Thermal Requirement and Development of *Liriomyza sativae* (Diptera: Agromyzidae) on Cucumber

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ABSTRACT The effect of temperature on developmental rate of vegetable leafminer, *Liriomyza sativae* Blanchard (Diptera: Agromyzidae), was determined at seven constant temperatures (10, 15, 20, 25, 30, 35, and 40°C) on cucumber, *Cucumis sativus* L. 'Negin'. The total developmental period (oviposition to adult emergence) decreased with increasing temperature, although no development occurred at 10 and 40°C. Using the linear model, the estimated lower temperature threshold for the egg, larval, pupal, and entire developmental period was 9.20, 9.75. 11.01, and 10.20°C and the effective accumulative temperatures for these stages were 64.10, 81.97, 106.38, and 250 degree-days (DD), respectively. Data also were fitted to nonlinear temperature-dependent models. Evaluation of the models was based on fit to data, number and biological value of the fitted coefficient, number of measurable parameters, and accuracy of the estimation of the thresholds. Conclusively, linear and Briere models are recommended as the most efficient for the description of temperature-dependent development of *L. sativae*. Temperature-based developmental data can be used to predict occurrence, number of generations, and possibly population dynamics.

KEY WORDS *Liriomyza sativae*, cucumber, temperature dependent, development, degree-days

Temperature affects insect development, allowing species-specific traits, including optimal, lower, and higher temperature thresholds. Developmental rate models and biological parameters help to determine whether synchrony exists between pests and natural enemies (Roy et al. 2002, 2003; Kontodimas et al. 2004). Temperature is a critical abiotic factor influencing the dynamics of insects and limiting biological activities in arthropods, in a way that optimal, lower, and higher temperature thresholds can be estimated in all major life processes. However, in these processes, thermal characteristics may vary between species, populations, developmental stages, and with other ecological factors such as food sources (Gilbert and Raworth 1996, Bybee et al. 2004). Models are effective tools for organizing, expressing, and analyzing knowledge about systems. The philosophy of integrated pest management (IPM) has led to widespread interest in the use of system analysis (Smerage et al. 1980). Temperature-dependent models are most often used to predict the activity and seasonal population dynamics of pests and natural enemies (Lamb 1992).

Cucumber, *Cucumis sativus* L., is the main greenhouse vegetable in Iran, and this crop is attacked by different pests such as leafminers (Fathipour et al. 2006). Vegetable leafminer, *Liriomyza sativae* Blanchard (Diptera: Agromyzidae), is a major pest of different kinds of vegetables and ornamental plants throughout the world (Reitz and Trumble 2002). Vegetable leafminer creates light-colored, irregular winding mines in leaves, which are generally S-shaped and may be enlarged at one end (Spencer 1986, Murphy and LaSalle 1999). Infested leaves are favorable habitats for invading bacterial and fungal plant pathogens (Capinera 2001). Besides the damage caused by the larvae, feeding punctures cause loss of vigor and reduce the photosynthetic capacity of plants (Johnson et al. 1983). Yield losses in general can be considerable (Waterhouse and Norris 1987).

Very little information exists on the biology of *L. sativae* on cucumber (Haghani et al. 2006). Biological studies on *Liriomyza* spp., including *L. sativae*, have been conducted on different host plants but not on cucumber (Charlton and Allen 1981, Tryon and Poe 1981, Parrella 1987, Parkman et al. 1989, Minkenberg and Helderman 1990, Petitt et al. 1991, Petitt and Wietlisbach 1994, Palumbo 1995, Sakamaki et al. 2003). Parrella et al. (1983) had warned against the generalization of *L. trifolii* biology from different host plants. Charlton and Allen (1981), Schuster et al. (1992), and Parrella (1983) showed that the biology of

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L. trifolii varied considerably on different species of host plants. Because of important effect of host plant on biology and population growth of *L. sativae*, the species of host plant should be considered in IPM programs of this pest.

