Developmental Times and Life Table Statistics of *Aulacorthum solani* (Hemiptera: Aphididae) at Six Constant Temperatures, With Recommendations on the Application of Temperature-Dependent Development Models

S. E. JANDRICIC,[1,2] S. P. WRAIGHT,[3] K. C. BENNETT,[1] AND J. P. SANDERSON[1]

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ABSTRACT *Aulacorthum solani* (Kaltenbach) (known as foxglove aphid or glasshouse potato aphid) is a pest of increasing economic importance in several agricultural crops worldwide, including greenhouse vegetables and ornamentals. Developmental rates and age-specific life tables for a North American population of *A. solani* on pansy (*Viola* × *wittrockiana*) (Gams.) were determined at six constant temperatures, and comparisons were made to previous studies of *A. solani* from differing geographic regions and host crops. On pansy, *A. solani* developed fastest at 25°C, passing through the four nymphal instars in an average of 6.9 d. The highest intrinsic rates of population increase (0.410 and 0.445) and shortest population doubling times (1.69 and 1.56 d) were recorded at 20 and 25°C, respectively. Average total fecundity remained high from 10 to 20°C (74–68 nymphs/adult); a significant decrease to 39 nymphs/adult occurred at 25°C. For calculating developmental thresholds, we present here a method of adjusting the lower developmental threshold (t_{min}) using estimates from nonlinear models to provide an improved estimate of the thermal constant (K, in degree-days). We also call attention to the necessity of using a simulation method to estimate the true upper developmental threshold (T_{max}) and optimum developmental temperature (T_{opt}) from the Lactin-2 model of temperature-dependent development.

KEY WORDS foxglove aphid, *Aulacorthum solani*, developmental rate, Lactin model, greenhouse floriculture pests

Greenhouse floriculture growers are finding foxglove aphid (*Aulacorthum solani*) to be an increasing problem in many areas of the northeastern United States (J.P.S., personal observation; Van Driesche et al. 2008). Native to Europe (Blackman and Eastop 1984), *A. solani* is now a cosmopolitan pest. In recent years, this aphid has gone from an occasional pest to a major pest of many agricultural and greenhouse crops worldwide, including pepper (Down et al. 1996; Sanchez et al. 2007), potato (Down et al. 1996), and lettuce (Palumbo 2003, Lee et al. 2008a). It is also an important pest of soybean in Japan and Korea, but not in North America (Kim et al. 1991, Takada et al. 2006). In a 2006 survey of floriculture greenhouses conducted in Massachusetts and New York state, *A. solani* was found to be the second most common aphid species infesting floriculture crops, more common than both melon aphid (*Aphis gossypii*) and potato aphid (*Macrosiphum euphorbiae*) and second only to the green peach aphid, *Myzus persicae* (Van Driesche et al. 2008). It has been suggested that the change in pest status of *A. solani* in some crops may be caused by recent widespread reduction of pesticide sprays for other pests because of increasing adoption of integrated pest management (IPM) practices (Sanchez et al. 2007), although this is unlikely to be the case in greenhouse floriculture crops in the United States, where insecticides are still heavily used.

Although originally described from potato (*Solanum tuberosum*) (Blackman and Eastop 1984), *Digitalis purpurea* L. (common foxglove) and *Hieracium* spp. (common perennial hawkweed) are the important primary hosts for *A. solani* in North America (Patch 1928, Wave et al. 1965). The anholocyclic stage of *A. solani* uses an extremely wide variety of secondary hosts, including mono- and dicotyledonous, herbaceous, and woody plants (Blackman and Eastop 1984, 1994, 2006). Some populations are entirely anholocyclic (Müller 1970). *A. solani* is known as a pest on 95 different plant species from 25 families (Kim et al. 1991), but the actual number of plant hosts may be much higher than this. For example, to date, we have successfully maintained colonies of *A. solani* on pansy (*Viola* × *wittrockiana*), Victoria blue salvia (*Salvia farinacea*), scarlet sage (*Salvia splendens*), garden chrysanthemums (*Chrysanthemum morifolium*), potted mums (*Dendranthema* × *grandiflora*), million bells

[1] Department of Entomology, Comstock Hall, Cornell University, Ithaca NY 14850.
[2] Corresponding author, e-mail: sej48@cornell.edu.
[3] USDA–ARS Robert W. Holly Center for Agriculture and Health, Tower Road, Cornell; University, Ithaca NY 14853.

(*Calibrachoa hybrida*), pentas (*Pentas lanceolata*), and poinsettia *(Euphorbia pulcherrima*). Our population of *A. solani* has successfully reproduced on every floral crop species we have provided. *A. solani* has also been reported from other important ornamentals such as carnations, lilies, gladiolas, tulips, and orchids (Blackman and Eastop 1984).

