## ORIGINAL RESEARCH PAPER

# Temperature-dependent development and life table parameters of *Thrips palmi* (Thysanoptera: Thripidae) on eggplant

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Abstract The life history of *Thrips palmi* Karny on eggplant (Solanum melongena L.) leaves was studied based on the age stage and two sex-life tables at 16, 19, 22, 25, and 31 °C. The intrinsic rate of increase (r) at these temperatures was 0.0427, 0.0566, 0.0979, 0.1738, and 0.2237 day<sup>-1</sup>, respectively. The relationship among the gross reproductive rate (GRR), the net reproductive rate  $(R_0)$ , and the pre-adult survivorship  $(l_a)$  is consistent with  $R_0 < l_a \times GRR < GRR$  for all results at different temperatures. The mean generation time was 47.52, 38.33, 29.52, 19.81, and 13.88 days, respectively. The developments of pre-adult and adult stages were faster in males than in females. The means of developmental periods for each developmental stage decreased with increases of temperature. The maximum life span of female adults was noted at 56.67 days, whereas that of males was 50.66 days at 16 °C. The maximum female fecundity (64.18 eggs/female) was recorded at 25 °C and the lowest (23.38 eggs/female) at 16 °C. Life table data could be used to project population growth, to design mass rearing programs, and to establish management tactics to control insect pests.

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#### Introduction

Thrips palmi Karny, commonly known as melon thrips, is a serious pest of fruited vegetables, legumes, fiber crops, and flower plants in tropical and sub-tropical regions (Cannon et al. 2007). T. palmi quickly develop heavy infestations causing severe damage. Both larvae and adults feed gregariously on leaves, flowers, stems, and fruits. Due to their feeding, oviposition, and virus transmission to eggplant, fruits become scarred, deformed, and aborted (Reitz et al. 2011). These results in damaged eggplant fruits and severe economic losses up to 75 % compared to original nondamaged fruits in Taiwan. In addition to feeding on various economic crops, T. palmi can complete its life history in several weed species (Tsai et al. 1995). Life stages of the T. palmi are egg, two larval instars, two pupal instars, and adult. The adult, egg, and the larval stages are found on the host plants, whereas pupae are found in the soil or among leaf litter. A complete generation may be completed in about 20–30 days. Melon thrips are able to multiply during any season; however, warm weather is most favorable (Chang 1995).

Several studies have been conducted on the effect of temperature on the development of *T. palmi* (Nonaka et al. 1982; Tsai et al. 1995; McDonald et al. 1999; Park et al. 2010). However, many of these studies and reviews have been reported in languages such as Japanese (e.g., Kawai 1985; Koyama and Matsui 1992) and Chinese (e.g., Huang and Chen 2004; Wang and Chu 1986), limiting the use of published information. Furthermore, many published reports on life table analysis of *T. palmi* focused only on



female populations, although both males and females are economically important. In addition, there are differences in the development rate of male and female populations of T. palmi. Moreover, the effectiveness of various chemical or biological control agents to control melon thrips might differ depending on their growth stages and sexes. A life table study explains the development, survival, and fecundity of a cohort and provides basic data on population growth parameters. Yu et al. (2005) explained the relationship among gross reproductive rate, net reproductive rate, and pre-adult survivorship. Successful control of T. palmi requires a basic demographic study of the life history, age-stage-specific survivorship, and rate of population growth in a specific crop at different climatic conditions. Therefore, temperature-dependent development and life table parameters at different temperatures are fundamental and crucial for ecologically based pest management of T. palmi in Taiwan. For a complete understanding of the development and reproduction of T. palmi on eggplant, we collected its life history data at five different temperatures and analyzed them using age stage and two sex life tables.

#### Materials and methods

The experiment was conducted from February 2011 to January 2012 at the Department of Plant Medicine's laboratory, National Pingtung University of Science and Technology (NPUST), Taiwan.

# Eggplant transplantation

Eggplant seedlings were transplanted in plastic pots (12 cm diameter) with pores underneath. The seedlings were grown in greenhouse conditions under fine net cages ( $90 \times 90 \times 100$  cm) to prevent infestation from other insects.