The main objective of this study is to estimate the temperature thresholds (lower, higher, and optimal) and thermal constant of immature stages of *L. sativae* reared on cucumber at seven constant temperatures (10, 15, 20, 25, 30, 35, and 40°C). Our findings may provide necessary information for predicting population occurrence and growth. This information can be used in IPM programs of vegetable leafminer on cucumber.

Materials and Methods

Colony Maintenance. *L. sativae* used in this study was originally collected on greenhouse cucumber in Tehran suburbs, Iran, in July 2004. The colony of the leafminer was established on bean, *Phaseolus vulgaris* L. 'Sunray' in growth chamber at 25 ± 1°C, 65 ± 5% RH, and a photoperiod of 16:8 (L:D) h. The flies used in this study had been reared on beans for 3 mo. To reduce any inbreeding effects, regular infusion of the wild flies was made into the colony.

Seeds of cucumber 'Negin' were placed in 12-cm pots, each containing standard nursery mixed soil, and then the pots were placed in the growth chamber under supplemental fluorescent light. Plants were fertilized every 2 wk with a modified HortGrow (HortiLand Inc., The Netherlands) and Grow More (Grow More Inc., CA) solutions. All the plants were 1.5 mo old with a total leaf area of 70–80 cm^2 when were used for the experiments.

Effect of Temperature on Development. The effect of seven constant temperatures (10, 15, 20, 25, 30, 35, and 40°C) on the development of *L. sativae* was determined. The experiments were conducted in controlled temperature incubators operated at assigned constant temperatures. *C. sativus* plants, each with seven fully expanded leaves (upper and two lower leaves were removed) were exposed to a colony of adult *L. sativae* for 4–8 h in well-ventilated cages at 25 ± 1°C, 65 ± 5% RH, and a photoperiod of 16:8 (L:D) h. To avoid negative effect of intraspecific competition among *L. sativae* larvae (Parrella 1983, Reitz and Trumble 2002), exposure time was regulated according to the number of flies (i.e., shorter exposed time for high fly density). Because it was impossible to follow individual larvae, higher densities of the fly were not used. Larval density was restricted to a maximum six per leaf by killing the surplus. In the course of experiments, finally 40 first instars of *L. sativae* were randomly selected from the plants and were left to develop at constant temperatures (10, 15, 20, 25, 30, 35, and 40°C).

Newly eclosed larvae (an estimate of viable eggs) were determined by inspecting the leaves by stereomicroscope every day. Developmental time of eggs, larvae, pupae, and total immature stages were measured by regular observation until adult emergence. The development study was based on observations with 24-h intervals. At the end of third instar, the larvae were separated by clip-cages to determine pupation period of individuals, which also included the time spent by larva outside the leaf before pupation (prepupa). After pupae turned black, accurate adults emergence time (eclosion) was determined.

Statistical Analysis of Developmental Rate. On the basis of the recorded duration of each immature stage on different temperatures, developmental rate (i.e., 1/developmental time) was calculated. The effect of temperature on developmental rate was calculated using the following formula: $Y = a + bT$, where T is the temperature, Y is the developmental rate; a and b are constants. In this calculation, only the rate of development included in the linear part of developmental curve was used. The lower temperature threshold (T_0) was calculated by means of the x-intercept method ($T_0 = -a/b$). Furthermore, the thermal constant (degree-days) of each stage was calculated from regression equation ($K = 1/b$).

The relationship between temperature and developmental rate also was fitted by five nonlinear developmental rate models (Table 1), chosen because they are commonly used for such purposes. The nonlinear models were suggested by Logan et al. (1976), Lactin et al. (1995), and Briere et al. (1999). Evaluation of the models took place based on fit to data, number and biological value of the fitted coefficient, number of measurable parameters, and accuracy on the estimation of the thresholds.

