Influence of Temperature and Tomato Maturity on Development and Survival of *Keiferia lycopersicella* (Lepidoptera: Gelechiidae)

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ABSTRACT Tomato pinworm, *Keiferia lycopersicella* (Walsingham), growth and survival were studied at selected temperatures from 11–41°C. Eggs did not hatch at 11 or 41°C. Development time from egg to adult ranged from 118.4 days at 14°C to 18.6 days at 35°C. Mortality was greater at extreme temperatures (11, 14, 35, 38, and 41°C) than at moderate temperatures (17, 20, 26, and 32°C). Lower thermal thresholds were determined by extrapolation as 11.4, 10.9, and 11.0°C for eggs, blotch leafmining stage (L1 + L2), and tentiform leafmining stage (L3 + L4), respectively. Pupa development was not linear and no lower threshold was estimated. Second and third instars had significantly greater survival than first instars on nearly all stages of foliage and fruit maturity examined. Within each instar, there were no significant differences in rate of development regardless of stage of host maturity. However, development time for each instar was generally longer and mortality was significantly greater on senescing foliage.

THE TOMATO PINWORM (TPW), *Keiferia lycopersicella* (Walsingham), has caused considerable economic losses to tomato growers, particularly in southern California, Texas, and Florida (Mickel 1929, Elmore and Howland 1943, Lin and Trumble 1983). Although the first- and second-instar larvae (L1, L2) feed primarily as leaf blotch miners, and third- and fourth-instar larvae (L3, L4) feed primarily as tentiform leafminers, contamination of the fruit results when larvae enter the fruit, typically just beneath the calyx (Oatman 1970). Infested tomatoes are unmarketable and must be discarded.

TPW introduced into the United States from Mexico was first discovered in the United States in 1923 in Imperial County, California (Morill 1925). Since then, the known distribution has increased dramatically, but low temperatures have limited the distribution to the southern United States (Elmore 1937). However, in 1964 and 1966 TPW caused serious and widespread damage to tomatoes in northern California. Batistie et al. (1970) concluded that transplants from southern California were the major source of the infestations and speculated that, although TPW may have the potential to survive the winter under sheltered tomato plants which were left in the field after harvest, low temperatures were probably limiting distribution. Weinberg and Lange (1980) investigated the relationship between moderate temperatures (20–35°C) and TPW survival and development on 'Red Cherry Tomato', *Lycopersicon esculentum* (Milhouse) var. *cerasiforme*. However, leaves of this cultivar have a different form and thickness than foliage of the economically more valuable fresh market tomato cultivars (Luckwill 1943); therefore, we compared existing developmental information of TPW on 'Red Cherry Tomato' with development on a common fresh market tomato cultivar in a wider range of temperatures (8–44°C).

A second objective was to document the survival and growth rates of larvae attacking fruit and foliage in selected stages of maturity. This information is of considerable value in making pest management decisions as well as providing useful data for modeling pest–host interactions.

Materials and Methods

A TPW colony was initiated from larvae collected in 1982 from the University of California's South Coast Field Station in Orange County, California. The culture was maintained at 26°C in a photoperiod of 14:10 (L:D) on commercial tomato plants 'VFN 7718' grown from seed in a greenhouse. For all tests, 50 pairs of newly emerged moths were confined in a cage supplied with a 10% honey solution for 2 days to allow mating. Tomato plants were then exposed to gravid females for 2 h to obtain eggs of a similar age.

Effect of Temperature on Development. The development times of eggs, the blotch leafmining stage (L1 + L2), the tentiform leafmining stage (L3 + L4), and pupae were obtained using environmental chambers set for constant temperatures of 8, 11, 14, 17, 20, 26, 32, 35, 38, 41, and 44°C (±0.5°C) and a 12:12 photoperiod (1.8×10^3 lx). Relative humidity was adjusted with sulfuric acid to 50–70% (Hodgman 1948).

Table 1. TPW development times (in days ± SE) and cumulative percent mortality by growth stage in selected temperatures

Temp (°C)	Developmental days (±SE)/cumulative % mortality[a]				
	Egg stage	Blotch leafminer (L1 + L2)	Tentiform leafminer (L3 + L4)	Pupa stage	Egg to adult
11	—/100	—	—	—	—
14	28.3 ± 1.1/0	34.3 ± 1.0/45	37.5 ± 2.8/60	18.4 ± 1.4/60	118.4 ± 4.2/60
17	13.7 ± 0.2/0	16.3 ± 0.7/30	18.3 ± 1.1/40	19.0 ± 1.5/50	67.4 ± 2.6/50
20	9.1 ± 0.1/0	11.2 ± 1.9/0	13.2 ± 2.1/40	16.5 ± 2.9/50	49.9 ± 3.9/50
26	5.6 ± 0.0/0	5.8 ± 0.0/0	6.2 ± 0.1/16	8.4 ± 0.1/30	26.0 ± 0.0/30
32	3.8 ± 0.0/0	5.1 ± 0.1/0	5.3 ± 0.1/30	6.6 ± 0.0/30	20.8 ± 0.1/30
35	3.4 ± 0.3/0	4.3 ± 0.9/50	4.5 ± 1.0/65	6.5 ± 1.1/65	18.6 ± 1.0/65
38	2.9 ± 0.0/40	3.7 ± 0.1/40	4.7 ± 1.2/80	—/100	—
41	—/100	—	—	—	
—					

n = 50 larvae per temperature.
[a] —, no survival.

