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EFFECT OF PHOTOPERIOD AND TEMPERATURE ON THE LIFE TABLE PARAMETERS OF ONION THRIPS (*THRIPS TABACI*) LINEAGES

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ABSTRACT

This study investigated the effect of photoperiod and temperature on the bionomics of the three *Thrips tabaci* lineages (L1 and L2 – leek-associated, and T – tobacco-associated). The experiment was performed in the laboratory under the following conditions: 23 °C 16L/8D and 8L/16D, and 15 °C under 8L/16D. Reproductive diapause was detected in the T lineage at 23 °C and 8L/16D, but not in the L1 and L2 lineages, while all three lineages diapaused at 15 °C and 8L/16D. Adult longevity of L1, L2, and T lineages were 29.51, 25.69, and 29.76, respectively, at 23 °C under 16L/8D; 30.9, 28.52, and 38.06, respectively, at 23 °C under 8L/16D; and 48.9, 34.22, and 76.89 days, respectively, at 15 °C. Mean fecundity of L1, L2, and T lineages were 89.30, 80.31, 86.76, respectively, at 23 °C under 16L/8D; 40.14, 46.94, and 39.34, respectively, at 23 °C under 8L/16D; and 7.0, 13.85, and 17.87, respectively, at 15 °C. The difference in responses to photoperiod and temperature could be a factor to cause a sympatric population variation of the different *T. tabaci* lineages under the same environmental condition.

Key words: arrhenotoky, light, lineage, onion thrips, reproductive diapause, temperature

INTRODUCTION

Onion thrips, *Thrips tabaci*, Lindeman, 1889 (Thysanoptera: Thripidae) is a cosmopolitan and polyphagous insect pest since it has been reported to occur worldwide and has been recorded on more than 300 plant species (McKinlay 1992). It is one of the most important pests of onion and several other crops both outdoors and indoors. It is estimated that direct feeding damage of onion thrips causes crop losses of more than $1 billion annually worldwide (Balan et al. 2018). Besides direct damage to its host plants, *T. tabaci* is a vector for different economically significant viral pathogens, such as Iris yellow spot virus (IYSV) (Cortês et al. 1998), Tomato spotted wilt virus (TSWV) (Pittman 1927; Macharia et al. 2015), Tomato yellow ring virus (TYRV) (Rotenberg et al. 2015), and Alstroemeria yellow spot virus (AYSV) (Hassani-Mehraban et al. 2019). The IYSV pathogen is estimated to cause an annual loss of $90 million in onion production in the United States alone (Gent et al. 2006), and the TSWV can cause over $1 billion in crop losses annually worldwide (Goldbach & Peters 1994). Like other insect species, onion thrips are ectothermic (cold-blooded) and exhibit a biological response to unfavorable environmental conditions (Beck 1980).

Reproductive diapause is one way of insect adaptation that is used to prevent reproduction (Danks 2004). The reproductive diapaused females laid no eggs, and this provided them insurance against unsuitable moisture, temperature, photoperiod, and food. Temperature and photoperiod are the two environmental factors that induce reproductive diapause and affect lifetable parameters of different insect species (Kamm 1972; Lewis 1973; Pullin 1986;

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McKinlay 1992; Brødsgaard 1994; Ekesi et al. 1999; Trudel et al. 2002; Danks 2004). The diapause effect occurs at an egg, larval, prepupal, pupal, or adult developmental stages (Murai 1987; Aroga & Coderre 2001). Insects living at higher latitudes subsequently show overwintering diapause when the autumn night length falls short of critical value (Saunders et al. 2002).