The extreme polyphagy of *A. solani* is of concern to floriculture growers, considering the damage this pest can cause. *A. solani* is responsible for the usual suite of problems caused by aphids, including the growth of sooty molds as a result of honeydew excretion (Miller and Stoetzel 1997), the unacceptable appearance of aphids and their cast skins in crops grown for esthetic beauty (Heinz 1998), leaf discoloration (Okubu 2001), plant defoliation at high aphid densities (Okubu 2001, Sanchez et al. 2007), and transmission of 45 different plant viruses (Miller and Stoetzel 1997), including leaf roll viruses (Wave et al. 1965), soybean dwarf virus (Tamada 1970) (both readily transmitted), mosaic viruses (Wave et al. 1965), and tomato aspermy virus (which can affect chrysanthemums) (Govier 1957). In addition to this, *A. solani* also secrete salivary toxins that can cause leaf vein yellowing, local tissue necroses (which can result in leaf death), and severe twisting and curling of plant tissue (Wave et al. 1965, Miles 1990, Sanchez et al. 2007). Tolerance for this aphid in ornamental crops may be lower compared with other aphids because of its tissue-distorting feeding damage.

Recent genetic studies have provided no evidence that *A. solani* includes cryptic species (Valenzuela et al. 2007, Miller et al. 2009) despite morphological variability within the species (Müller 1976, Damsteegt and Voegtlin 1990). However, observations of damaging infestations on soybean in Asia (Kim et al. 1991, Nagano et al. 2001) but not in North America suggest that the species comprises multiple biotypes (Miller et al. 2009), a phenomenon known to occur in other aphid species (ex. *Myzus persicae*, *Acyrthosiphon pisum*) (Mittler and Wilhoit 1990, Peccoud et al. 2008). Other than these apparent host range differences, however, the biological variability of *A. solani* populations worldwide remains largely uncharacterized. To date, only one multi-temperature life table study has been reported for this aphid, based on a Korean population reared on lettuce (Lee et al. 2008a, b). The objective of this study was to estimate developmental times and life table statistics for a North American population of *A. solani* reared on a greenhouse ornamental crop and to compare these statistics to those reported by Lee et al. (2008a, b) and others. Given the importance of *A. solani* as a pest in the greenhouse vegetable and floriculture industries in the northeastern United States, we sought to describe the development of this aphid over a range of temperatures common to greenhouse production systems in temperate climes.

Materials and Methods

Plant Material. Pansies (*Viola* × *wittrockiana*) (variety Majestic Giant; Stokes Seeds, Buffalo, NY) were chosen as the host plant because of their popularity as a bedding plant in greenhouse ornamental production. Pansies were grown from seed in a Cornell University greenhouse at ≈15–22°C and transplanted into 10-cm pots filled with Pro Mix BX (Premier Horticulture, Quakertown, PA). Plants were fertilized three to four times weekly with Excel 21:5:20 (N-P-K) at 300 ppm (Scotts-Sierra Horticultural Products, Marysville, OH), and supplemental lighting was used to ensure a 12-h daylength. After 4–6 wk, the pansy leaves were large enough to be used for experiments. New pansies were planted every 2–4 wk as needed.

Source and Maintenance of Insects. *Aulacorthum solani* were collected from blue saliva and pentas from a garden center in Ithaca, NY, and reared on pansy for more than five generations before starting experiments. Aphid-infested plants were kept in screened cages (60 by 60 by 60 cm, 104 by 26 mesh/2.54 cm, BugDorms; Bioquip Products, Rancho Dominguez, CA) in a greenhouse compartment (temperature range: 20–30°C, L:D = 16:8; RH = 30–50%). New plants were introduced approximately twice a week. The colony consisted mainly of apterous aphids, but some alates (≈10–20% of adults) were present at all times, regardless of aphid density.