#### Insect collection

Leaves containing T. palmi males and females were collected from a farmer's field in Pingtung county, southern Taiwan. By using a dissecting microscope  $(20\times)$ , pairs of males and females were identified from infested leaves. With the help of a fine camel hair brush, a male and female pair was transferred to 1-month-old eggplant seedlings. A total of ten pairs of T. palmi were transferred to ten seedlings for each temperature study. The seedlings containing T. palmi males and females were placed in glass cages  $(36 \times 20 \times 20 \text{ cm})$  and were reared for 6 h at 25-28 °C, 70-80 % RH, and a photoperiod of 12:12 (L:D) h for the purpose of egg laying.



All the egg-bearing leaves were removed from the plants, cut into pieces  $(2 \times 2 \text{ cm})$ , and placed in petri dishes (9 cm diameter) with the bottom covered by water-soaked filter paper to prevent desiccation of eggs and leaflets (Park et al. 2010). The petri dishes were placed in a growth chamber at 16, 19, 22, 25, and 31 °C, 70–80 % RH, and a photoperiod of 12:12 (L:D) h. The egg development period was determined by the appearance of larva; however, egg mortality could not be determined. After the emergence of the first instar larvae, the experiment was continued for larva rearing with the same conditions.

## Larva rearing

By using a fine camel hair brush and a dissecting microscope, a single larva was placed in each petri dish (9 cm diameter) containing eggplant leaf  $(2 \times 2 \text{ cm})$ . The petri dish was sealed with parafilm (Park et al. 2010) and placed in growth chamber. A total of 120, 80, 80, 80, and 130 larvae of first instars were studied at 16, 19, 22, 25, and 31 °C, respectively. The growth chamber was maintained at 70-80 % RH and a photoperiod of 12:12 (L:D) h at all temperatures. Moist cotton was placed in each petri dish for maintaining sufficient moisture. Leaves were transferred every alternate day. Observations were made every 24 h. During the observation the larvae that developed minute wing pads were transferred for pre-pupa and pupa rearing at the same conditions. Development duration and survival of first and second instar larvae were recorded daily.

## Pupae rearing

Pre-pupae were transferred individually to petri dishes containing fresh leaves ( $2 \times 2$  cm) and were monitored for development. Pupal stages were observed as pre-pupae and pupae at all temperatures except 31 °C. Because of the fastest development at 31 °C and data recording period every 24 h, we studied total pupa duration only. When newborn adults were noted during the observation, their sexes were identified, and they were used for rearing adults.

## Adult rearing

After emergence of new born adults, each male and female pair of T. palmi was placed separately on eggplant leaves  $(2 \times 2 \text{ cm})$  in a petri dish (9 cm) diameter) containing moist filter paper. The petri dishes were placed in growth chamber for egg laying at 16, 19, 22, 25, and 31 °C, 70–80 % RH, and 12:12 (L:D) h. The leaves with laid eggs



were replaced daily by new leaves until the female adult died. The leaves with laid eggs were again placed for egg development study at the same temperature conditions as for adult rearing. The egg development period was determined by the emergence of larvae. The larvae that emerged from the egg development study were again used continuously for pupae and adult rearing in the same conditions. Fecundity and survival were recorded daily until the death of each female at every temperature. Longevity of male and female adults was measured at all temperatures condition.

# Identification of stages and sexes

Identification of *T. palmi*, their stages, and sex differentiation was done on the basis of morphological characters reported by different authors (OEPP/EPPO 2001) at the Department of Plant Medicine, NPUST, Taiwan.

#### Life table parameters

The life history data of all individuals at different temperatures were analyzed using the age-stage, two-sex life table approach (Chi and Liu 1985; Chi 1988). The agestage-specific survival rate  $(S_{xi})$ , age-stage-specific fecundity  $(f_{xi})$ , age-specific survival rate  $(l_x)$ , and age-specific fecundity  $(m_x)$  were measured. The intrinsic rate of increase (r), the finite rate of increase  $(\lambda)$ , net reproduction rate  $(R_0)$ , and the mean generation time (T) were calculated. The intrinsic rate of increase was estimated using the iterative bisection method from  $\sum_{x=0}^{\infty} e^{-r(x+1)} l_x \times m_x = 1$ with age indexed from 0 (Goodman 1982). The mean generation time is defined as the length of time that a population needs to increase  $R_0$  fold of its size (i.e.,  $e^{rt} = R_0$  or  $\lambda^T = R_0$ ) at stable age distribution. The mean generation time was calculated as  $T = lnR_0/r$ . The cumulative reproductive rate to age x was calculated as  $R_x = \sum_{i=0}^x l_i \times m_i$ . The gross reproductive rate (GRR) was calculated as  $\sum m_x$ . The age-stage life expectancy is the time that an individual of age x and stage j is expected to live. The life expectancy for an individual of age x and stage y was calculated as  $e_{xy} = \sum_{i=x}^{n} \sum_{j=y}^{m} S_{ij}$ , where n is the number of age groups and m is the number of stages.  $S_{ii}$ is the probability that an individual of age x and stage y will survive to age i, and stage j and is calculated by assuming  $S_{xy} = 1$  (Chi and Liu 1985; Chi 1988).