Based on mitochondrial DNA sequences *T. tabaci* is not a single pest species but rather a cryptic species complex (Brunner et al. 2004). The currently recognized *T. tabaci* lineages are arrhenotokous leek (L1), thelytokous leek- (L2), and arrhenotokous tobacco-associated (T). The L1 and T *T. tabaci* lineages reproduce through arrhenotoky reproduction mode (females are produced from fertilized eggs and males are produced from unfertilized eggs), whereas L2 *T. tabaci* lineage reproduces through thelytoky reproduction mode (females are produced from unfertilized eggs) (Brunner et al. 2004). The L1 and L2 lineages perform well on cabbage plants, and the T lineage performs well on tobacco plants (Li et al. 2014). Two types of leek-associated *T. tabaci* lineages (L1 and L2) were found to form sympatric populations outdoors (two genetically distinct lineages coexist in the same host plant), but the proportions of these two forms in such populations varied greatly (Jenser et al. 2006). These differences gave rise to the hypothesis that the different *T. tabaci* lineages could undergo different responses in the incidence of reproductive diapause, preoviposition, oviposition, longevity, and fecundity at different photoperiod and temperature levels.

To emphasize the above hypothesis, laboratory research was initiated to investigate how the leek- (L1 and L2), and the tobacco-associated (T) *T. tabaci* lineages respond to different photoperiod and temperature regimes, with regard to reproductive diapause, preoviposition period, oviposition period, longevity, and fecundity. The study of reproductive diapause and different lifetable parameters of the three *T. tabaci* lineages is necessary to understand the causes of the sympatric population variation among the different *T. tabaci* lineages. Understanding of factors responsible for sympatric population variations is essential for developing effective biocontrol strategies aim at disrupting reproduction. It could also be used to quantify the reproductive fitness of the L1, L2, and T lineages under different photoperiod regimes and different temperature levels as well as useful for designing effective pest management systems in these lineages.

MATERIALS AND METHODS

Insect

The stock cultures of the *T. tabaci* lineages were maintained in the laboratory at 23 °C under long daylight (16L/8D) regime. Cabbage leaf discs excised from head-forming leaves were used in the bioassays of the L1 and L2 *T. tabaci* lineages, and tobacco leaf discs excised from middle-aged leaves were used in the bioassays of the T lineage. The number of mothers in the experiment was different in each treatment. In the treatment of 16L/8D and 23 °C it was 48, 49, and 48 for L1, L2, and T, respectively; in the treatment 8L:/6D and 23 °C it was 50, 50, and 29, for L1, L2, and T, respectively; and in the treatment 8L/16D and 15 °C it was 11, 22, and 32 for L1, L2, and T, respectively (Table 1).

Table 1. The number of mothers in particular combinations

Treatment number	Treatment temperature and photoperiod	Number of mothers for linaeges L1, L2, and T, respectively
I	23 °C, 16L/8D	48, 49, 48
II	23 °C, 8L/16D	50, 50, 29
III	15 °C, 8L/16D	11, 22, 32

Effect of photoperiod and temperature on preoviposition period and reproductive diapause

Newly emerged virgin female adults of the L1, L2, and T lineages were kept isolated individually and transferred to a new microcentrifuge tube containing a leaf disc of their preferred host plant every 24 h. The preoviposition period was calculated as the time from adult emergence to the beginning of oviposition. Leaf discs were changed daily until the observation of the first egg using the bottom light of a stereomicroscope (Alpha, NSZ-606, Novel optics, Ningo Yongxin, China). When females began laying eggs, leaf discs were changed regularly at 48 h and diapausing females were provided new leaf discs in a similar way until they died.

To measure the incidence of reproductive diapause, the oviposition of females was monitored during their entire lifetime. The criteria employed to detect females in reproductive diapause was the failure to oviposit during their lifetime. Females that did not lay a single egg during their lifetime were considered to be in reproductive diapause, and females that laid eggs during their lifetime were considered reproducing females. However, some females died within a relatively short period of time without laying a single egg. Those females that died before reaching the age of the upper bound of the 95% confidence interval of average preoviposition time were excluded from this test. Therefore, the females that lived longer than the upper bound of the 95% confidence interval of an average preoviposition time and produced some eggs were considered reproducing, and those that did not lay a single egg as being in reproductive diapause.