Temperature-Dependent Development and Mortality of *A. solani* Nymphs. Embedded leaves were used as the experimental arena to enable comparisons with previous *A. solani* studies, which were conducted on excised leaves. To embed, single leaves (abaxial side up) were pressed gently into 2.5% Difco agar (Fisher, Pittsburgh, PA) before it solidified in a petri dish. Nymphs (<8 h old) were obtained for experiments by placing 6–10 apterous, adult *A. solani* onto an excised, embedded pansy leaf in a 60-mm petri dish. Dish lids had 1-cm-diameter ventilation holes covered with thrips-proof screening. Dishes were placed in an incubator at 25 ± 1°C, 16:8 L:D, and ≈40–50% RH. After 8 h, the newly born nymphs were transferred to embedded pansy leaves in new dishes (one aphid per dish) for experiments using a fine camel-hair brush. Two tests were conducted (1 wk apart), with a slight modification in methods between them. Test date 1 used 90-mm petri dishes with ventilated lids (2 by 1 cm diameter holes covered with the above-described mesh); slightly bigger leaves were used in these dishes, and they were sealed with Parafilm "M" (Pechiney Plastic Packaging, Chicago, IL) to prevent aphid escape. Test date 2 used the 60-mm dishes described above, which had tight-fitting lids making Parafilm unnecessary. Dishes with individual aphids (14 replicates per temperature treatment in test date 1; 18 in test date 2) were placed in an incubator set at one of six temperatures: 10, 15, 20, 25, 30, or 35 ± 1°C. Chamber temperature was recorded every 2 h using a Hobo electronic data logger (Onset Computer, Bourne, MA). Nymphs were observed every 12 h (0700 and 1900 hours) for molting (as evidenced by the presence of a cast skin) until adult emergence. Mortality was also recorded; if a nymph carcass could not be found, the replicate was recorded as "missing." Leaves were changed as needed at each temperature. Typically,

this was every 12–24 h at 35°C, 24–48 h at 30°C, 48–96 h at 25°C, 72–96 h at 20°C, and 96–120 h at 15 and 10°C. The above methodology was used for all trials involving embedded leaves.

As would be expected, we observed much more rapid declines in the quality of the excised, embedded leaves under the high versus low temperature conditions of our tests. Because of concerns over possible effects of high temperatures on excised leaf quality, and thus aphid development and survival, we conducted tests using embedded leaves versus leaves on whole plants to confirm the validity of the embedded leaf results. First, longevity was determined at 35°C using whole pansy plants (4–6 wk; 10-cm pots). An individual aphid nymph (<8 h old) was placed on the underside of a leaf and confined to the leaf by a clip cage ($n = 16$). Simultaneously, an individual nymph (<8 h old) was confined on an embedded pansy leaf for the control treatment ($n = 7$). To eliminate the possibility that first-instar aphids died at 35°C because they were too fragile to survive the heat shock, we also placed 7- to 12-d-old adult aphids ($n = 13$; reared at 25°C) into the 35°C chamber on embedded pansy leaves (one aphid per leaf) to determine adult longevity at this temperature. All aphids were checked every 12 h until death. Second, we used clip cages and whole plants at 30°C (using the same methods as above) and followed aphid developmental time from first instar (<8 h old) until third instar ($n = 16$). Observations were made every 12 h; the presence of a cast skin on the leaf or within the cage indicated that a molt had taken place. Again, embedded pansy leaves were used as the control ($n = 7$).

Fecundity, Larviposition, and Longevity of *A. solani*. Observations of survival and reproduction for each aphid that became an adult in the developmental tests were continued at the same temperature regimen. Observations were made every 24 h (at 1600 hours) until death, and leaves were changed as needed. Offspring were counted and removed daily.

Statistical Analyses. All analyses were done in SAS v. 9.13 (SAS Institute 2003). Analyses of variance (ANOVAs) to determine the effects of temperature and test date on the development of each life stage were conducted on all aphids that completed that life stage. In all cases, time of molt was estimated as the midpoint of the time interval during which the molt was observed. Developmental time data, an example of time-to-event data (whose distributions are commonly skewed to the right), were $\ln(x + 1)$ transformed to better meet the assumption of normality for the parametric ANOVAs. ANOVAs were also conducted to determine effects of temperature on fecundity and longevity; daily fecundity data were $\ln(x + 1)$ transformed, and adult longevity data were ln-transformed before analysis. Additionally, results from the parametric analyses for developmental time, total reproduction, and adult longevity were confirmed by ANOVA of the data after rank transformation, a nonparametric approach essentially equivalent to the Kruskal-Wallis test (Conover 1999; Stokes et al. 2001). To accommodate two-way designs that included test date as a factor, we opted to apply the aligned rank transformation technique (Mansouri 1999) using the PROC RANK function in SAS. Significance of main effects and interactions were compared between the parametric and nonparametric ANOVAs, and if in agreement, the results were accepted (Conover 1999, Zar 1999), and the *F*-test results from the parametric analyses are reported herein.

