Life Table Parameters of *Thrips palmi* Karny (Thysanoptera: Thripidae) as Related to Its Management Strategy

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ABSTRACT

The life table parameters of *Thrips palmi* Karny were determined at four constant temperatures, 15, 21, 25, and 30°C, on eggplant leaves for three generations. The results indicated that the age-specific fecundity (m_x), the daily fecundity (f_{x5}), and the age-specific maternity ($l_x m_x$) were highest at 25°C. The intrinsic rate of increase (r) rose from 0.033 day^{-1} at 15°C to between 0.046 and 0.157 day^{-1}, then dropped to 0.118 day^{-1} at 21, 25° and 30°C, respectively. The net reproductive rate (R_0) was highest at 25°C at 18.6 eggs/individual. The mean generation time (T) shortened gradually from 15 to 30°C, but was only one day shorter at 30°C than at 25°C. The standard error of r, λ, R_0, and T were estimated by using the Jackknife method. Accordingly, the management strategy for *T. palmi* was suggested based on this study.

Key words: *Thrips palmi*, temperature, life table parameters, eggplant

Introduction

Thrips palmi Karny has been commonly found on cucumber plants in the central and southern Taiwan since 1975. It is a very serious pest for many vegetable crops such as cucumbers, eggplants, sweet peppers, water melons, and many ornamentals (Wang and Chu, 1986). *Thrips palmi* larvae and adults feed on the leaves, stems, flowers and fruits of crops, producing many scars and deformities, thereby decreasing yield and marketability. In addition, they also transmit some plant tospoviruses, such as the *Watermelon silvery mottle virus* (WSMoV) and the *Melon yellow spot virus* (MYSV) on cucurbit, and the *Calla lily chlorotic spot virus* (CCSV) on calla lily (Yeh *et al.*, 1992; Kato *et al.*, 1999; Chen *et al.*, 2005), which further increases crop damage and economic losses.

Numerous studies have been carried out on *T. palmi*, including the effect of temperature, humidity and various host plants on its development (Kawai, 1985, 1986a; Tsai *et al.*, 1995; McDonald *et al.*, 1999; Huang and Chen, 2004; Park *et al.*, 2010); its reproductive mechanism (Wang

et al., 1989; Chu and Wang, 1990); its population fluctuation (Su *et al*., 1985; Ho and Chen, 1992); sampling plans and spatial distribution, population ecology and control (Kawai, 1983, 1986b, c, 1988, 1995; Kawai and Kitamura, 1987, 1990), as well as its susceptibility to insecticides (Hsu *et al*., 2002). Studies on the life table parameters of *T. palmi* at different temperatures and on various host plant have been reported in the past (Kawai, 1985; Tsai *et al*., 1995), but they focused on the intrinsic rate of increase (r), the net reproductive rate (R_0), and the mean generation time (T). This article will take into account the variations in developmental rate among individuals and between the sexes to analyze the data and to compare the life table parameters of *T. palmi* at four temperatures, including r, R_0, T, the gross reproduction rate (GRR), and the reproductive value. In addition we tried to determine the proper management strategy for *T. palmi* control in the field based on the life table data.

Materials and Methods

Eggplant (*Solanum melongena* L.) seedling culture

To obtain clean insect-free leaves, seedlings from seeds of the eggplant were cultured in a walk-in growth chamber equipped with fluorescent plant growth light (GRO-LUX® , Sylvania, USA), set at 27 ± 1°C, 16L:8D and 70-85% RH (Huang and Su, 1997).