The curtailed intrinsic rate of increase is the effect of longevity and fecundity on the intrinsic rates of *T. palmi*. The curtailed intrinsic rate  $r(\delta)$  is defined as the solution of  $\sum_{x=0}^{\delta} e^{-r(x+1)} l_x \times m_x = 1 \text{ where } r(\delta) \text{ is the intrinsic rate of the population by assuming that it survives only to age <math>\delta$  and discarding all  $l_x$  and  $m_x$  beyond age  $\delta$ . The  $r(\delta)$  gives

the actual intrinsic rate of a population surviving only to age  $\delta$ . The cumulative contribution  $(r_y)$  of age y was calculated as  $r_y = r \times \sum_{x=0}^y e^{-r(x+1)} l_x \times m_x$ . The cumulative contribution of  $r_y$  is not an intrinsic rate; however, it describes the cumulative input of individuals surviving to age y to the intrinsic rate r. The relationship between the net reproductive rates  $(R_0)$  and the mean female fecundity (F) was determined by using formula as  $R_0 = F \times (N_f/N)$ , 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 that emerged (Chi 1988).

#### Results and discussion

In this study, T. palmi completed development and produced offspring on eggplant leaves at all temperatures tested. The means of developmental periods for each developmental stage decreased with increases of temperature (Table 1). The developments of various stages were observed faster in males than females at all temperatures. The mean life span of female adults ranged from 18.68 to 56.67 days and that of males ranged from 15.48 to 50.66 days. The mean of female pre-adult duration ranged from 9.76 to 35.85 days and that of male 9.17 to 35.44 days. According to Park et al. (2010), pre-adult durations of T. palmi at different temperatures on cucumber leaf were 40.8, 20.5, 12.7, and 9.8 days at 15, 20, 25, and 30 °C, respectively. However, Tsai et al. (1995) documented longer pre-adult durations of 43.3, 16.4, and 10.9 days at 15, 26, and 32 °C on eggplant. According to Huang and Chen (2004), pre-adult durations of T. palmi at 15, 21, 25, and 30 °C were 29.9, 19.6, 12.3, and 10.4 days, respectively. Our results of pre-adult durations are higher than those of Huang and Chen (2004) and lower than those of Park et al. (2010) and Tsai et al. (1995). These differences are due to differences in the host plant, temperature, and two-sex life table principle.

The adult pre-oviposition period (APOP) and total pre-oviposition period (TPOP) are listed in Table 1. The APOP of females ignores the length of the pre-adult stage. The TPOP is the time interval from the birth of a female individual to its first oviposition day. The mean of APOP decreased from 8.26 days at 16 °C to 1.8 days at 31 °C, and that of TPOP decreased from 44.1 days at 16 °C to 11.56 days at 31 °C. This finding shows that *T. palmi* can quickly build up its population at high temperatures compared to low temperature. This finding is supported by Huang and Chen (2004). They recorded 7.1, 6.8, 2, and 2.3 days of APOP at 15, 21, 25, and 30 °C.