Two nonlinear equations were used to model developmental rate (1/development time) across temperature using the PROC NLIN procedure in SAS, which generates the best-fit model by iterating initial parameters. The Logan model is given as $r(T) = e^{\rho T} - e^{[\rho T_{max} - (T_{max} - T)/\Delta]}$, where ρ (rate of increase at optimal temperature), T_{max} (upper developmental threshold), and Δ (difference between optimal and upper temperature threshold) are fitted parameters (Logan et al. 1976); the redundant Ψ parameter was removed as suggested by Lactin et al. (1995). The second model used was the Lactin-2 model (Lactin et al. 1995), which will be referred to henceforth as the Lactin model. Given as $r(T) = e^{\rho T} - e^{[\rho T_{max} - (T_{max} - T)/\Delta]} + \lambda$, the Lactin model is simply the Logan model with an additional parameter λ that forces the curve to intercept the *x*-axis, allowing the estimation of a low-temperature developmental threshold (Lactin et al. 1995). Initial parameter values for both models were based on previously reported aphid developmental time data (i.e., from Diaz et al. (2007), who used the Lactin model for the lettuce aphid *Nasonovia ribisnigri*, and from Lamb (1992), who used the Logan model for the pea aphid *Acyrthosiphon pisum*). To determine the goodness-of-fit of each model, the residual sum of squares (RSS) and the pseudo-R^2 of each model were compared (Roy et al. 2002). The pseudo-R^2 is calculated as $R^2 = 1 - (S_r/S_m)$, where S_r is the variance of the residuals and S_m is the mean squared error of developmental rate (Medeiros et al. 2004).

Although T_{max} is a parameter in the Lactin equation, it does not actually represent the upper temperature at which the growth rate equals zero (the upper developmental threshold) as in the underlying Logan model (see Discussion). The true developmental threshold predicted by the model can be obtained only via simulation: the temperature parameter in the models was iterated using R statistical software (v. 2.9.0) (Crawley 2007) until $r(T) = 0$ (identifying the upper point at which the model crossed the *x*-axis). Optimum temperature for development (T_{opt}) can be calculated for both models as $T_{max} - \Delta$. However, because of the above-described problem with T_{max} from the Lactin model, an additional estimate of T_{opt} was obtained from the Lactin equation by iterating the temperature parameter until the developmental rate was maximized. The lower developmental threshold (T_{min}) was estimated from the Lactin equation by iterating the temperature parameter to determine the lower point at which the model crossed the *x*-axis. In the case of the Logan model, the lower threshold

cannot be calculated as the function approaches zero asymptotically.

The linear model $y = a + bx$ (Campbell et al. 1974) was used to provide an additional estimate of the lower developmental threshold ($t_{min} = -a/b$), as well as the thermal constant ($K = 1/b$) for all developmental stages of *A. solani.* The SE for K was calculated as in Campbell et al. (1974). Developmental rates were regressed against temperature for 10, 15, 20, and 25°C (a range of temperatures over which the response was approximately linear) (Kontodimas et al. 2004, Diaz et al. 2007) using the PROC REG procedure in SAS. Estimation of K using the linear model is the accepted method given that nonlinear models cannot estimate K (Kontodimas et al. 2004). However, this linear approach disregards the estimate of the lower developmental threshold estimated from the nonlinear model. We propose that an improved estimate of K can be obtained by adding the value of the lower threshold predicted by the Lactin model (T_{min}) to the data set used for the linear regression. We included this derived data point in a linear regression to produce a new estimate of the *y*-intercept. Then, we removed the derived data point and repeated the regression of the empirical data constrained to the new *y*-intercept to generate an adjusted slope and SE for determination of an adjusted K value and its SE. This approach provides a simple mechanism by which the lower threshold predicted by the nonlinear Lactin model contributes toward estimation of the thermal constant.

Product limit (Kaplan-Meier) survival estimates and median survival times (ST_{50}) were generated for each temperature using PROC LIFETEST in SAS (Allison 1995). All data were censored for aphids that went missing (0–6 per treatment; most were lost within the first 48 h) or were eliminated because they became alate (only two alate were encountered). To determine whether the main effects of test date and temperature significantly affected survival and whether it was appropriate to pool the data between test dates, data were submitted to proportional hazard analysis (PROC PHREG in SAS) (Allison 1995). ST_{50} values were also regressed on temperature (PROC REG).

ANOVAs and Tukey-Kramer tests were conducted to determine differences between temperatures for prelarviposition period, larviposition period, total fecundity, daily lifetime fecundity (=total offspring produced divided by age at death), and adult longevity. Effect of test date was also determined for total fecundity and adult longevity. To generate a graph of age-specific fecundity, we used the mean number of offspring produced per surviving female per day of adult age (which differs from the cohort-based fecundity rate, m_x, used in the Euler equation).

To calculate life table statistics, we used the Euler equation, given as $\Sigma e^{-rx} l_x m_x = 1$, where x is the time in days (including immature stages), l_x is the proportion of individuals in the original cohort alive at time x (including immature mortality), and m_x is defined as the mean number of offspring produced per surviving aphid during time interval x (1 d) (Davis et al. 2006). Intrinsic rate of increase was determined by iterating r in the Euler equation until $\Sigma e^{-rx} l_x m_x = 1$ (see Southwood 1978). Net reproductive rate ($R_o = \Sigma l_x m_x$), generation time ($GT = \ln R_o/r$), and doubling time ($DT = \ln 2/r$) for each temperature were also calculated as per Birch (1948).