Collection of life history data

For the life table study, *T. palmi* were collected from an eggplant field in Ershuei Township, Changhua County in central Taiwan. The eggplant leaves were cut into small pieces (1.5 × 1.5 cm) and placed in a glass vial (1.6 cm in diameter × 4.5 cm high), and then the 2nd-instar larvae were put into the vial. The vial was sealed with two layers of Parafilm® (Bemis Company Inc.). Once the adults emerged they were immediately removed and placed into a new set of rearing vials, three pairs per vial, for feeding and oviposition. The new leaf-slices were carefully examined by a stereomicroscope on dark field to verify that the leaf tissue was egg-free before being used. During oviposition, the leaf-slices were removed daily to examine and count the number of eggs on the leaf tissue using a stereomicroscope on dark field. The leaf-slices that contained eggs were then placed in a petri dish with hydro-polymeracrylate (SuperSorb-F, Aquatrols Co.) to maintain moisture (Huang and Su, 1997).The newly hatched larvae were then individually placed in a vial for daily observation. The cohort life history data was recorded. Once the adults emerged, a female and a male were paired and placed into an individual rearing vial for oviposition. The leaf-slice was renewed daily. Since the eggs of thrips are pale white or semi-transparent, the leaf-slices that were kept at 15 and 21°C were checked on the 14th day and those that were kept at 25 and 30°C were checked on the 7th day, in order to reduce any counting errors. The leaves were then immersed in 1% fuchsin solution at 4°C for 4-5 days, and then inspected again using a stereomicroscope. These dyed eggs were regarded as infertile. This experiment was performed for three consecutive generations at four temperatures (15, 21, 25, 30°C) with a 16L:8D photoperiod and 65-75% RH. At least 30 eggs were observed in each generation. However, as the vials were not sealed with parafilm tight, some larvae escaped from the vials during the experiments, only 77 individuals at 25°C could complete the life history.

Life table analysis

We used the age-stage, two sexes life table theory (Chi and Liu, 1985; Chi, 1988) to analyze the life table data and the estimated standard error of the life table parameters by the Jackknife method (Sokal and Rohlf, 1995) using computer

program TWOSEX-MSChart (Chi, 2005). The age-stage specific survival rate (s_{xj}) and the age-stage-specific fecundity (f_{xj}) where x is the age in days and j is the stage, including egg, first larval stage, second larval stage, pupal stage, female and male.

The intrinsic rate of increase, r, was estimated using the Euler-Lotka formula (Lotka, 1922) $\sum e^{-r(x+1)} l_x m_x = 1$ with age x indexed from zero (Goodman, 1982). The age-specific survival rate (l_x), and the age-specific fecundity (m_x) were calculated as

$$l_x = \sum_{j=1}^{m} s_{xj}$$

and

$$m_x = \frac{\sum_{j=1}^{m} s_{xj} f_{xj}}{\sum_{j=1}^{m} s_{xj}}$$

where m is the number of stages. The gross reproduction rate (GRR) is the sum of m_x. The net reproductive rate, R_0, is given by $R_0 = \sum l_x m_x$; the mean generation time, T, in days, is given by $T = \frac{\ln R_0}{r}$; the finite rate of increase, λ, is given by $\lambda = e^r$. Since $t \rightarrow \infty$, the age-stage structure will trend to steady and the stable stage distribution can be derived from $N_{t+1} = \lambda N_t$ (Chi and Liu, 1985; Yu *et al.*, 2005). These parameters were obtained from the computer program, TWOSEX-MSChart, for the age-stage, two-sex life table analysis (Chi, 2005).

Results

Age-stage specific survival rate and stable stage distribution

The age-stage specific survival rate (s_{xj}) of *T. palmi* at four constant temperatures is shown in Fig. 1. It indicates that *T.*

palmi has significant stage overlap, and that the survival rate from egg to adult was the highest at 25°C. Adult males at 15, 21 and 25°C had higher survival rates than females but not at 30°C. The trend of the overall survival rate differed at four temperatures (Fig. 2, l_x). At 15°C the survivorship curve was diagonal after age 10 days, characterized by a constant mortality rate for all ages, and the curve was the same as type II of the survivorship curves in Slobodkin (1961). At both 21 and 30°C, the survivorship curve showed a gradual and constant mortality at each age (type III). At 25°C the survivorship curve began as type III, indicating an optimal condition for the first half-life (more than 60% survival rate to age 20-days), and then declined sharply like type I.