The age-stage-specific survival rate  $(S_{xj})$  of T. palmi at different temperatures (Fig. 1) showed the probability that



**Fable 1** Means and standard errors (in parentheses) of the developmental time, longevity, adult pre-oviposition period, total pre-oviposition period, and fecundity of T. palmi at different emperatures

Statistics	Temperatures (°C)	(°C)								
	16		19		22		25		31	
	Н	M	ц	M	Н	M	Н	M	Н	M
E duration (days)	12.67 (0.12)	12.50 (0.13)	10.16 (0.09)	9.90 (0.14)	6.24 (0.12)	5.94 (0.17)	5.08 (0.08)	4.92 (0.08)	3.19 (0.05)	2.97 (0.12)
L <sub>1</sub> duration (days)	4.26 (0.07)	4.22 (0.07)	3.52 (0.10)	3.48 (0.11)	3.09 (0.10)	3.12 (0.12)	1.79 (0.08)	1.58 (0.1)	1.12 (0.04)	1.03 (0.03)
L <sub>2</sub> duration (days)	7.90 (0.14)	7.84 (0.10)	5.80 (0.10)	5.38 (0.13)	4.47 (0.11)	4.12 (0.12)	3.54 (0.09)	3.42 (0.12)	2.24 (0.06)	2.10 (0.06)
P <sub>1</sub> duration (days)	3.92 (0.09)	3.84 (0.09)	3.32 (0.11)	3.19 (0.13)	2.24 (0.07)	2.25 (0.11)	1.18 (0.06)	1.00 (0.00)	3.22 (0.06)	3.07 (0.10)
P <sub>2</sub> duration (days)	7.10 (0.11)	7.03 (0.11)	4.44 (0.14)	4.38 (0.13)	3.50 (0.09)	3.31 (0.12)	3.05 (0.07)	2.92 (0.08)		
Pa duration (days)	35.85 (0.25)	35.44 (0.24)	27.24 (0.31)	26.33 (0.22)	19.53 (0.20)	18.75 (0.34)	14.64 (0.81)	13.83 (0.21)	9.76 (0.10)	9.17 (0.17)
Adult duration (days)	20.82 (0.36)	15.22 (0.39)	19.36 (0.24)	16.14 (0.29)	19.26 (0.34)	15.88 (0.42)	17.13 (0.26)	11.46 (0.35)	8.92 (0.22)	6.31 (0.27)
Mean longevity (days)	56.67 (0.44)	50.66 (0.39)	46.6 (0.36)	42.48 (0.38)	38.79 (0.36)	34.62 (0.57)	31.77 (0.23)	25.29 (0.41)	18.68 (0.23)	15.48 (0.34)
APOP (days)	8.26 (0.13)	0	7.28 (0.14)	0	5.85 (0.10)	0	2.15 (0.10)	0	1.80 (0.06)	0
TPOP (days)	44.10 (0.27)	0	34.52 (0.29)	0	25.38 (0.25)	0	16.79 (0.17)	0	11.56 (0.12)	0
Fecundity (eggs/female)	23.38 (0.53)	0	27.96 (0.71)	0	42.32 (0.99)	0	64.18 (1.30)	0	49.14 (0.59)	0

E egg, L<sub>I</sub> first instar larva, L<sub>2</sub> second instar larva, P<sub>I</sub> pre-pupa, P<sub>2</sub> pupa, Pa pre-adult, APOP adult pre-oviposition period, TPOP total pre-oviposition period, F female, M male

survival rate of first instar larvae (0.98), second instar larvae (0.93), pre-pupae (0.86), and pupae (0.78) were recorded at 25 °C, whereas above or below this temperature the survival rate of all stages was found in declining order. This highest value for survival rate at 25 °C is supported by Huang and Chen (2004). The second instar larval survival rate ranged from 0.76 to 0.93, whereas pupal survival ranged from 0.59 to 0.78 at different temperatures. The curve  $S_{xi}$  describes the probability that an individual at age i and stage j growing to age i + 1 but remaining in stage j after one age interval (the age-stage-specific growth rate,  $g_{ij}$ ), and the probability of developing to stage j + 1and be in age i + 1 after one age interval (the age-stagespecific development rate,  $d_{ij}$ ). Due to variable development rates among individuals, significant overleaping between stages can be observed. According to Chi (1988), if survival curves are constructed based on the means of each stage, the stage overlap would not be observed, and it would result in errors in the survival curves. This error is due to differences in the sum of the means of the pre-adult stage and the mean of the total pre-adult development period for all individuals. The maximum female fecundity (64.18 eggs/female) of