In the tests comparing longevity and developmental time on whole plants versus embedded leaves, nonparametric *t*-tests (i.e., the Wilcoxon-Mann-Whitney test; PROC NPAR1WAY in SAS) were used to compare treatment means. Replicates where aphids went missing were removed from the data before analysis. The same test was used to compare longevity of adult aphids and nymphs at 35°C on embedded leaves.

Results

Comparison of Data Between Test Dates. The proportional hazard analysis indicated no significant effect of test date on aphid survival ($\chi^2_{1df} = 0.099$ $P = 0.75$), and there was no test date × temperature interaction ($\chi^2_{1df} = 0.006$ $P = 0.94$). Data for the two test dates were therefore pooled for determination of the Kaplan-Meier survival curves.

In the parametric ANOVAs, test date was not a significant factor in developmental time for any of the four instars (P values from 0.08 to 0.86), total developmental time ($F_{(1,105)} = 2.27$ $P = 0.14$), total reproduction ($F_{(1,105)} = 0.17$ $P = 0.68$), or adult longevity ($F_{(1,105)} = 0.03$ $P = 0.86$). The nonparametric ANOVAs confirmed that test date was not a significant effect in total reproduction ($F_{(1,105)} = 2.28$ $P = 0.14$), adult longevity ($F_{(1,105)} = 1.07$ $P = 0.31$), or developmental time of first ($F_{(1,133)} = 0.07$ $P = 0.79$) and third instars ($F_{(1,114)} = 1.47$ $P = 0.229$). However, test date was a statistically significant factor in total developmental time ($F_{(1,105)} = 4.85$ $P = 0.03$) and developmental time of second ($F_{(1,125)} = 4.42$ $P = 0.04$) and fourth instars ($F_{(1,105)} = 10.67$ $P = 0.002$).

There were no significant test date × temperature interactions in any of the parametric analyses of duration of each stadium (P values ranging from 0.16 to 0.70 for the four instars), total developmental time ($P = 0.20$), total reproduction ($P = 0.88$), or adult longevity ($P = 0.95$). The nonparametric tests supported these findings ($P = 0.15$–0.97) with the single exception of a marginally significant interaction detected in the third-instar data ($F_{(4,114)} = 2.5$, $P = 0.048$).

Because results from the two test dates were generally similar and consistent across temperatures, data were pooled for determination of life table statistics. In the ANOVA/Tukey-Kramer tests of temperature effects, test date was retained in the model statements as a blocking factor to potentially reduce error variance. All presented results are means (±SE) expressed in the original (untransformed) scale.

Temperature-Dependent Development and Mortality of *A. solani* Nymphs. Temperature had a significant effect on developmental rate ($F_{(4,105)} = 253.10$ $P < 0.0001$). Total developmental times were comparable to those found in previous research (Tables 1 and 2). From 10 to 25°C, developmental time of *A. so-*

Table 1. Duration (mean ± SE) of each stadium of *A. solani* incubated at constant temperatures

Temperature	Initial *n*	Duration of each stadium (d)[a]				
		First instar	Second instar	Third instar	Fourth instar	Nymph to adult
10	32	6.20 ± 0.173 a (24)	5.18 ± 0.172 a (24)	5.02 ± 0.177 a (22)	5.91 ± 0.160 a (22)	21.81 ± 0.360 (22) a
15	32	3.32 ± 0.143 b (29)	2.36 ± 0.142 b (29)	2.51 ± 0.129 b (29)	3.19 ± 0.117 b (29)	11.37 ± 0.262 (29) b
20	32	2.72 ± 0.162 c (26)	1.61 ± 0.161 c (26)	2.14 ± 0.146 c (26)	1.92 ± 0.132 c (26)	8.37 ± 0.296 (26) c
25	32	2.02 ± 0.157 d (26)	1.31 ± 0.155 c (26)	1.44 ± 0.143 d (25)	2.11 ± 0.130 c (25)	6.88 ± 0.291 (25) d
30	32	2.22 ± 0.145 d (29)	1.74 ± 0.196 c (21)	2.38 ± 0.230 bc (13)	3.74 ± 0.368 b (4)	9.48 ± 0.825 (4) bc
35	32	—[b]	—	—	—	—

[a] Means within columns followed by same letter are not significantly different (Tukey-Kramer test, $\alpha = 0.05$). The numbers of aphids that completed each stadium (versus dead or missing) are presented in parentheses for each temperature.
[b] All aphids died within 48 h at 35°C.

lani significantly decreased as temperature increased (Table 1). *A. solani* nymphs developed significantly faster at 25°C than at all other temperatures, growing from newly laid nymph to adult in an average of 6.9 d. Developmental time increased to 9.5 d at 30°C; however, only four aphids of an original 32 were able to complete development at this temperature. No *A. solani* incubated at 35°C were able to complete even the first molt. The first and fourth stadia and the second and third stadia tended to have similar duration at the nonlethal temperatures of 10–25°C, with the first and fourth stadia being longer than the middle stadia (Table 1). An exception occurred at 20°C, at which temperature the third stadium exceeded the fourth by >10%.

