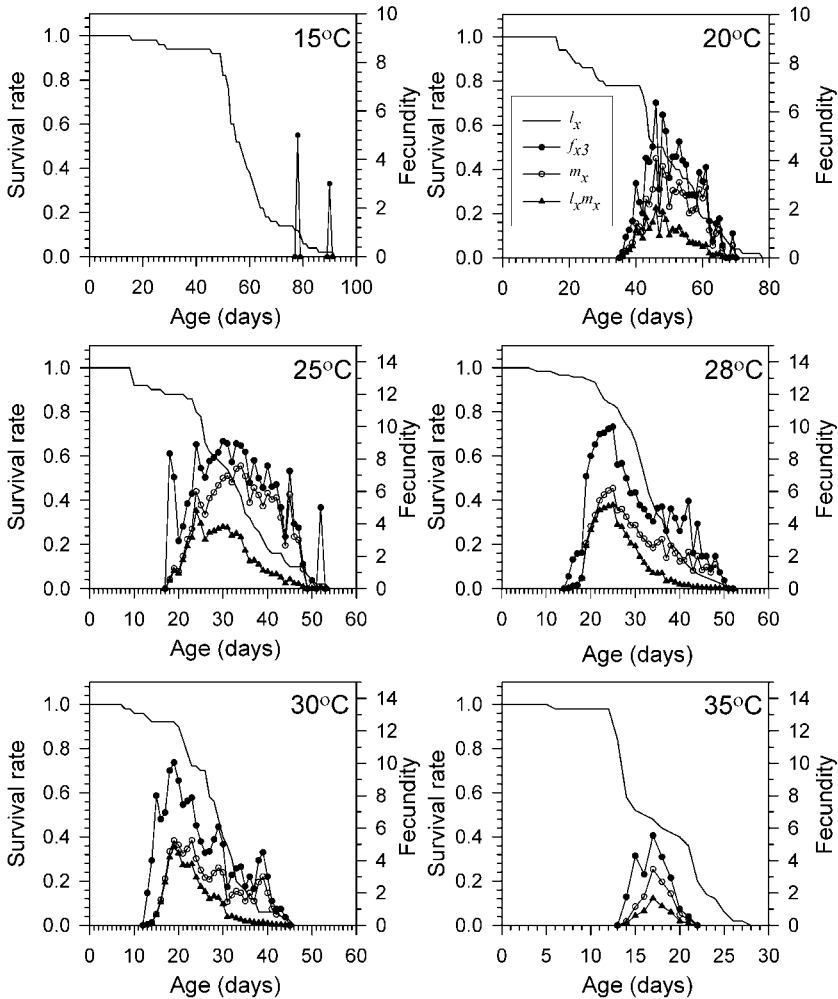


Fig. 3. Age-specific survival rate (l_x), female age-specific fecundity (f_{x3}), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) of *B. argentifolii* at different temperatures.

(e.g., Fig. 8.5 of Pianka 1994, Tables 4-4, 4-5, 6-14, and 6-12 of Carey 1993), the stage overlap would not have been observed, and it would have resulted in errors in the survival curves.

At different temperatures, the mean fecundity per female ranged from 2.0 to 114 eggs (Table 1). They are lower than that the values found by Nava-Camberos et al. (2001a) on cantaloupe and cotton. The mean number of offspring produced by individual *B. argentifolii* of age x and stage j per day is shown with the age-stage fecundity (f_{xj}) in Fig. 3. Because only females produce offspring, there is only a single curve f_{x3} (i.e., the female is the third life stage). At 15°C, oviposition was very low; however, 90% *B. argentifolii* survived longer than a month and 20% survived longer than 2 mo. This survivorship is sufficient for *B. argentifolii* to survive the short, mild winter in Taiwan. The age-specific survival rate (l_x), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) show that *B. argentifolii* can successfully survive and reproduce in the range of

20–35°C. This is one of the main contributing reasons that *B. argentifolii* is as successful as it is as a major agricultural pest in Taiwan.

The population parameters of *B. argentifolii* at different temperatures are listed in Table 2. The intrinsic rate of increase at 15°C is -0.0176 d^{-1} . The negative intrinsic rate shows that the whitefly population will decrease at lower temperatures. The maximum of intrinsic rate of increase (0.1745 d^{-1}) was obtained at 30°C. The fecundity curve at 35°C begins much earlier than that at 25°C, however, because the total fecundity at 35°C is much lower than that at 25°C, the intrinsic rate of increase at 25°C is higher than that at 35°C. The maximal gross reproductive rate is 157.5 offspring at 25°C. The net reproductive rate is 0.16, 24.8, 63.8, 58.3, 46.6, and 5.7 offspring at 15, 20, 25, 28, 30, and 35°C, respectively. Liu and Stansly (1998) reported an intrinsic rate as 0.105 d^{-1} at 26.7°C and the net reproductive rate (R_0) as 17.0, whereas the mean fecundity (F) was 9.75 eggs/adult on hibiscus 'Pink Versicolor'.