Effects of temperature and photoperiod on oviposition period, longevity, and fecundity

The length of the oviposition period (in days) was calculated as the period between the first and the last egg laid. Longevity (in days) was measured as the period between the emergence and the death of the adult. Fecundity was calculated as the total number of eggs laid for each female.

Statistical analyses

All data analyses were performed using IBM SPSS 25 (SPSS, Chicago, USA). Means of female lifespan, fecundity, preoviposition, and oviposition period were analyzed separately using GLM of univariate analysis of variance to test the hypothesis that there would be meaningful differences between the lineages and treatments. All means are reported with their 95% confidence interval. Prior to analysis, data were checked for normality using nonparametric Kolmogorov–Smirnov and Shapiro–Wilk tests ($p > 0.05$) as well as studying skewness and kurtosis. The normality of lifespan and preoviposition data were violated, and to normalize the distributions, these variables were log-transformed. Prior to conducting a series of follow-up t-tests, the homogeneity of variance assumption was tested, and for multiple pairwise comparisons, the Games–Howell post-hoc test was performed.

RESULTS AND DISCUSSION

Effect of temperature and photoperiod on preoviposition period

The average preoviposition periods of females in the L1, L2, and T lineages at different photoperiod regimes and temperature levels are given in Table 2. The females in the three lineages examined at 23 °C under 16L/8D periods laid eggs within 3 days. The photoperiod 8L/16D at the same temperature increased the preoviposition period for T lineage by 1–2 days. The temperature of 15 °C significantly extended the period of preoviposition by 13, 4, and 3 times for L1, L2, and T, respectively, compared to treatment 2. The differences between lines in this treatment were significant at $p < 0.001$.

The duration of the preoviposition periods of the L2 lineage at 23 °C under short daylight was about 5 days, but it was less than 3 days in the L1 and T lineages. Thus, the differences of females in the preoviposition period, due to photoperiod responses, could be one of the causes of the population fluctuations among the different *T. tabaci* lineages. Because a lineage that has a shorter preoviposition period can easily build up its population, while a lineage that has a longer preoviposition can build up its population slowly (Woldemelak et al. 2021). Murai (1990) reported prolonged preoviposition period in the thelytokous type of *T. tabaci* under short photoperiod. Additionally, the preoviposition periods of L1, L2, and T *T. tabaci* lineages were increased at 15 °C. Murai (2001) and Sakimura (1937) found a longer preoviposition period in the thelytokous females of *T. tabaci* at 15 °C.

Effect of temperature and photoperiod on reproductive diapause

Photoperiod and temperature both influenced the incidence of reproductive diapause of the *T. tabaci* lineages as shown in Table 3. The incidence of reproductive diapause in the T lineage was increased as the length of daylight decreased, and in the L1 and L2 lineages increased as temperature decreased. Dissections of females exposed to 23 °C under 8L/16D revealed that 40% of the females tested in the T lineage enter reproductive diapause. However, reproductive diapause was not detected in the females of L1 and L2 lineages at this condition. However, it was detected in 50, 42, and 28% of the L1, L2, and T lineage females tested, respectively, at 15 °C. There was no significant difference in reproductive diapause in the T lineage between 23 and 15 °C. All females of the three lineages laid eggs at 23 °C under 16L/8D.

Reproductive diapause was not detected in the arrhenotokous type of *T. tabaci*, but it was detected in the thelytokous *T. tabaci* type under short photoperiod (Murai 1990). Woldemelak et al. (2021) reported reproductive diapause in the L1 and T lineages at 15 °C under 16L/8D. Therefore, reproductive diapause seems to occur in the T lineage likely due to the effect of short daylight, and in L1 and L2 lineages likely due to the effects of low temperature. Photoperiod does not induce diapause in the development of *T. tabaci* rather the adult has a temperature-induced reproductive quiescence (Jenser & Szénási 2004). Murai (1987) has also reported that under 10L/14D at 23 °C *F. intonsa* females produce eggs, but 100% of these females entered reproductive diapause at 20, 16, and 12 °C under 10 h daylight. Kamm (1972) reported reproduction diapause induced in the *Anaphothrips obscurus* (Müller) by exposing larvae to short days (10L/14D), and Lewis (1973) also observed it in *Limothrips cerealium* (Haliday). The incidence of reproductive diapause varied across different geographical locations in the *Haplothrips brevitubus* (Karny) (Fujimoto et al. 2014).