The stable stage distribution of *T. palmi* at four constant temperatures is shown in Table 1. It shows that the proportion of egg stage was the highest, with more than 50% of the population at 25 and 30°C in the egg stage. The adult stage was the lowest, and the female adult stage was lower than the male one except at 30°C.

Population parameters

The age-stage-specific fecundity (f_{xj}) indicates the average number of eggs deposited daily by a female of age x in stage j. Because only adult females produce eggs, the f_{xj} is shown as f_{x5}. As evidenced by the curve of f_{x5}, the mean pre-oviposition period of a female, including the pre-adult stages became shorter as the temperature increased (34.7, 25.1, 13.5, 11.4 days, at 15, 21, 25 and 30°C, respectively). The age-specific fecundity (m_x) and the daily fecundity were highest at 25°C, and lowest at 15°C. The age-specific maternity ($l_x m_x$) was highest at 25°C, ranging from 1-2 eggs from the 11th to the 21st day (Fig. 2). The reproductive value (v_{xj}) denotes the contribution of individuals at age x and stage j to the future
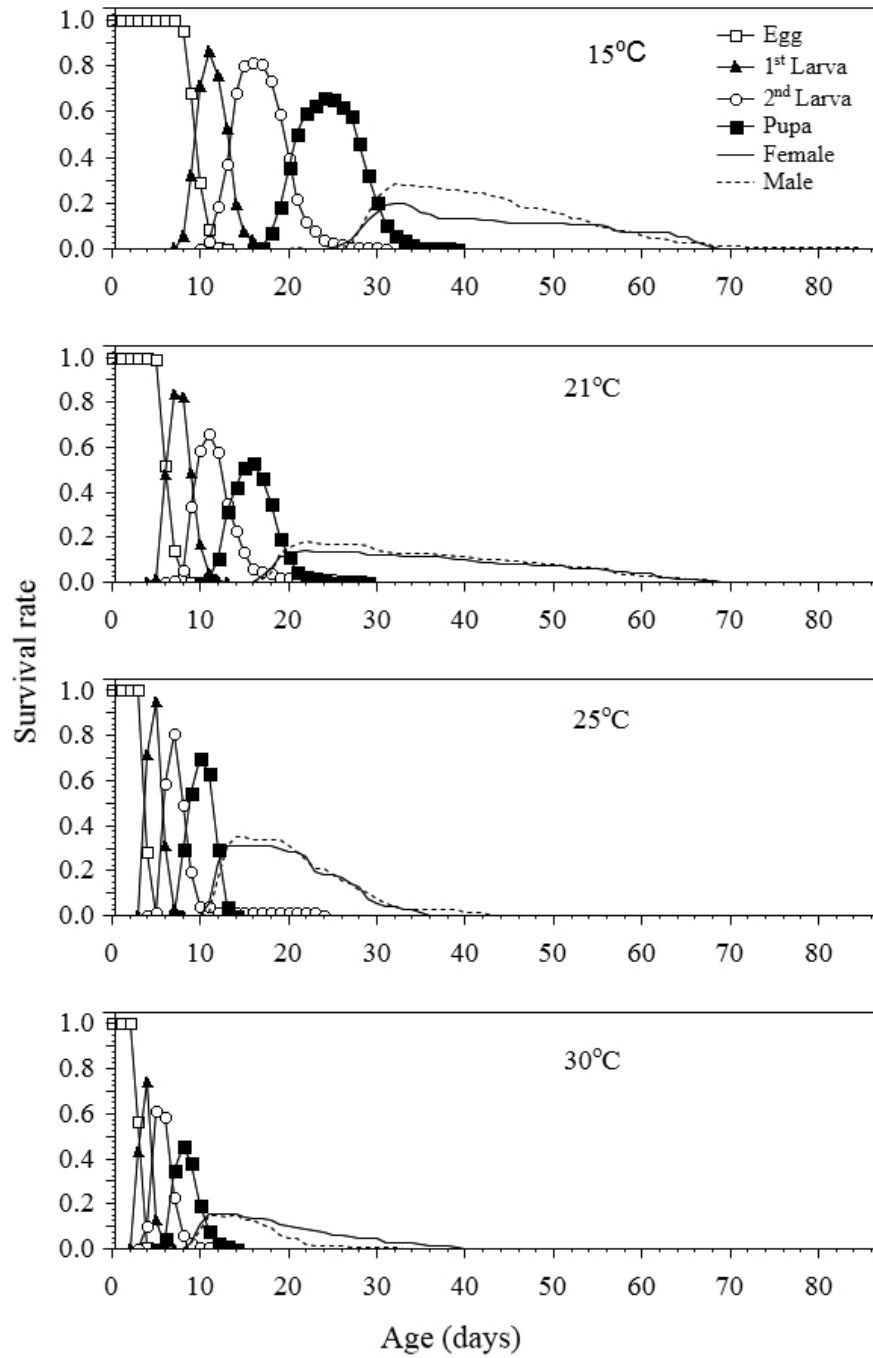
Fig. 1. Age-stage-specific survival rate of *Thrips palmi* at four constant temperatures.