Temperature-dependent nymphal mortality is shown in Table 3. Nymphal mortality was highest at 35°C, where all aphids died within the first 48 h, followed by 30 and 10°C, with 85.7 and 33.3% mortality, respectively. Nymphal mortality was lowest at 15°C (0%).

Using linear regression, the lower developmental thresholds for instars 1–4 were estimated at between 2.3 and 5.8°C (Table 4), with the lower threshold for total development estimated as 3.1°C (Table 4). The thermal constant (K) for nymph to adult development is estimated as 141.0 DD.

The Logan and Lactin models for developmental rate of *A. solani* are depicted in Fig. 1 and parameter values are given in Table 5. In general, both models seemed to fit the data well, having high pseudo-R^2

Table 2. Mean total developmental times (±SE), intrinsic rate of increase (r_m), net reproductive rate (R_o), total fecundity, and doubling times (DT) of *A. solani* reared on various crops

Temperature (°C)	Crop	*n*	Total developmental time (d)	r_m	R_o	Total fecundity	DT (d)	Reference
2.0	Potato	41	0[a]	—	—	—	—	Pozarowska 1987
5.0	Potato	50	63.15 ± 1.08	—	—	45.3	—	Pozarowska 1987
10.0	Pansy	32	21.8 ± 0.36	0.0964	61.7	74.4	7.19	This study
	Pepper	100[b]	16.7 ± 0.24	0.1240	59.2	—	5.59	Vasicek et al. 2001
	Soybean	20	20.2 ± 4.50	—	—	—	—	Kim et al. 1991
	Lettuce	20[c]	23.7 ± 0.43	0.078	29.8	—	8.89	Vasicek et al. 2003
	Eggplant	20[c]	21.8 ± 0.62	0.089	42.0	—	7.79	Vasicek et al. 2003
	Pea	20[c]	18.8 ± 0.58	0.079	10.2	—	8.76	Vasicek et al. 2003
	Fennel	20[c]	23.8 ± 0.50	0.083	30.7	—	8.37	Vasicek et al. 2003
12.5	Lettuce	30	16.9 ± 0.15	0.1292	36.3	—	5.37	Lee et al. 2008a, b
15.0	Pansy	32	11.4 ± 0.26	0.3045	75.4	74.9	2.28	This study
	Lettuce	30	10.3 ± 0.15	0.2284	58.7	—	3.04	Lee et al. 2008a, b
	Soybean	20	13.4 ± 2.6	—	—	—	—	Kim et al. 1991
17.5	Lettuce	30	7.9 ± 0.13	0.2631	35.4	—	2.63	Lee et al. 2008a, b
20.0	Pansy	32	8.4 ± 0.30	0.4098	64.5	68.4	1.69	This study
	Lettuce	30	7.2 ± 0.13	0.2747	33.8	—	2.52	Kim et al. 1991
	Potato	50	7.9 ± 0.06	—	—	84.8	—	Pozarowska 1987
	Soybean	20	7.8 ± 1.20	—	—	—	—	Kim et al. 1991
22.5	Lettuce	30	6.6 ± 0.14	0.2625	17.9	—	2.64	Lee et al. 2008a, b
avg. 22.6	Potato	37	9.3[d]	—	—	60.3	—	MacGillivray and Anderson 1958
25.0	Pansy	32	6.9 ± 0.29	0.4435	37.7	39.1	1.56	This study
	Lettuce	30	7.4 ± 0.30	0.2625	17.9	—	2.64	Lee et al. 2008a, b
	Soybean	20	7.0 ± 1.0	—	—	—	—	Kim et al. 1991
27.5	Lettuce	30	0[a]	—	—	—	—	Lee et al. 2008a, b
30.0	Pansy	32	9.5 ± 0.83[e]	0.0961	—	—	—	This study
	Soybean	20	0[a]	—	—	—	—	Kim et al. 1991
35.0	Pansy	32	0[a]	—	—	—	—	This study

[a] All nymphs died before reaching adulthood at this temperature.
[b] Data for one cohort (of four) were randomly chosen, because there were no significant differences among cohorts.
[c] Data were chosen from the best performing cohort (of two cohorts).
[d] No SE available.
[e] Based on four nymphs that developed into adults.