Table 2. Effect of photoperiod and temperature on the preoviposition period of *T. tabaci* lineages (days) (mean ± 95% confidence interval)

Lineages	Treatments		
	I (23 °C, 16L/8D)	II (23 °C, 8L/16D)	III (15 °C, 8L/16D)
L1	2.55 ± 0.2a (n = 49)	2.78 ± 0.4a (n = 50)	27.72 ± 6.9b (n = 11)
L2	2.40 ± 0.3a (n = 48)	4.50 ± 0.5b (n = 50)	17.80 ± 2.8c (n = 22)
T	2.76 ± 0.3a (n = 49)	3.37 ± 1.1a (n = 29)	9.03 ± 1.6b (n = 32)

Note: Different letters indicate a significant difference between photoperiod (column) and temperature (column) within lineages (column) (Games–Howell, $p < 0.05$)

Table 3. Incidence of reproductive diapause among the lineages at different treatments (%)

Lineages	Treatments		
	I (23 °C, 16L/8D)	II (23 °C, 8L/16D)	III (15 °C, 8L/16D)
L1	0	0	50 (n = 11/22)
L2	0	0	42 (n = 16/38)
T	0	40a (n = 21/50)	28a (n = 14/50)

Note: see Table 2

Effect of temperature and photoperiod on oviposition period

The average oviposition periods of females in the L1, L2, and T lineages at different photoperiod regimes and temperature levels are given in Table 4. The length of oviposition periods of female L1 and T lineages was significantly influenced by the photoperiod treatment ($p = 0.001$), but the oviposition periods of the L2 lineage showed no difference due to the photoperiod effect. The shortest oviposition period was observed in the L1 and L2 lineages of treatment 3. In all three lineages, there was no significant difference in oviposition period between 15 and 23 °C under the 8L/16D photoperiod.

The egg production of females in all three lineages was irregular and sporadic at 15 °C and 23 °C under 8L/16D. Females of L1, L2, and T lineages reared at 15 °C under 8L/16D laid very few eggs. Ekesi et al. (1999) also observed irregular and sporadic egg production under long daylight (16L/8D) at 29 °C in the *M. sjostedti*. The effect of photoperiod at low temperature on oviposition periods in lineages L1, L2, and T contradicts the report of Ishida et al. (2003) where *F. occidentalis* continuously oviposited at 15 °C under short daylight (10L/4D). However, females in the L1, L2, and T lineages did not lay eggs continuously under short daylight at 15 °C and 23 °C.

Effects of temperature and photoperiod on the survival of females

Fifty percent of adult L1 females survived at 8L/16D at 23 °C for periods from 30 to 40 days, whereas about 71% survived under short photoperiod (Fig. 1). The longevity of L1 lineage at 15 °C and short photoperiod was much lower because only about 10% of adult female survived periods of 30 and more days and about 40% survived for 10–20 days. The longevity of adult L2 females was similar under different experimental conditions because they survived in about 40% for 20–40 days. The longevity of T lineage was different from that of L1 and L2. 50% of T females survived 20–30 days at 23 °C and 16L/8D, and about 25% survived 30–50 days in the shorter photoperiod. Nevertheless, the differences were at 15 °C and 8L/16D. Under this condition, about 20% survived for 100–110 days. Generally, such conditions were conductive to extend live time of all lineages but especially the lineage T (Table 5).