population. The v_{xj} at the four temperatures showed that the peak reproductive values were on about the 36th, 28th, 13th, and 11th day at 15, 21, 25 and 30°C, respectively.
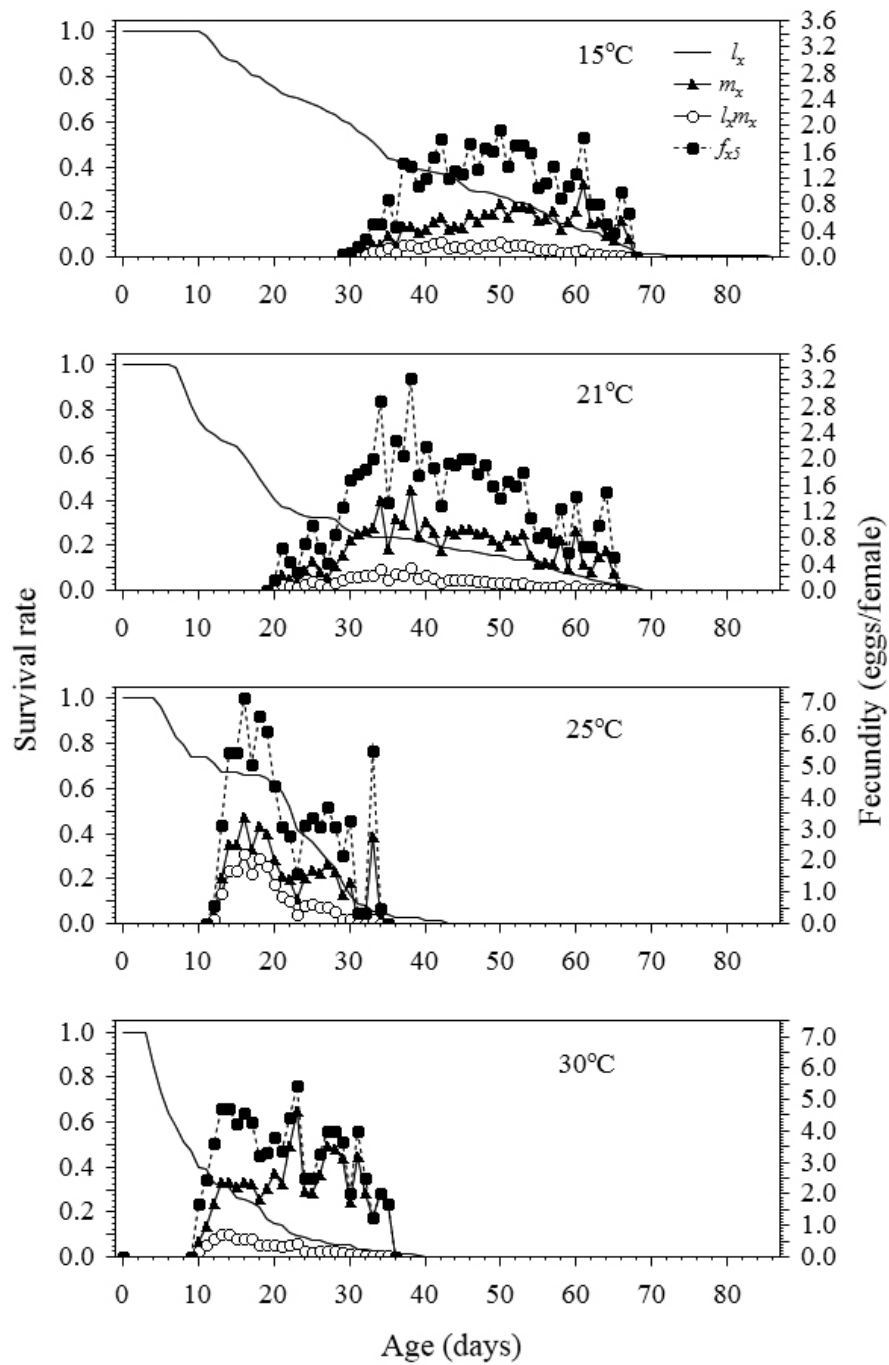
Fig. 2. Age-specific survival rate (l_x), age-specific fecundity (m_x), age-specific maternity ($l_x m_x$), and age-stage specific fecundity of the female adult stage (f_{x5}) of *Thrips palmi* at four constant temperatures.