Criteria for Model Selection

The following criteria were used to assess the performance of each model:

1. The model should describe the data accurately. Two statistics were used to evaluate accuracy: the adjusted coefficient of determination (R^2), and the residual sum of squares (RSS), which provide complementary information on goodness-of-fit and usefulness for predicting observation (Draper and Smith 1998).
2. The models should allow estimation of parameters with biological significance (Briere et al. 1999). For development, the key biological parameters needed are the lower (T_0), optimal (T_{opt}), and higher (T_{max}) temperature thresholds, as defined previously (Roy et al. 2002).

A good model must explicitly include thermal maximum or thermal minimum, or both (Logan and Hilbert 1983, Kontodimas et al. 2004).

One-way analysis of variance (ANOVA) was used to determine significant difference in developmental time of each stage at constant temperatures (Minitab 2000). If significant difference was detected, multiple comparisons were made using the least significant difference (LSD) test ($P < 0.05$). Data were checked for normality before analysis. The temperature-de-

Table 1. Parameter estimated for the temp-dependent models for describing development of *L. sativae*

Equation	Model	Reference
$Y = a + bX$	Linear	Stathas (2000), Roy et al. (2002)
$D(T) = \Delta \times \left[e^{\rho.T} - e^{\left(\rho.T\max - \frac{T\max - T}{\Delta T} \right)} \right]$	Logan-6	Logan et al. (1976), Tobin et al. (2001)
$D(T) = e^{\rho.T} - e^{\left(\rho.T\max - \left(\frac{T\max - T}{\Delta T} \right) \right)}$	Lactin-1	Lactin et al. (1995), Roy et al. (2002)
$D(T) = e^{\rho.T} - e^{\left(\rho.T\max - \left(\frac{T\max - T}{\Delta T} \right) \right)} + \lambda$	Lactin-2	Lactin et al. (1995), Roy et al. (2002)
$D(T) = a \times T(T - T_0) \times (T_{\max} - T)^{1/2}$	Briere-1	Briere et al. (1999)
$D(T) = a \times T(T - T_0) \times (T_{\max} - T)^{1/m}$	Briere-2	Briere et al. (1999)

In Logan-6 model, T is the rearing temperature (°C), Δ is the maximum developmental rate, ρ is a constant defining the rate of optimum temperature, $T_{\max}$ is the lethal maximum temperature, and ΔT is the temperature range over which physiological breakdown becomes the overriding influence. In both Lactin models, T, ρ, $T_{\max}$, and ΔT are as in the Logan-6 model, and in the Lactin-2 model λ forces the curve to intercept the y-axis at a value below zero and thus allows estimation of a low temperature threshold. In both Briere models, T is the rearing temperature (°C), a is an empirical constant, T_0 is the low temperature developmental threshold, $T_{\max}$ is the higher temperature threshold, and in the Beriere-2 model, m is an empirical constant.

pendent models were analyzed using the SPSS statistical program (SPSS Inc. 2004).

Results

Developmental Rate. Mean developmental time and developmental rate of each immature stage at constant temperatures are shown in Table 2. The total developmental time (oviposition to adult emergence) decreased with increasing temperature at 15–35°C, although no development occurred at 10 and 40°C.

At 15°C, *L. sativae* took ≈40 d to complete its development, and comparatively dropped to 27, 14, and 9 d at 20, 30, and 35°C, respectively. Development of the leafminer lasted 21 d at 25°C. Total developmental time was much longer at 15°C, and 10 and 40°C were lethal temperatures to *L. sativae*.

Model Evaluation. The relationship between temperature and developmental rate of all immature stages was adequately described with linear regression. The regression P value showed a high linear relationship between the mentioned variables (Table 3).