Table 2. Means and standard errors (in parentheses) of intrinsic rate of increase (r), gross reproductive rate (GRR), net reproductive rate (R_0), mean generation time (T), and life expectancy of newborn (e_{01}) of *B. argentifolii* at different temperatures

Pop parameter	Temp (°C)					
	15	20	25	28	30	35
r (d^{-1})	-0.0176 (0.0113)	0.0667 (0.0049)	0.1469 (0.0061)	0.1611 (0.0043)	0.1745 (0.0082)	0.0989 (0.0198)
GRR (offspring/individual)	6.8 (2.9)	60.0 (10.3)	157.5 (21.9)	97.3 (12.8)	81.0 (16.5)	12.3 (3.7)
R_0	0.16 (0.12)	24.8 (5.7)	63.8 (11.2)	58.3 (6.0)	46.6 (7.6)	5.7 (1.9)
T (d)	81.9 (8.5)	48.6 (0.8)	28.4 (0.7)	25.3 (0.3)	22.1 (0.5)	18.2 (0.3)
e_{01} (d)	58.4 (2.0)	47.2 (2.2)	31.8 (1.5)	32.6 (0.8)	28.5 (1.1)	18.0 (0.7)

In their report, the net reproductive rate was higher than the mean fecundity, i.e., $R_0 > F$. Because the net reproductive rate (R_0) takes the age-specific survival rate into consideration, it is always true that $R_0 \leq F$. If there is preadult mortality, it is inevitable that $R_0 < F$. This suggests that there is a miscalculation in their results. Bayhan et al. (2005) reported the fecundity of *Aphis punicae* (Passerini) (Homoptera: Aphididae) as 31.34 progeny/female, whereas the R_0 is 31.51, and the survivorship of the total immature stages is 90% (Tables 2 and 3 in Bayhan et al. 2005). Their results showed a similar miscalculation where their $R_0 > F$.

Chi and Liu (1985) and Chi (1988) showed that the variable developmental rate among individuals resulted in stage overlapping in the survival curves (Fig. 3 in Chi and Liu 1985 and Fig. 2 in Chi 1988). Liu and Stansly (1998) showed similar curves of stage overlapping (Fig. 2 in Liu and Stansly 1998); however, they ignored the variable developmental rates among individuals and plotted the survival curves and fecundity curves based only on the adult age (Fig. 3 in Liu and Stansly 1998). In entomological journals, many authors have constructed survival rates and fecundity curves based on "adult age." For example, Tsai and Wang (1996) constructed the curves of age-specific survival rates and fecundity of *B. argentifolii* on five host plants based on the adult age. Calvitti and Remotti (1998) studied the life tables of *B. argentifolii* on weeds by using the female age-specific life table and constructed the survival rate and fecundity curves based on the adult age. As Chi (1988) and Yu et al. (2005) pointed out, when the survival rate and fecundity are constructed based solely on the adult age, the differences in preadult development are ignored, and it is assumed that all adults emerged on the same day. These manipulations and assumptions consequently result in errors in the survival and fecundity curves.

The relationship between the net reproductive rate R_0 and the mean female fecundity F was proven by Chi (1988) for two-sex life table as

$$R_0 = F \cdot \left(\frac{N_f}{N} \right) \quad [2]$$

where N is the total number of eggs used for life table study at the beginning, and N_f is the number of female adults emerged. In this study, N is 120 for 28°C and 50 for all other temperatures, whereas N_f are 4, 23, 28, 64, 25, and 17 for 15, 20, 25, 28, 30, and 35°C, respectively. All data of R_0 and F are consistent with the relationship of equation 2. Yu et al. (2005) proved the relationship

among the GRR , R_0 , and preadult survivorship (l_a) as $GRR > l_a \cdot GRR > R_0$. All of our results at different temperatures are consistent with this relationship. Chi (1988) and Chi and Yang (2003) discussed in detail the differences between the traditional female age-specific life table and the age-stage, two-sex life table and pointed out possible errors in the survival and fecundity curves based on the adult age.