All plants were grown from the same seedlot with identical fertilization practices (slow release 14:14:14 initially, followed by weekly application of liquid fertilizer). Plants were utilized as hosts when they reached the five true-leaf stage (ca. 5–7 weeks old). Ten plants, each with five TPW eggs (2 h old), were confined at each temperature (n = 50 larvae per temperature). Each potted plant was covered with a 0.95-liter translucent polyethylene container ventilated through 100-mesh brass screen fixed on the top and opposite sides. Developmental stage of TPW was recorded every 8 h. Larva stage was determined in situ from head-capsule width measurements (Walz 1948).

The reciprocals of the mean development time in days (=development rate) for each life stage were regressed against temperature. The PROC GLM procedures of SAS (Helwig and Council 1979) were used to generate the polynomial regression lines. A linear regression line was used, only when the F value was significant ($P \leq 0.05$). From the linear regression line, lower thermal threshold temperatures were determined by extrapolation.

Influence of Host Maturity. Development and survival of TPW were evaluated at a constant temperature of 26 ± 1°C on plants in the 6 (preblossom) or 12 (blossom) true-leaf stages. Foliage on these plants was further defined as young (upper foliage <2 weeks old), mature (2–4 weeks old), and senescing leaves (located near the bottom of the plant, with visual signs of senescence). Five larvae of the first, second, or third instar were confined on each foliage category of 10 test plants with a 0.95-liter translucent polyethylene container. This experiment was replicated three times for a total of 150 larvae per instar in each plant stage. Developmental stage and survival were recorded at 8-h intervals.

Two leaves of each maturity stage from three randomly chosen plants were analyzed for water content and percent total organic nitrogen, using a micro-Kjeldahl technique (McKenzie and Wallace 1954).

Similar data were collected using tomato fruit (5.1–7.6 cm diam) as the host substrate. Three fruit stages were defined by color standards as follows: green, mature green (first signs of red color), and red (mature). Tomatoes were placed on a base of white sand and covered with a 0.95-liter translucent polyethylene container ventilated with wire screen on the top and opposite sides. Each fruit stage was infested with three first-, second-, or third-instar larvae. Forty replicates of each stage of fruit were used for each of the three instars, thus providing 120 larvae per instar for each fruit stage. Survival and development were observed weekly in 10 randomly chosen fruit for each stage of fruit and larval instar. These tests were conducted at a temperature of 26 ± 1°C and a photoperiod of 12:12.

Results and Discussion

Effect of Temperature on Development. Development from egg to adult ranged from 118.4 days at 14°C to 18.6 days at 35°C (Table 1). The egg-to-adult development time obtained at 20°C (49.9 days) was 12.1 days longer than that found by Weinberg and Lange (1980) for TPW on *L. esculentum* var. *cerasiforme*, but at 26, 32, and 35°C was 3.8 days, 4.0 days, and 2.0 days shorter, respectively. At temperatures ≤11°C or >41°C there was no survival. Mortality at the extreme temperatures (14, 35, and 38°C) was greater than at the moderate temperatures (17, 20, 26, and 32°C). Where total mortality was highest (100%), death most often occurred during the egg stage (11, 38, and 41°C). Larva stages also suffered substantial mortality at all temperatures.

Linear and nonlinear regression equations and coefficients of determination (R^2) are presented in Fig. 1. The lower thermal thresholds were calculated as 11.4, 10.9, and 11.0°C for the eggs, the blotch leafmining stage, and the tentiform leafmining stage, respectively. These values are 1–3°C higher than those estimated by Weinberg and Lange (1980).

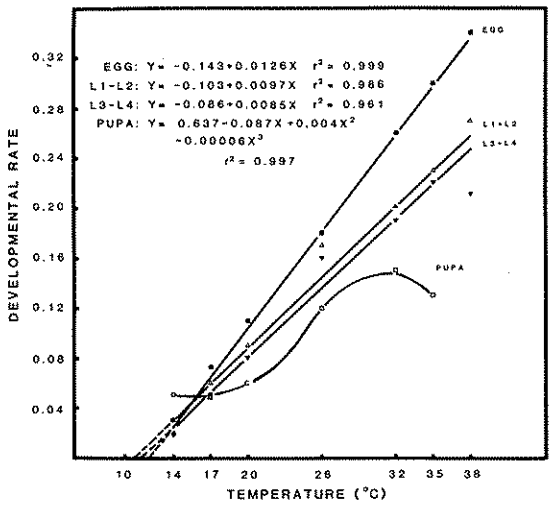

Fig. 1. Relationships between temperature and development times of selected tomato pinworm life stages.