Egg developmental rate (Y) increased linearly with temperature (T) up to 35°C. *L. sativae* egg developmental time decreased from 7.8 to 2.4 d as temperature increased from 15 to 35°C, respectively. Larval developmental time decreased from 12.5 at 15°C to 3.2 d at 35°C, respectively; however, increase in larval developmental rate (Y) was linear in the range of temperatures in which larvae completed development (15–35°C). Developmental rate of pupal stage increased linearly with increasing temperature until 35°C. Pupal developmental time decreased from 19.7 to 3.7 d as temperature increased from 15 to 35°C, respectively. Total developmental rate also increased linearly with increasing temperature from 15 to 35°C (Tables 2 and 3).

The estimated lower temperature threshold for egg, larva, pupa, and whole development of *L. sativae* were 9.20, 9.75, 11.01, and 10.20°C, and the thermal constant of these stages was 64.10, 81.97, 106.38, and 250 degree-days (DD), respectively. Our findings indicated that egg stage had the lowest T_0 and thermal constant (K) in comparison with other immature stages for completing its development (Table 3). The estimated

Table 2. Developmental time (DT; mean ± SE) and development rate (DR; 1/d) of immature stages of *L. sativae* on cucumber at different temperatures

Stage	Temp (°C)[a]				
	15	20	25	30	35
Egg					
DT ± SE	7.8 ± 0.12a	6.4 ± 0.09b	4.4 ± 0.11c	3.1 ± 0.09d	2.4 ± 0.12e
DR	0.128	0.156	0.227	0.323	0.417
Larva					
DT ± SE	12.5 ± 0.21a	8.7 ± 0.17b	5.8 ± 0.13c	4 ± 0.0.12d	3.2 ± 0.12e
DR	0.080	0.115	0.172	0.250	0.313
Pupa					
DT ± SE	19.7 ± 0.08a	11.5 ± 0.08b	10.2 ± 0.11c	6.8 ± 0.09d	3.7 ± 0.08e
DR	0.051	0.087	0.098	0.147	0.270
Total					
DT ± SE	40.4 ± 0.08a	26.6 ± 0.08b	20.6 ± 0.11c	13.5 ± 0.09d	9.3 ± 0.08e
DR	0.025	0.038	0.049	0.074	0.108

Means followed by different letters in the same row are significantly different ($P < 0.05$).

[a] No development occurred at 10 and 40°C.

Table 3.   Linear regression between developmental rate (*Y*) and temperature (*T*; °C) for immature stages of *L. sativae* on cucumber

Stage	Regression equations (*T*, temp)	Slope	R^2	*P*	Lower threshold (°C)	Thermal constant (DD)
Egg	$Y = 0.0156\,T - 0.143$	0.0156	0.97	<0.0001	9.20	64.10
Larva	$Y = 0.0122\,T - 0.119$	0.0122	0.99	<0.0001	9.75	81.97
Pupa	$Y = 0.0094\,T - 0.103$	0.0094	0.90	<0.01	11.01	106.38
Egg to adult	$Y = 0.004\,T - 0.0408$	0.004	0.97	<0.0001	10.20	250.00

threshold for total immature development is apparently only a vague indicator for the observed threshold for development. Actually, the highest rate of temperature threshold of different immature stages should be considered as a threshold for development (Minkenberg and Helderman 1990).

The values of fitted coefficients and measurable parameters of the nonlinear models are shown in Table 4. Considering the value of R^2, RSS, and temperature thresholds, there was not substantial difference between the models of Logan-6, Lactin-1, Briere-1, and Briere-2. In general, it seems that the Briere-1 and Briere-2 are more suitable models for estimating temperature thresholds of *L. sativae* because of estimating

Table 4.   Estimated parameters of development rate models for describing total development of *L. sativae*