a newborn will survive to age x and stage i. The maximum

T. palmi was recorded at 25 °C and that of the lowest (23.38 eggs/female) at 16 °C (Table 1). These values are slightly higher than the values found by Huang and Chen (2004). Mean fecundity of T. palmi was influenced by temperature. The age-stage-specific fecundity  $(f_{xj})$  is the number of offspring produced by individual T. palmi of age i and stage j per day (Fig 2). Since only females produce offspring, there is only a single curve f (i, female). At 16 °C, oviposition was very low; however, 69 % of T. palmi survived longer than 1 month, and 40 % survived longer than 50 days. This survivorship is sufficient for T. palmi to survive the short, mild winter in Taiwan. The age-specific survival rate  $(l_x)$ , age-specific fecundity  $(m_x)$ , and age-specific maternity  $(l_x \times m_x)$  show that T. palmi can successfully survive and reproduce in the range of 16-31 °C. This is one of the main contributing reasons that T. palmi is so successful as a major agricultural pest in Taiwan. The maximum of the cumulative reproductive rate  $(R_x = \sum_{i=0}^x l_i \times m_i)$  is the net reproductive rate  $(R_0)$ at that temperature. The maximum cumulative reproductive rate was recorded at 31.29 at 25 °C after 24 days and the lowest 7.6 at 16 °C after 55 days (Fig. 2). Chi (1988) discussed that if the fecundity curves are constructed based on the adult stages, it will be different from  $m_x$  in Fig. 2.

The population parameters calculated by using the agestage, two-sex life tables for *T. palmi* are listed in Table 2. The lowest intrinsic rate of increase (r = 0.0427) and the finite rate of increase ( $\lambda = 1.0436 \text{ day}^{-1}$ ) are accompanied



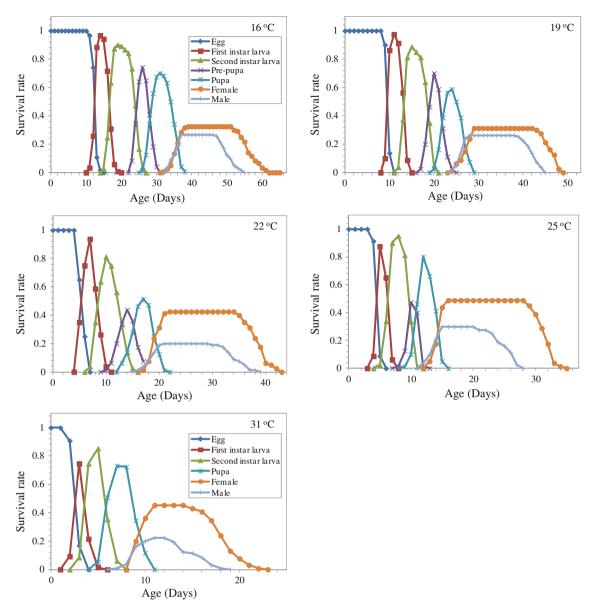


Fig. 1 Age-stage-specific survival rate  $(S_{xj})$  of T. palmi on eggplant at different temperatures (legends for 16, 19, 22, and 25 °C are the same)

by a long mean generation time (T=47.52 days), and low net reproductive rate ( $R_0=7.6$  offspring/individual) at 16 °C. These results at 16 °C showed that if the population reaches the stable age-stage distribution and if there are no mortality factors other than physiological ones, T. palmi populations can multiply 1.0436 times per day for an average of 47.52 days with an exponential rate of 0.0427 day $^{-1}$ . The maximum of female fecundity, net reproductive rate, and gross reproductive rate was recorded at 25 °C; however, the maximum intrinsic rate (0.2237 day $^{-1}$ ) was recorded at 31 °C. This is due to the longer mean generation time (19.81 days) at 25 °C than at 31 °C (13.88 days). Table 2 also shows that when the temperature increased from 16 to 31 °C, the mean

generation time became shorter and the population increase rate became higher. The maximum finite rate of increase (1.25) was recorded at 31 °C. Tsai et al. (1995) reported an intrinsic rate of 0.039, 0.094, and 0.153 day<sup>-1</sup> at 15, 26, and 32 °C in eggplant leaf. According to Kawai (1990), the intrinsic rates of *T. palmi* in cucumber leaves were 0.035, 0.080, 0.134, and 0.144 day<sup>-1</sup> at 15, 20, 25, and 30 °C. These differences may be due to consideration of both male and female populations in the two sex-life tables, differences in female fecundity, and variation in survival rates of immature insects and dissimilar temperatures.