Table 1. Stable stage distribution (%) of *Thrips plami* on eggplant leaf at four constant temperatures

Temperature (℃)	Egg	1st-instar larva	2nd-instar larva	Pupa	Female	Male
15	42.8	12.0	17.1	13.6	5.8	8.7
21	43.7	15.0	14.1	11.5	7.3	8.4
25	53.4	15.4	12.0	9.0	5.1	5.1
30	51.1	14.2	14.2	10.1	5.9	4.6

The v_{xj} at 25 and 30°C were higher and their peak period shorter than at 15 and 21°C (Fig. 3).

The intrinsic rate of increase (r) rose from 0.033 to 0.046 to 0.157 day^{-1}, and then dropped to 0.118 day^{-1} at 15, 21, 25 and 30°C, respectively. The finite rate of increase (λ) was 1.033, 1.047, 1.170 and 1.125 day^{-1}, respectively. The net reproductive rate (R_0) at 25°C was 18.5 eggs/individual, and was below 10 eggs/individual for the other three temperatures. The *GRR* rose with the increase in temperature. The mean generation time (T) was 46.8, 38.1, 18.6, 17.7 days at 15, 21, 25, 30°C, respectively.

In order to determine the variation in the population parameters, the mean and standard error of $r, \lambda R_0, T$ and *GRR*, were estimated by the Jackknife method, as shown in Table 2. The variation of r, R_0 and T at 25°C were lower than at the other three temperatures.

Discussion

Since the development rate varies among individuals, the stage overlap is significant at the same age-day. We used Chi's TWOSEX-MSChart computer program (Chi, 2005) for calculating the life table parameters for *T. palmi* , because it takes the variation in development rate among individuals into consideration. The results of the age-stage-specific survival curve, the extent of the stage overlapping and the survival rate each age and stage (Fig. 1) demonstrated indeed that the development rate among individuals is variation, so we used the age-stage, two

sexes life table theory (Chi and Liu, 1985; Chi, 1988) to analyze. However, the paper from Tsai *et al*. (1995) only provided the survival rate of the larvae and pupae using age-specific survivorship, and thus they could not fully interpret the dimension of the development of *T. palmi*.