The mean generation time is 81.9, 48.6, 28.4, 25.3, 22.1, and 18.2 d at the temperature tested, and the life expectancy of newborns is 58.4, 47.2, 31.8, 32.6, 28.5, and 18.0 d at 15, 20, 25, 28, 30, and 35°C, respectively (Table 2). The age-stage specific life expectancy (e_{xj}) (Fig. 4) gives the lifespan that an individual of age x and stage j is expected to live at different temperatures. It shows that the age-stage specific life expectancy decreases with temperature. The life expectancy is calculated using the age-stage survival rate (s_{xj}) without assuming that the population reaches the stable age-stage distribution. Thus, it can be used to predict the survival of a population at that condition. For example, at 25°C a female adult of age 20 d will live on average another 16.7 d, whereas a male adult of age 20 d will live on average another 11.2 d. The life expectancy based on age-stage, two-sex life table distinguishes the difference among individuals of the same age but of different stages or different sexes.

Fisher (1930) defined the reproductive value as the contribution of an individual to the future population. The age-stage reproductive value (v_{xj}) of *B. argentifolii* describes the contribution of an individual of age x and stage j to the future population. The reproductive value of a newborn (v_{01}) is exactly the finite rate of increase. The reproductive value significantly increases when reproduction begins. For example, at 25°C an adult emerged on age 18 d (Fig. 2) and began to produce offspring (Fig. 3), the reproductive value jumps from a value <20 for a nymph to 42.3 for female on that day (Fig. 5). However, if an old female no longer produces offspring, the reproductive value will become and remain 0 thereafter. For example, the survival curve of female *B. argentifolii* ended on age 28 d at 35°C (Fig. 2), but the fecundity curve stopped at age 22 d (Fig. 3), the reproductive values are 0 after age 22 d (Fig. 5). Because the contribution of males to the future population is not defined by Fisher (1930), there is no curve for males.

Liu and Stansly (1995) noticed that there were variations in susceptibility to insecticides among different developmental stages of *B. argentifolii*. Nava-

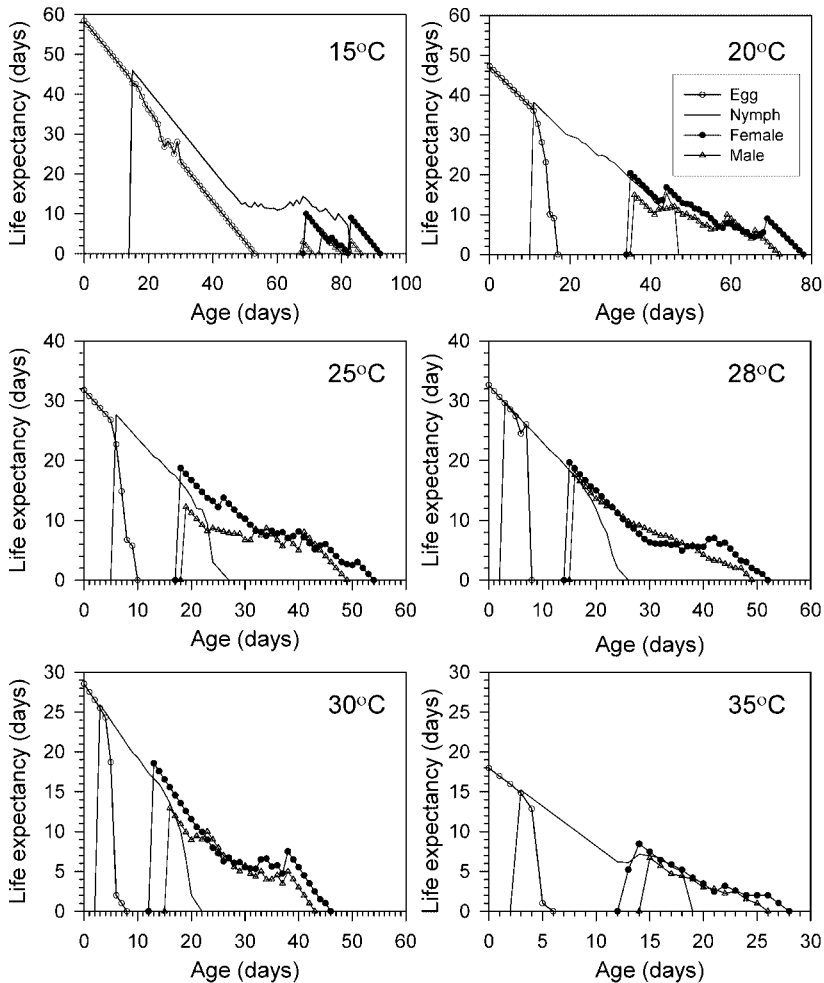


Fig. 4. Age-stage specific life expectancy (e_{xj}) of *B. argentifolii* at different temperatures.