Chi (1988) elucidated the relationship between the net reproductive rates and the mean female fecundity in two sex-life tables by using



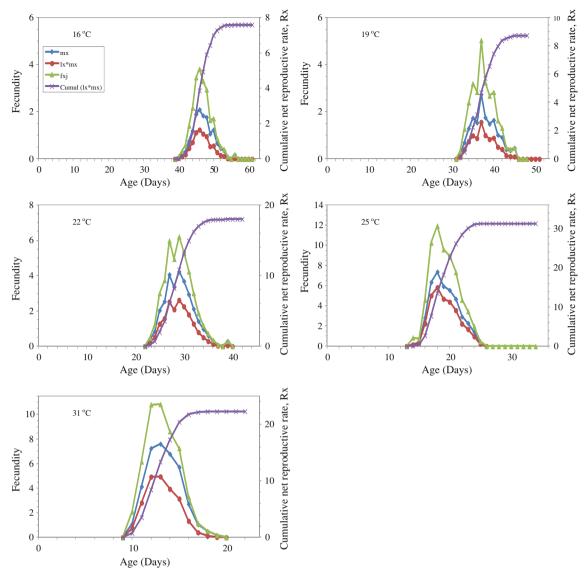


Fig. 2 Age-stage-specific fecundity  $(f_{xj})$ , age-specific fecundity  $(m_x)$ , age-specific maternity  $(l_x \times m_x)$ , and cumulative net reproduction rate  $(R_x)$  of T. palmi on eggplant at different temperatures

$$R_0 = F \times (N_f/N) \tag{1}$$

In our study N was 130 for 31 °C, 120 for 16 °C, and 80 for all other temperatures, whereas  $N_f$  was 39, 25, 34, 39, and 59 for 16, 19, 22, 25, and 31 °C, respectively. Our finding of  $R_0$  and F are consistent with the relationship of Eq. (1). Yu et al. (2005) proved the relationship among GRR, pre-adult survivorship ( $l_a$ ), and net reproductive rate ( $R_0$ ) as  $R_0 < l_a \times \text{GRR} < \text{GRR}$ . For example, at 31 °C,  $R_0$  is 22.3,  $l_a$  is 0.68, and GRR is 37.07 (Table 2). Thus, the relationship 22.3 < 0.68 × 37.07 < 37.07 is consistent. All of our results at different temperatures are consistent with this relationship. Chi (1988) explained the difference between traditional female-based age-specific life tables and age-stage two-sex life tables, and indicated

possible errors in the survival and fecundity curves based on the adult age.

The age-stage-specific life expectancy  $(e_{xj})$  of T. palmi is reported in Fig. 3. The life expectancy gives the life span that an individual of age x and stage j is expected to live at different temperatures. The life expectancy of newborns is 42.45, 33.94, 27.81, 25.36, and 14.18 days at 16, 19, 22, 25, and 31 °C, respectively. Figure 3 shows that age-stage 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 16 °C female adults aged 15 days will live on average another 10.67 days, whereas a male adult of age 15 days



**Table 2** Means and standard errors (in parentheses) of the intrinsic rate of increase (r), gross reproductive rate (GRR), net reproductive rate  $(R_0)$ , mean generation time (T), finite rate of increase  $(\lambda)$ , life

expectancy of new born  $(e_{01})$ , and pre-adult survivorship  $(l_a)$  of T. palmi at different temperatures

Population parameters	Temperatures (°C)					
	16	19	22	25	31	
$r (day^{-1})$	0.0427 (0.00)	0.0566 (0.00)	0.0979 (0.00)	0.1738 (0.01)	0.2237 (0.00)	
GRR (offspring/individual)	14.2 (1.42)	16.27 (2.09)	29.82 (2.84)	40.38 (4.00)	37.07 (2.38)	
$R_0$ (offspring/individual)	7.6 (1.02)	8.74 (1.47)	17.99 (2.39)	31.29 (3.66)	22.3 (2.17)	
T (days)	47.52 (0.27)	38.33 (0.33)	29.52 (0.24)	19.81 (0.15)	13.88 (0.12)	
$\lambda  (\mathrm{day}^{-1})$	1.0436 (0.00)	1.0582 (0.01)	1.1028 (0.01)	1.1898 (0.01)	1.2508 (0.01)	
$e_{01}$ (days)	42.45 (1.36)	33.94 (1.47)	27.81 (1.44)	25.36 (0.93)	14.18 (0.48)	
$l_{ m a}$	0.59	0.57	0.62	0.80	0.68	