At 15°C the age-specific survival rate (l_x) gradually declines linearly, while at 21°C and 30°C it first decreases sharply and then gradually, and is optimal at 25°C as demonstrated by its sharp drop at about 0.6 before peak reproduction (Fig. 2). The survivorship curve of *T. palmi* at 15, 21, 25, and 30°C was similar to that of Slobodkin's type II and III, showing that the major mortality of *T. palmi* occurs in the early ages and stages (Slobodkin, 1961). The area of the $l_x m_x$ curve at 25°C was the largest, and showed that 25°C was optimal for both the development and reproduction of *T. palmi*. Consequently, the intrinsic rate of increase at 25°C was the highest (Table 2). At 30°C females laid eggs 2 days earlier than at 25°C, and the gross reproductive rate (60.5 eggs) was also higher than at 25°C (37.8 eggs), but the l_x at 30°C was significantly lower than at 25°C. As a result, the R_0 at 30°C was 50% less than that at 25°C. These results confirm that in the first couple of days of adult life the intrinsic rate of increase was determined to a much greater extent by the rate of oviposition than by the total number of eggs laid in the life span of the adults (Birch, 1948; Cole, 1954).

Compared to the existing data, our results, notably, r (0.157 day^{-1}) and R_0 (18.5 eggs) at 25°C in were higher than those reported by Kawai's (1986a) 0.102
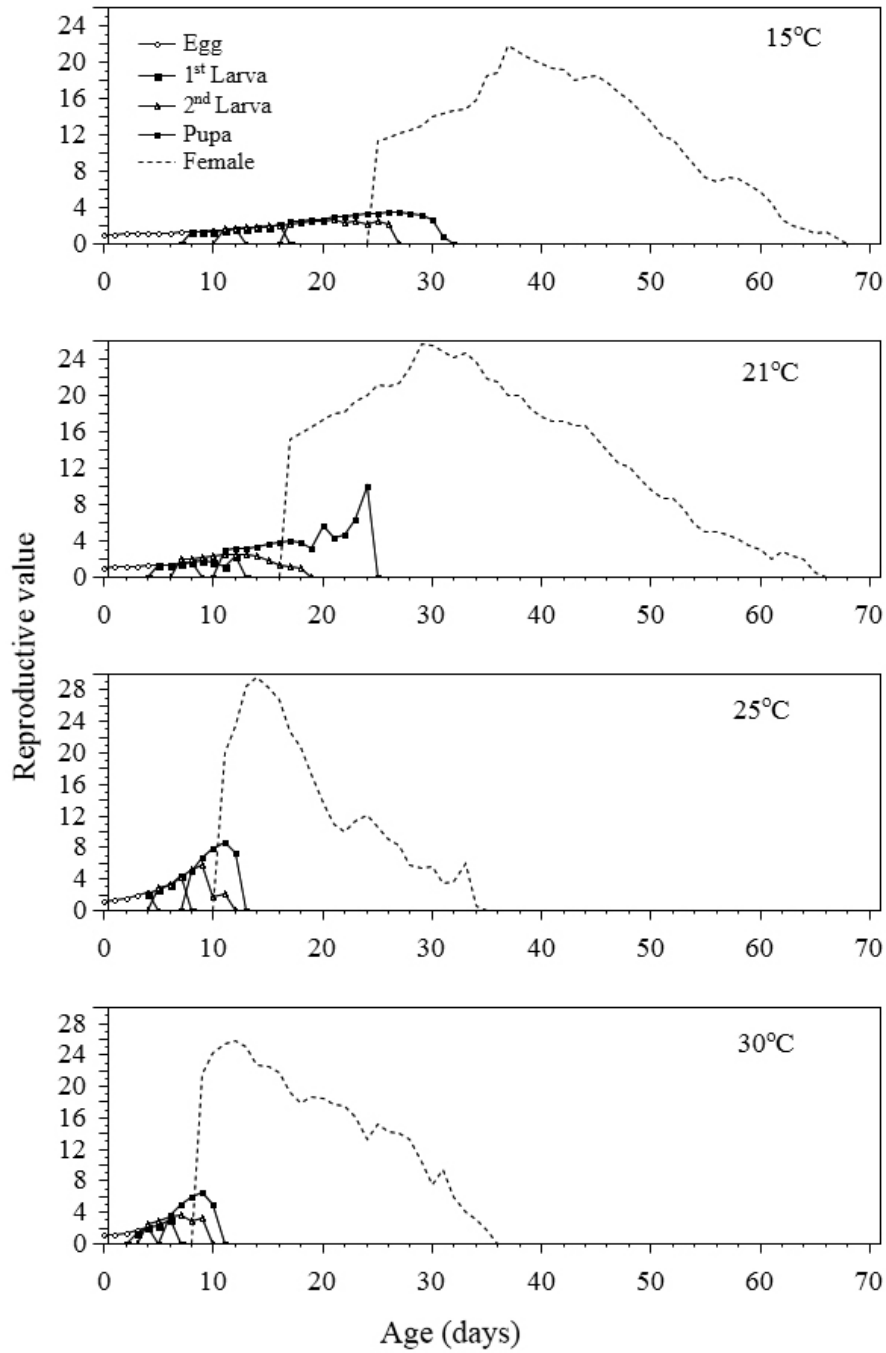
Fig. 3.   Age-stage reproductive value (v_{xj}) of *Thrips palmi* at four constant temperatures.