Camberos et al. (2001b) reported that the economic injury levels (EILs) varied as a function of whitefly density, whitefly stage, and other factors. Because the susceptibility of an individual to both chemical and biological control agents may vary widely with sex and developmental stage, and the two-sex life table is capable of precise calculation of the sex and stage structure of a two-sex population, use of the two-sex life table can be extremely helpful in timing pest management decisions (Chi 1990). Liu et al. (1997) studied the life table of *Nephaspis oculatus* (Coleoptera: Coccinellidae), a predator of *B. argentifolii*. Their data showed that the consumption of whitefly eggs by predator larva increased from first instar to third instar. They also found that adult females consumed an average of 78.0 *B. argentifolii* eggs per day over a 5-wk period, whereas males consumed 123.0 eggs per day. The differences in predation rate among stages and between sexes are important for biological control and can only be properly included by using stage-structured two-sex model (Chi and Yang 2003). Headrick

et al. (1999) developed the life table for *Eretmocerus eremicus* (Hymenoptera: Aphelinidae), a parasitoid of *B. argentifolii* on cotton and sweet potato. They found there were differences in life table parameters of the parasitoid on different host plants. For biological control, it is not only necessary to study the life tables of both pests and their natural enemies on different host plants but also to incorporate the stage-specific predation rate of predators or the parasitism rate of parasitoids with the life table of their natural enemies (Chi and Yang 2003). However, because of the tedious and time-consuming process of data gathering inherent in life table studies conducted under different environmental conditions and on different host plants, especially for long-lived insects, the application of life tables in pest management programs is far from satisfactory. Nevertheless, with the increasing awareness on the importance of sustainable agriculture and environmentally friendly pest management, life table studies on key pests and their natural enemies are certainly worth pursuing.

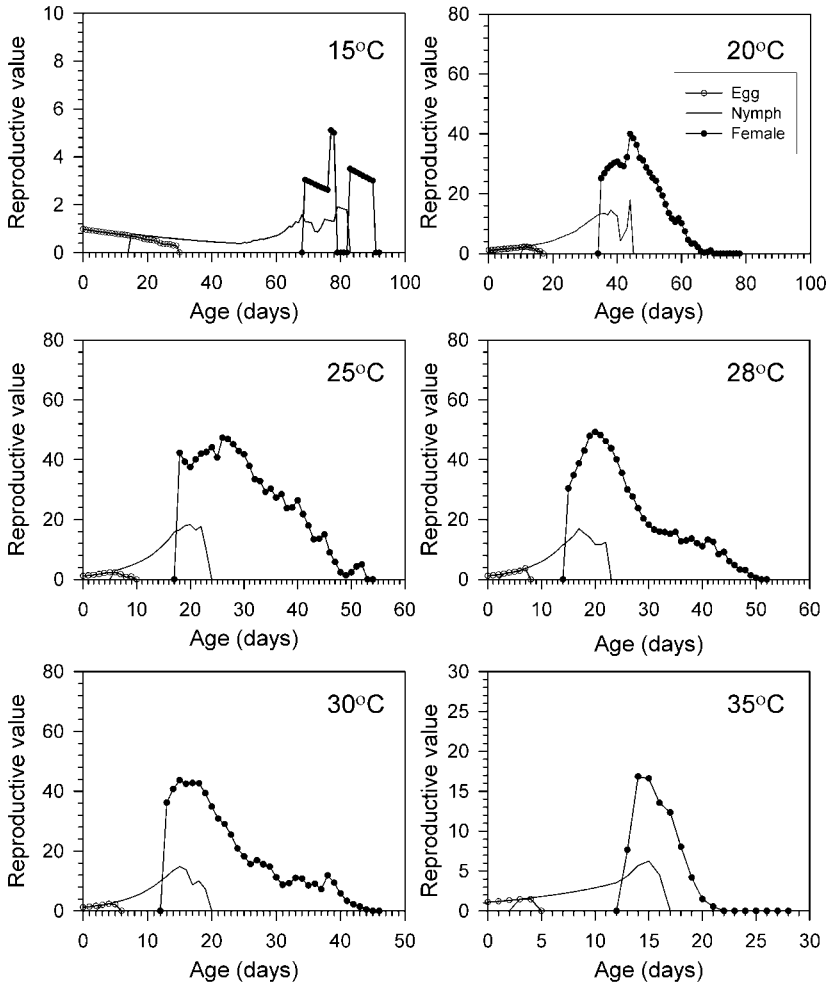


Fig. 5. Age-stage reproductive value (v_{xj}) of *B. argentifolii* at different temperatures.

Acknowledgments

We thank Cecil L. Smith for generous help with the editing. This research is supported by the Bureau of Animal and Plant Health Inspection and Quarantine, Taiwan [90AS-6.2.3-BQ-B1(9),91AS-7.2.3-BQ-B1(2),92AS-1.8.1-BQ-B4(2)] to H.C.

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Received 26 May 2005; accepted 16 February 2006.