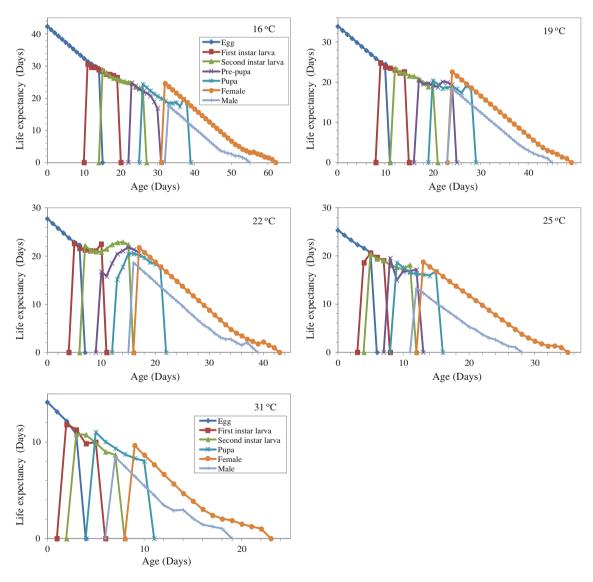


Fig. 3 Age-stage-specific life expectancy  $(e_{xj})$  of T. palmi on eggplant at different temperatures (legends of 16, 19, 22, and 25 °C are the same)



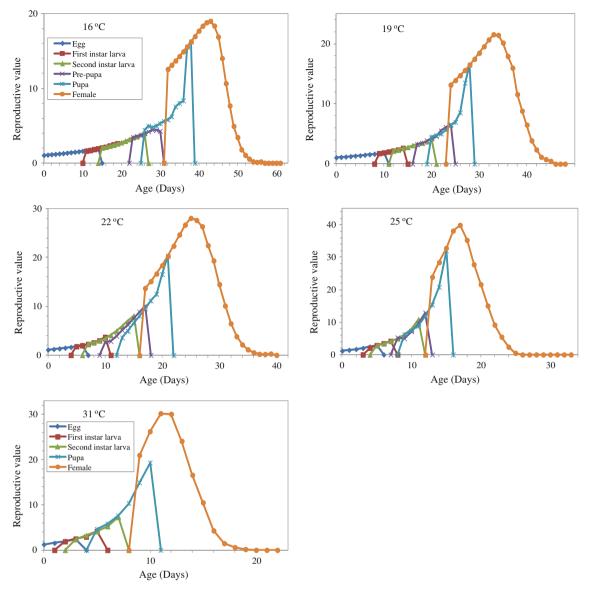


Fig. 4 Age-stage-specific reproductive value  $(V_{xj})$  of T. palmi on eggplant at different temperatures (legends of 16, 19, 22, and 25 °C are the same)

will live on average another 4.66 days (Fig. 3). The life expectancy based on age-stage, two-sex life tables distinguishes the difference among individuals of the same age but of different stages or different sexes.

Fisher (1930) explained the reproductive value as the contribution of an individual to the future population. The age-stage reproductive value  $(v_{xj})$  of T. palmi illustrates the contribution of an individual to age x and stage j to the future population (Fig. 4). The reproductive value significantly increases when female adults emerge. In our study, at 25 °C females started to emerge at 13 days and began to produce offspring (Fig. 2). The corresponding reproductive values increased sharply to 39.89 in 17 days at 25 °C (Fig. 4). The reproductive value of a newborn  $(v_{01})$  is

exactly the finite rate of increase. However, if older adults no longer produce offspring, the reproductive value becomes zero. In our study, the survival curve of *T. palmi* females at 25 °C ended at age 35 days (Fig. 1); however, the fecundity curve stopped at 26 days (Fig. 4).

The curtailed intrinsic rate of increase at different temperatures is shown in Fig. 5. The curtailed intrinsic rate of increase  $(r_{\delta})$  at different temperatures gives the actual intrinsic rate of a population surviving only to age  $\delta$ . The curve of the cumulative contribution of  $r_y$  in Fig. 5 is not an intrinsic rate but a descriptive value of the cumulative input of individuals surviving to age y to the intrinsic rate r. For example, at 25 °C all  $m_x$  are zeros before age 14 days, and the curves of  $r_{\delta}$  and  $r_y$  start at age 14 days.