day^{-1} and 13.3 eggs, respectively, and 0.094 day^{-1} and 15.5 eggs at 26°C by Tsai *et al.* (1995). However, our T (18.6 days) was lower than Kawai's (25.4 days) and Tsai's (29.1 days). Because the 95% confidence intervals of *r*, R_0 and *T* at 25°C estimated

Table 2. Life table parameters[1] of *Thrips palmi* on eggplant leaf at four constant temperatures

Temperature (℃)	n	Pooled data					Jackknife estimates				
		r	λ	R_0	T	GRR	r	λ	R_0	T	GRR
		(1/day)	(1/day)	(eggs)	(days)	(eggs)	(1/day)	(1/day)	(eggs)	(days)	(eggs)
15	158	0.033	1.033	4.6	46.8	18.4	0.033 (0.005)[2]	1.034 (0.006)	4.6 (1.1)	46.8 (1.1)	18.4 (4.1)
21	159	0.046	1.047	5.7	38.1	30.1	0.046 (0.007)	1.048 (0.008)	5.7 (1.6)	38.2 (1.4)	30.1 (7.7)
25	77	0.157	1.170	18.5	18.6	37.8	0.158 (0.011)	1.171 (0.013)	18.5 (3.5)	18.6 (0.4)	37.8 (8.2)
30	136	0.118	1.125	8.1	17.7	60.5	0.120 (0.015)	1.127 (0.017)	8.1 (2.0)	17.8 (0.63)	60.5 (10.0)

[1] r: Intrinsic rate of increase; λ: Finite rate of increase; R_0: Net reproductive rate; T: Mean generation time; GRR: Gross reproductive. rate

[2] Mean, standard error in parentheses.

by the Jackknife method were 0.136-0.18 day^{-1}, 12.5-24.5 eggs and 17.8-19.4 days, respectively (Table 2), we could say that the r and T in Kawai's and Tsai's papers are significantly different from our present study, but the R_0s were not different from ours. This difference could be due to the method of collecting life history data and the method of counting the eggs laid inside eggplant leaves, resulting in a higher survival rate and reproductive rate in the present study. Moreover, the geographic biotype and the method of the population parameters obtained in the data analysis might be also involved. Viewed from the population parameters, r and R_0 especially, it is apparent that a temperature between 25 and 30°C was optimal for *T. palmi* population growth, as was also demonstrated by Huang and Chen (2004).