Model	Parameter	Estimate
Linear	*a*	−0.041
	b	0.004
	k	250
	T_0	10.20
	R^2	0.966
	RSS	0.0002
Logan-6	Δ	0.005
	ρ	0.089
	T_{max}	40.00
	ΔT	1.839
	T_{opt}	36.00
	R^2	0.974
	RSS	0.0002
Lactin-1	ρ	0.177
	T_{max}	40.02
	ΔT	5.652
	T_{opt}	34.40
	R^2	0.958
	RSS	0.0004
Lactin-2	ρ	0.004
	T_{max}	40.19
	ΔT	0.082
	T_0	10.00
	λ	−1.038
	T_{opt}	39.50
	R^2	0.976
	RSS	0.0002
Briere-1	*a*	0.0001
	T_0	10.36
	T_{max}	40.00
	T_{opt}	34.00
	R^2	0.908
	RSS	0.0001
Briere-2	*a*	0.0001
	m	4.859
	T_0	10.12
	T_{max}	40.00
	T_{opt}	36.80
	R^2	0.964
	RSS	0.0003

all temperature thresholds (T_0, T_{opt}, and T_{max}) and reasonable values of the parameters. The rate of optimal temperature threshold was overestimated by Lactin-2, and it seems that this model did not accurately predict the developmental rate of *L. sativae*. It is not possible for the lower temperature threshold to be estimated by Logan-6 and Lactin-1, because these models predict positive developmental rate even at 0°C. The curves of the influence of temperature on developmental rate of *L. sativae* for all models are depicted in Fig. 1.

Discussion

The current study provides more information on effect of a broad range of temperatures on development of *L. sativae*, which has never been thoroughly studied on cucumber. Developmental time observed in our study vary with that estimated for *L. sativae* on lettuce (Palumbo 1995), cowpea seedling (Wei et al. 2002), and bean (Pettit et al. 1991, Petitt and Wietlisbach 1994, Zeng et al. 1998, Hao and Kang 2001, Sakamaki et al. 2003). These contrasts indicate a possible effect of host plant species, techniques, and equipment of the experiments on development of *L. sativae*.

Zhang et al. (2000) reported regression equations for egg, larval and pupal development of *L. sativae* on bean that is very different from that obtained in our study (Table 3). Our findings on the temperature threshold and thermal constant of combined immature stages of *L. sativae* agree with those estimated on kidney bean by Wang et al. (2000) and Tokumaru and Abe (2003). Based upon Wang et al. (2000), the thermal constant for development of *L. sativae* on kidney bean (241 DD) was very close to results of our study on cucumber (250 DD), so lower temperature threshold for total immature stages was very similar (10.7 versus 10.2°C, respectively).

Our estimates on development of *L. sativae* conflict with the results of some studies. Some possible reasons for disagreements are physiological differences, depending on the host plants (Satio et al. 1995, Carolina et al. 1992) and genetic differences as a result of laboratory rearing (Petitt and Wietlisbach 1994, Petitt et al. 1991). Furthermore, techniques and equipment of the experiments could affect development of *L. sativae*.