Our data on development rates of TPW on fresh market tomatoes were substantially different from those on 'Red Cherry Tomato' due, in part, to the different tomato cultivars. Similar effects of tomato cultivars on damage potential of TPW, *Liriomyza* spp. leafminers, and *Heliothis zea* (Boddie) have been reported by Kelsheimer (1963), Schuster (1977), and Isman and Duffey (1982). Therefore, for TPW developing on fresh market tomatoes, degree-day models and plant–insect models generated with our data would be more realistic, than if based on other cultivars.

Influence of Host Maturity. Second- and third-instar larvae had significantly higher survival rates than first instars in nearly all maturity categories of the foliage and fruit ($P \leq 0.05$; Duncan's [1955] multiple range test) (Table 2). Lower survival of the first instars on the foliage is not surprising, since small insects are more susceptible to entrapment by the sticky exudates of the trichomes (Kisha 1981). On the fruit, they were less successful than later instars in penetrating the dense pericarp tissue beneath the calyx, perhaps because of small size of their mandibles.

Although the development times within each instar did not differ significantly with degree of maturity of the foliage or fruit, larvae confined on senescing foliage required longer to develop and generally exhibited significantly greater mortality than on the other foliage categories ($P \leq 0.05$) (Table 2). Development from the first through third instar required an additional 2.3 and 5.1 days for the 6 and 12 true-leaf stages, respectively. This suggests that senescing leaves were not as suitable as a host substrate.

The variation in development rates of TPW may be related to the significantly different total organic nitrogen content of the three leaf maturity stages tested: young = 4.16 + 2.16% (mean ± SD); mature = 3.50 + 1.86%; senescing = 2.47 + 1.16% ($P \leq 0.05$; Duncan's [1955] multiple range test). There was no difference in water content (range, 83.4–88.6%) between leaf ages. Many researchers have documented locational preferences for other species of arthropods in relation to leaf age (Ibbotson and Kennedy 1950, Wearing 1967, van Emden and Bashford 1969, Trumble 1982). Generally, these locational preferences were dependent on nitrogen content and the developmental physiology of the plant. Our data suggest that nitrogen level rather than water content might be the major factor responsible for differences in the suitability of the foliage within a plant.

Biological information of this nature is necessary to improve the decision-making process in integrated pest management programs and to develop models of insect–plant interactions. Changes in growth rates or survival of arthropods resulting from plant maturity are usually ignored when the effects of temperature are investigated. Information on plant maturity should be included when

Table 2. Development time in days (instar-to-adult emergence) and percent survival of TPW on tomato 'VFN 7718' foliage[a] and fruit[b] of selected stage of maturity[c]

Host stage	Maturity stage	TPW development days (±SE)/% survival		
		Instar 1	Instar 2	Instar 3
6-leaf	Young	20.7 ± 1.9/36.0b	16.5 ± 2.0/54.0ab	14.2 ± 1.4/76.0a
	Mature	20.4 ± 1.1/38.0b	16.2 ± 0.9/58.0ab	14.4 ± 1.0/74.0a
	Senescing	21.1 ± 0.9/32.0b	17.1 ± 1.2/36.0b	15.7 ± 1.0/67.5a
12-leaf	Young	20.5 ± 1.4/32.0b	17.1 ± 0.9/54.0ab	14.3 ± 1.2/78.0a
	Mature	20.6 ± 1.2/30.3b	17.2 ± 1.5/56.0ab	14.7 ± 1.1/76.0a
	Senescing	24.1 ± 0.7/22.0a	18.5 ± 0.8/34.0a	15.0 ± 1.1/46.0a
Fruit	Green	21.0 ± 1.1/17.6b	17.5 ± 1.3/36.7a	15.2 ± 1.1/49.2a
	Mature green	21.1 ± 1.4/15.8b	17.1 ± 1.8/30.8a	14.1 ± 1.1/54.2a
	Red	21.4 ± 1.2/11.7b	16.9 ± 1.2/36.7a	14.1 ± 1.4/54.2a

[a] n = 120 larvae per instar per treatment.
[b] n = 50 larvae per instar per treatment.
[c] Mean in rows followed by the same letter are not significantly different ($P = 0.05$; arcsine transformation; Duncan's [1955] multiple range test).

developing insect–plant models or life table data designed for use in integrated pest management programs (Gutierrez et al. 1977).

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