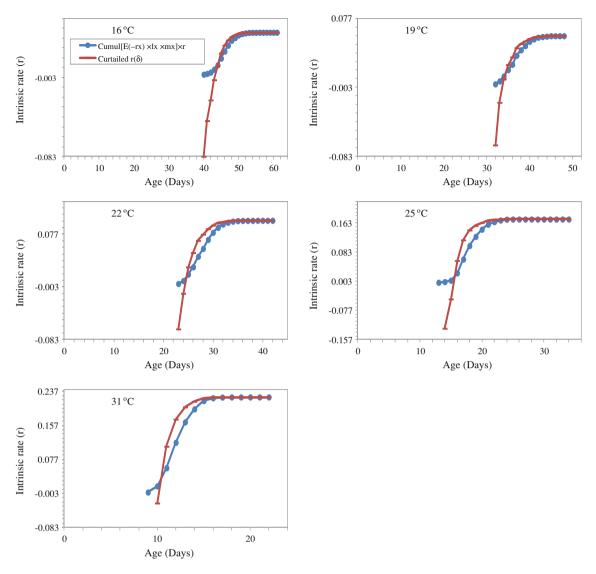


Fig. 5 Cumulative contribution to intrinsic rate of increase (Cumul $[E(-rx) \times l_x \times m_x] \times r$ ) and curtailed intrinsic rate of increase  $[r(\delta)]$  of T. palmi at different temperatures

In Fig. 5 at 25 °C, the  $r_y$  of T. palmi of age 14 days and age 15 days does contribute to the intrinsic rate of increase positively. However, the curve  $r_\delta$  shows that, if the population survives only to age 14–15 days, the intrinsic rate will be negative and the population will decrease. Therefore, the curtailed intrinsic rate at different temperatures is useful for describing the effect of the reduction of survivorship on the intrinsic rate of increase. In our study, we found that different age groups of T. palmi females contributed different weights to the value of r. For example at 25 °C, 83.97 % to the value of r was obtained in the first week of adult female life, and a 100 % contribution to r was obtained on the 12th day of adult female life.

There is variation in the susceptibility to biological control agents and chemical insecticides among different developmental stages of *T. palmi*. Seal (2005) found that

larval stages of T. palmi are more susceptible to the insecticide imidacloprid than egg, pupa, and adult stages. North et al. (2006) found that Lecanicillium muscarium Zare and Gams had a more significant impact on adult T. palmi than on juvenile stages. Application of the entopathogenic nematode Steinernema feltiae (Filipjev) was ineffective for killing pupae (Smith et al. 2005). Kuroki et al. (1997) found that Amblyseius cucumeris (Oudemans) consume more first instar larvae than second instar larvae of T. palmi during their life cycle. Therefore, the life history of T. palmi is useful information for farmers and researchers for selection of bio-agents and suitable chemicals in pest management. The deterministic economic threshold relies on knowledge of the age-specific parameters, pest density, and life process of the pest population (Pedigo et al. 1996).



Nagai and Yano (2000) studied the functional responses of different stages of *Orius sauteri* (Poppius) to densities of *T. palmi* and found that *O. sauteri* nymphs killed more larvae than adults. In addition, they reported *O. sauteri* adult females consumed more *T. palmi* larvae than *O. sauteri* adult males. They also documented that adult female *Orius* avoid consumption of *T. palmi* eggs. Therefore, the susceptibility of an individual to biological control agents varies widely with the sex of the natural enemies. Two-sex life tables are proficient for precise calculation of the sex and stage structure of a two-sex population, and use of two-sex life tables can be extremely useful in timing pest management decisions.

To estimate the biological control response it might be necessary to calculate the life table data for both the predator and crop pest and relate this to different temperature, time, and spatial dynamics. However, it is a very tedious and time-consuming process to collect data on pest and natural enemies in different host plants in different environmental conditions. Our study also focused on eggplant for developing pest management modules for *T. palmi* in conditions in Taiwan. This study identified different stages of *T. palmi* and their ages, survivorship of each stage and sex, and rate of population growth at different climatic conditions, information that is suitable for developing sustainable pest management of eggplant in Taiwan.

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**Conflict of interest** We declare that we have no conflict of interest.

**Ethical standard** The experiments reported in this paper comply with the current laws of Taiwan, Republic of China (ROC), where they were conducted.

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