The lower temperature threshold and thermal constant have been estimated by linear equation in numerous studies (Honek 1999, Lanzoni et al. 2002). Inherent deficiencies of the linear model are as follows: first, the assumed relationship holds only for a
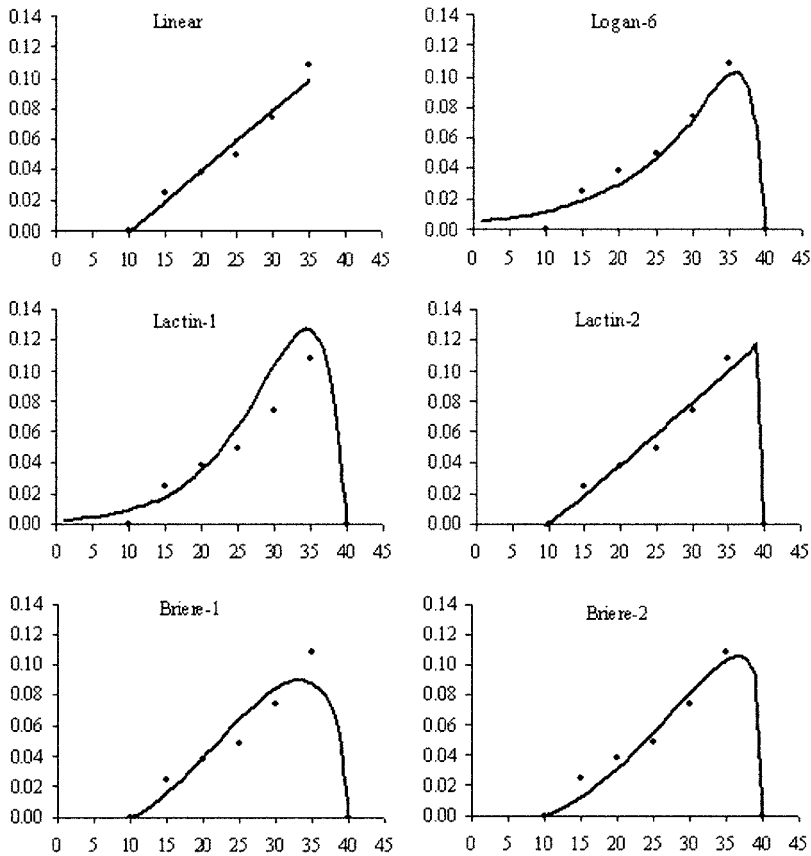
Fig. 1. Fitting the linear, Logan-6, Lactin-1, Lactin-2 Briere-1, and Briere-2 models to developmental rate of *L. sativae*. In all charts, the ordinate is the rate of development ($1/D$, in days^{-1}), and the abscissa is the temperature (°C). Dots represent observed rates.

medium range of temperatures (Gilbert et al. 1976, Syrett and Penman 1981). Second, the estimated threshold is an extrapolation of the linear portion of the relationship into a region where the relationship is unlikely to be linear (Jervis and Copland 1996). For these reasons, the lower temperature threshold and the thermal constant may be underestimated (Howe 1976). Despite these disadvantages, the linear model has been used widely, because it requires minimal data for formulation, it is very easy to calculate and apply, and usually yields approximately correct value with negligible differences in accuracy from more complex models. Moreover, it is the simplest and easiest method for estimation of thermal constant (K) (Worner 1992).

The nonlinear relationship between developmental rate and temperature for this species is similar to many other insects and mites (Briere and Pracros 1998). The data of the current study were fitted to nonlinear models, as indicated by the high values of R^2 and small RSS. The Lactin-2 model estimated realistic values for T_{max}, but it did not provide a realistic estimate of T_{opt} and overestimated this critical temperature. The models of Logan-6, Lactin-1, Briere-1, and Briere-2 were the favored nonlinear models for estimating thermal parameters of *L. sa-*

tivae. The Logan-6 and Lactin-1 models cannot estimate T_0, because there is no intersection with the temperature axis. As mentioned under *Results*, in general, it seems that the Briere-1 and Briere-2 are more suitable models for estimating temperature thresholds of *L. sativae* because of estimating all temperature thresholds (T_0, T_{opt}, and T_{max}) and reasonable values of the parameters.

The linear equation was not only very well fitted to experimental data but also easiest to calculate. Moreover, it is the only equation that enables calculation of the thermal constant (K). Conclusively, linear and some nonlinear models such as Briere-1 and Briere-2 are useful and efficient for description of temperature-dependent development of *L. sativae*.

The results of this study may provide some essential information on developmental and thermal requirements of *L. sativae* on cucumber. When this information to be used in association with other ecological data (such as intrinsic rate of increase, fecundity, and mortality) may be useful for predicting growing conditions conducive to *Liriomyza* outbreaks on cucumber and would be valuable in the development and implementation of pest management programs on cucumber. In addition, factors

such as host plant and population density also would affect leafminer development (Parrella et al. 1983, Parrella 1987). Therefore, further experiments with different host plants and fluctuation temperatures are recommended. After laboratory studies, more attention should be devoted to semifield and field experiments to obtain more applicable results in agricultural conditions.

Acknowledgments

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