Table 3. Temperature-dependent nymphal mortality of *A. solani* reared at six constant temperatures

Temperature (°C)	Stage	Number observed at start of each stage	Number dying in each stage	Number missing or discarded in each stage	Stage-specific percent mortality (minus missing aphids)	Percent of original cohort (minus missing aphids) dying in each stage
10	First instar	32	3	5	11.11	11.11
	Second instar	24	4	0	16.67	14.81
	Third instar	20	2	0	10.00	7.41
	Fourth instar	18	0	0	0.00	0.00
	Total	—	—	—	—	*33.33*
15	First instar	32	0	3	0.00	0.00
	Second instar	29	0	0	0.00	0.00
	Third instar	29	0	0	0.00	0.00
	Fourth instar	29	0	0	0.00	0.00
	Total	—	—	—	—	*0.00*
20	First instar	32	2	4	7.14	7.14
	Second instar	26	0	0	0.00	0.00
	Third instar	26	0	0	0.00	0.00
	Fourth instar	26	0	0	0.00	0.00
	Total	—	—	—	—	*7.14*
25	First instar	32	1	5	3.70	3.70
	Second instar	26	0	0	0.00	0.00
	Third instar	26	0	1	0.00	0.00
	Fourth instar	25	0	0	0.00	0.00
	Total	—	—	—	—	*3.70*
30	First instar	32	0	3	0.00	0.00
	Second instar	29	7	1	25.00	25.00
	Third instar	21	8	1	40.00	29.63
	Fourth instar	13	9	0	69.23	31.03
	Total	—	—	—	—	*85.66*
35	First instar	32	32	0	100.00	100.00
	Second instar	—	—	—	—	—
	Third instar	—	—	—	—	—
	Fourth instar	—	—	—	—	—
	Total	—	—	—	—	*100.00*

values (0.98 and 0.95 for the Logan and Lactin models, respectively). In the Lactin model, the parameter T_{max} (which we refer to as $T_{max\ modified}$; see Discussion) is given as 37.6°C. This parameter value seems to be an overestimation of the upper development threshold, because 37.6°C is not the point at which the model crosses the *x*-axis (Fig. 1). However, the simulation method with the Lactin model (described previously) produced an estimated T_{max} of 35.0°C, which is identical to the T_{max} predicted by the Logan model (Table 5). This estimate is confirmed by the experimental results: no aphids were able to complete development at constant 35°C. The optimal temperature for development (T_{opt}) was estimated between 25.5 and 27°C using the various methods and models. The lower developmental threshold estimated by simulation of the Lactin model is 4.0°C, which is ≈1°C higher than that estimated by the linear regression.

Adjusting for the higher T_{min} estimate from the nonlinear regression (as previously described), the adjusted lower developmental threshold was estimated to be 3.7°C, and K was reduced from 141 to 133 DD (Table 4).

Temperature-Dependent Survival of *A. solani*. Survivorship curves for *A. solani* at the six temperatures tested are shown in Fig. 2 and ST_{50} values are given in Table 6. A proportional hazards analysis shows that temperature had a significant effect on survival ($\chi^2_{1df} = 70.75, P < 0.0001$). Median survival time decreased from 96.7 to 0.4 d as temperature increased from 10 to 35°C. Aphids survived up to a maximum of 136 d total at 10°C.

Table 4. Linear regression equations for temperature-dependent development of *A. solani*

Life stage	Regression equation[a]	R^2	*P* value[b]	t_{min}[c]	K[d]
First instar	$r(T) = -0.0527 + 0.0232$ (T)	0.702	0.0001	2.27	43.0 ± 2.8
Second instar	$r(T) = -0.2947 + 0.0512$ (T)	0.246	0.0001	5.76	19.5 ± 3.4
Third instar	$r(T) = -0.1324 + 0.0355$ (T)	0.610	0.0001	3.73	28.2 ± 2.3
Fourth instar	$r(T) = -0.0810 + 0.0280$ (T)	0.441	0.0001	2.89	35.7 ± 4.0
Nymph to adult	$r(T) = -0.0217 + 0.0071$ (T)	0.874	0.0001	3.06	140.8 ± 5.3
Adjusted nymph to adult[e]	$r(T) = -0.0277 + 0.0075$ (T)	0.983	0.0001	3.69	133.3 ± 1.4

[a] $r(T)$ = growth rate (1/development time) at temperature *T*.
[b] *P* value from the test of significance of the regression coefficient.
[c] t_{min} = −intercept/slope; *t* represents the lower temperture threshold, expressed in °C.
[d] K = 1/slope; K represents the thermal constant, expressed in degree-days.
[e] Linear regression was re-calculated incorporating the lower threshold from the nonlinear model to provide adjusted *t* and K estimates.