The stable stage distribution indicated that immature stages comprised more than 85% of the population, and the egg stage as much as 50% (Table 1). Because the eggs require a longer development time than other stages (Kawai, 1985; Tsai *et al.*, 1995; McDonald *et al.*, 1999; Huang and Chen, 2004), they were adaptively deposited inside leaf tissue to be protected from predation or parasitism by natural enemies, thus increasing the opportunity of *T. palmi* population survival.

The reproductive value (v_{xj}) denotes the contribution an individual age x in stage j makes to the future population (Fisher, 1958), while m_x is the average female offspring produced by a female age x. Therefore, v_{xj} relates to both the adult and the immature stages, while m_x only relates to the adult female stage. The v_{xj} curves showed the same pattern under different temperatures, starting from 1 at newborn and increasing with age and stage to peak when egg-laying commenced, and then gradually declined to zero at the end of adult life (Wilson and Bossert, 1971; Carey, 1993). Fisher (1958) suggested that the reproductive value of a population was highest at the time of dispersal in order to raise the colonizing potential of individuals of new habitats. Our results showed that at 25 and 30°C the v_{xj} values were higher and the peak period shorter than at 15 and 21°C (Fig. 3). The higher v_{xj} at a higher temperature could promote colonists to establish new habitats in summer in Taiwan.

From the point of view of r, R_0, and T, *T. palmi* has the characteristic features of an r-strategist that normally tends to have a small body, strong dispersal ability, a fast growth rate and a short generation time. Conway (1984) argued that r-pests are the most difficult to control, because they frequently invade an area and cause outbreaks. Conway (1984) found that natural enemies cannot provide efficient control for r-pests, and that the timely use of pesticides is the main control for crop protection. This presents a more serious

long-term pesticide resistance problem (Immaraju *et al.*, 1992; Zhao *et al.*, 1995). Although some researchers proposed that the predators, *Orius* spp. could successfully control *T. palmi* for a long period of time (Kawamoto and Kawai, 1988; Nagai, 1990; Kawai, 1995), we believe that it would only work in a protected cultivation or using a mass release method in the fields. Furthermore, a natural enemy would not be appropriate for controlling *T. palmi* which is the vector of a plant virus. *Thrips palmi* larvae acquire the virus but only the adults can transmit it (Moritz *et al.*, 2004). Coincidentally, v_{xj} reaches its peak at adult stage when ready to disperse and colonize. If the viruliferous adult thrips could successfully colonize to a new habitat they might be able to cause a viral epidemic. We therefore suggest that the appropriate management strategy for *T. palmi* in the field is to detect the adult invasion and apply pesticides in time to protect the crop from establishing thrips, and control the second-instar larvae with a proper rotation of insecticides with different modes of action to avoid the thrips from becoming pesticide resistant. It would be best if an area-wide pest management was adopted and the source of metapopulation of *T. palmi* in the fields controlled.

Acknowledgments

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南黃薊馬 (*Thrips palmi* **Karny**) (**Thysanoptera: Thripidae**) 生命表介量及其管理策略

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摘　　要

　　本研究以年齡齡期兩性生命表之理論分析南黃薊馬 (*Thrips palmi* Karny) 以茄葉飼養在 15、21、25、30℃ 四種溫度下之生命表介量。結果顯示，齡別繁殖值 (m_x)、每日繁殖值 (f_{x5}) 及齡別繁殖淨值 ($l_x m_x$) 在 25℃ 下為最高。15、21、25、30℃ 四種溫度的內在增殖率 (r) 分別為 0.033、0.046、0.157 及 0.118 day^{-1}；淨增殖率 (R_0) 以 25℃ 的 18.6 粒卵/雌成蟲為最高。平均世代時間 (T) 隨溫度的升高而遞減，然而 30℃ 僅較 25℃ 少 1 天。本文也以 Jackknife 方法估算內在增殖率、終極增殖率 (λ)、淨增殖率及平均世代時間的平均值及標準機差 (standard error)。本文也利用生命表介量提出南黃薊馬田間管理策略上的建議。

關鍵詞：南黃薊馬、溫度、生命表介量、茄子。

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