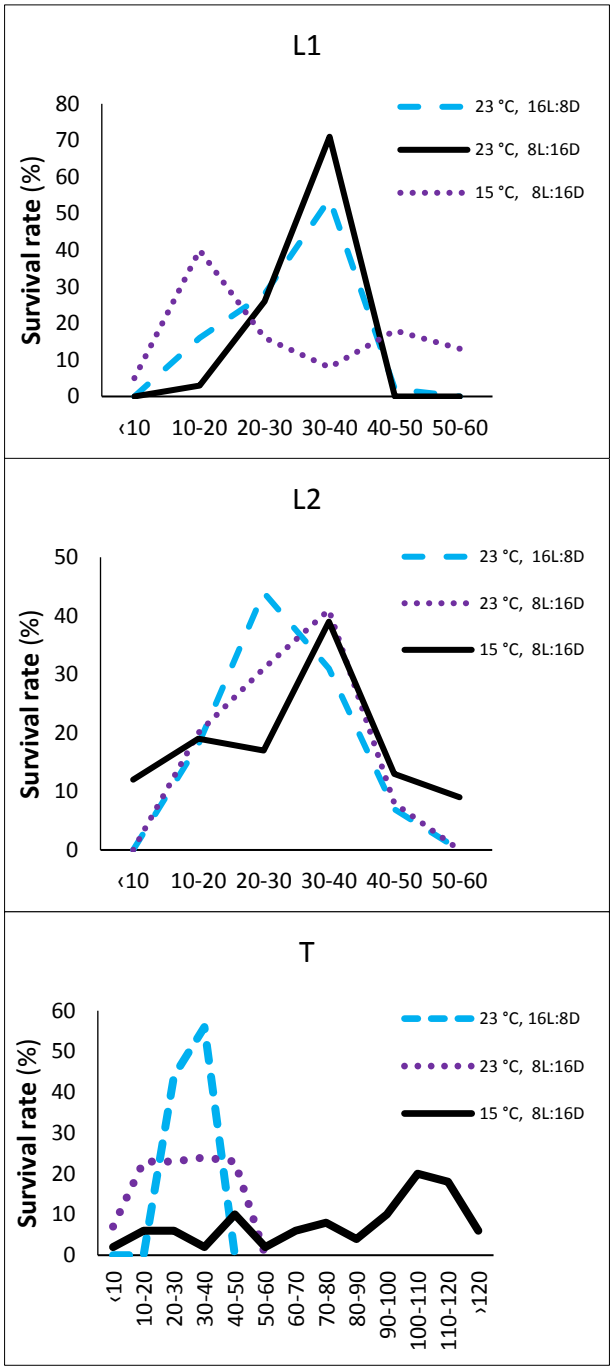

Figure 1. Effects of temperature and photoperiod on the survival rate of L1, L2, and T lineages of adult females at 23 °C under long and short daylight and at 15 °C under short daylight

All reproducing females in the L1 and L2 lineages reared under 8L/16D at 15 °C died within 49 days, whereas, reproducing females in the T lineage died within 76 days. The longest longevity under short daylight at 25 °C has been reported in *F. occidentalis* (Brødsgaard 1994), and adult longevity increased at 14 °C and 12L/12D in *M. sjostedti* (Ekesi et al. 1999) and at 10 °C under 16L/8D in *T. obscuratus* (Teulon

& Penman 1991). There was a difference in longevity between reproducing and diapausing females in lineages L1, L2, and T, where the reproducing females showed a shorter longevity than diapausing females, and it could be due to a direct relationship between fecundity and longevity. Fecundity is a key factor in terms of reducing longevity (Woldemelak et al. 2021). Therefore, diapausing females could have longer longevity due to the trade-off of lower investment in producing eggs, and reproducing females could have shorter longevity due to the overall cost of investment in producing eggs.

Effect of temperature and photoperiod on fecundity

The average fecundity of females in the L1, L2, and T lineages at different photoperiod regimes and temperature levels are given in Table 6. It was significantly ($p = 0.001$) influenced by temperature and photoperiod. In all three lineages, the lowest fecundity (7–17) was recorded at 15 °C and under 8L/16D compared to both treatments at 23 °C. Twice the highest fecundity was at 23 °C and 16L/8D (86–89) compared to 23 °C and 8L/16D (39–46). No significant differences were noted between lineages under treatment 1 and 3.

Short daylight is likely to have a direct negative effect on the fecundity of all three *T. tabaci* lineages. Based on the observed fecundity, the optimum photoperiod for maximum egg laying was 16L/8D. Furthermore, sharp fecundity reduction was recorded in the three lineages due to low temperature (15 °C). Murai (2001) and Sakimura (1937) found temperature as a factor to increase and decrease the fecundity of thelytokous (L2) females. *F. occidentalis* fecundity decreased under short daylight (Whittaker & Kirk 2004) and in *T. nigropilosus* (Nakao 1994) where fecundity decreased under short daylight and low temperature. There were few symptoms of damage on the leaf discs under short daylight (8L/16D) at 15 °C than under long daylight (16L/8D) at 23 °C. This implied that the feeding level of these lineages is directly interlinked with the temperature and length of the photophase. Murai (1987) has reported that the general activity, including feeding activity of thrips, is known to be higher in long daylight than in short daylight.

Table 4. Effect of photoperiod and temperature on oviposition period of *T. tabaci* lineages (days) (mean ± 95% confidence interval)

Lineage	Treatments		
	I (23 °C, 16L/8D)	II (23 °C, 8L/16D)	III (15 °C, 8L/16D)
L1	23.60 ± 1.9b (n = 49)	14.02 ± 1.8a (n = 50)	10.72 ± 2.7a (n = 11)
L2	20.31 ± 1.5b (n = 48)	16.80 ± 1.9ab (n = 50)	13.75 ± 5.4a (n = 22)
T	20.50 ± 1.5b (n = 49)	14.90 ± 3.2a (n = 29)	14.71 ± 3.1a (n = 32)

Note: see Table 2

Table 5. Effect of photoperiod and temperature on longevity of reproducing females of *T. tabaci* lineages (days) (mean ± 95% confidence interval)

Lineage	Treatments		
	I (23 °C, 16L/8D)	II (23 °C, 8L/16D)	III (15 °C, 8L/16D)
L1	29.51 ± 2.2a (n = 49)	30.90 ± 1.3a (n = 50)	48.90 ± 8.7b (n = 11)
L2	25.69 ± 1.8a (n = 48)	28.52 ± 2.5a (n = 50)	34.22 ± 6.3b (n = 22)
T	29.76 ± 1.2a (n = 49)	38.06 ± 4.3b (n = 29)	76.89 ± 12.4c (n = 32)

Note: see Table 2

Table 6. Effect of photoperiod and temperature on fecundity of *T. tabaci* lineages (in days) (mean ± 95% confidence interval)

Lineage	Treatments		
	I (23 °C, 16L/8D)	II (23 °C, 8L/16D)	III (15 °C, 8L/16D)
L1	89.30 ± 5.5a (n = 49)	40.14 ± 5.4b (n = 50)	7.00 ± 1.6c (n = 11)
L2	80.31 ± 8.3a (n = 48)	46.94 ± 4.3b (n = 50)	13.85 ± 4.9c (n = 22)
T	86.76 ± 6.6a (n = 49)	39.34 ± 10.3b (n = 29)	17.87 ± 3.3c (n = 32)

Note: see Table 2

CONCLUSIONS

The overall conclusion of the above results is that reproductive fitness of *T. tabaci* lineages was significantly influenced by short daylight and low temperature. The determination of the reproductive diapause and lifetable parameters of distinct *T. tabaci* lineages could improve our understanding of population dynamics and the proper management of these distinct lineages in the future. However, to complement this work, it would be interesting to compare in further studies with more photoperiod regimes and temperature levels to verify if there are difference between these distinct lineages in the termination of reproductive diapause.

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Conflict of Interest Statement

The authors have not declared any conflict of interests.

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