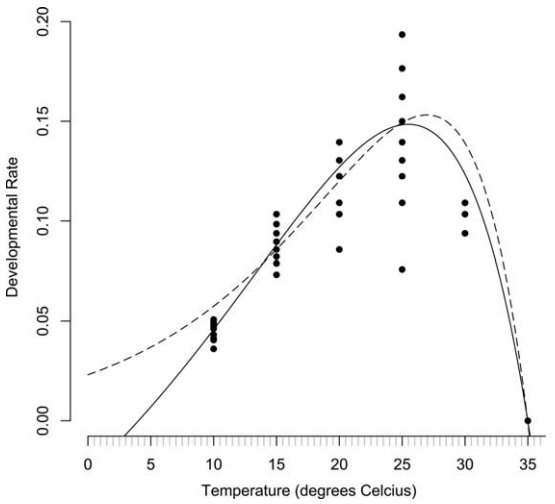

Fig. 1. Constant temperature-dependent developmental rate of *A. solani* based on the Lactin model (solid line) and the Logan model (dashed line).

A linear regression of ST_{50} versus temperature revealed a highly significant model, with temperature explaining nearly all of the variation ($F_{(1,5)} = 178.0, P = 0.0002, R^2 = 0.98$). The regression equation is given as $ST_{50} = 143.36 - 4.21$ (temperature).

Longevity and Development on Whole Plants Versus Embedded Leaves. In tests comparing the two experimental arenas at 35°C, there was no significant difference in longevity of nymphs held on embedded leaves versus whole plants (18.6 ± 2.2 versus 27.5 ± 3.7 h, respectively; Wilcoxon-Mann-Whitney test, $z = -1.66$, $P = 0.096$). In both cases, all aphids were dead within 48 h. Adults survived significantly longer than nymphs on embedded leaves at 35°C (27.2 ± 1.5 versus 18.6 ± 2.2 h, respectively, $z = -2.57$, $P = 0.01$), but none of the aphids survived past 36 h. At 30°C, time spent in the first and second stadia was not significantly different whether embedded leaves or whole plants were used ($z = -0.78$, $P = 0.44$ and $z = -0.96$, $P = 0.34$ for first and second instars, respectively).

Fecundity, Larviposition Period, Adult Longevity, and Population Dynamics. Mean prelarviposition time, larviposition time, total fecundity, daily fecundity, and adult longevity for aphids reared at each temperature are presented in Table 7. Each of these five parameters was significantly affected by temperature ($F_{(4,102)} = 21.13\ P < 0.0001$; $F_{(4,105)} = 61.25\ P < 0.0001$; $F_{(4,105)} = 31.54\ P < 0.0001$; $F_{(4,105)} = 19.59, P < 0.0001$; and $F_{(4,105)} = 33.99\ P < 0.0001$, respectively). Aphids at 10, 15, and 20°C had similar total fecundity (with 74, 75, and 68 offspring/female on average, respectively). Total fecundity was markedly lower at 25°C, with an average of 39 offspring/adult, a 57% reduction in fecundity from the 20°C treatment. Daily fecundity was nominally highest at 20°C, with 1.58 nymphs/d; however, this rate was not significantly higher than the rate of 1.48 nymphs/d recorded at 25°C (Table 7). Of the four aphids that survived to adulthood at 30°C, only one reproduced, bearing two offspring on 1 d. The prelarviposition (prereproductive) period decreased with increasing temperature between 10 and 20°C; this trend was reversed at 25°C, although the increase between 20 and 25°C was not significant. The larviposition period decreased with increasing temperature. Adult longevity increased as temperature decreased.

Age-specific fecundity per surviving aphid showed an expected decrease in the number of offspring produced over time (Fig. 3). Maximum larviposition occurred at days 12, 7, and 6 of adulthood for temperatures 15, 20, and 25°C, respectively. At 10°C, the mean number of offspring per day was fairly consistent from day 5 to day 49 of adulthood; maximum offspring production occurred on day 37 of adulthood.

The life table statistics for *A. solani* are presented in Table 8. The intrinsic rate of increase (r_m) was highest for aphids reared at 25°C ($r_m = 0.445$). Similarly, generation and doubling time were fastest for aphids reared at 25°C (8.18 and 1.56, respectively), whereas net reproductive rate (R_o) was highest at 15°C. Life table statistics from other studies of *A. solani* are presented in Table 2 for comparison.

Table 5. Parameter estimates (mean ± SE) and estimated temperature thresholds of the Logan and Lactin models for the development of *A. solani*

Model	df	Fitted model parameter estimates				Simulation estimates			$T_{opt}(= T_{max} - \Delta)$	Pseudo R^2	RSS
		ρ	T_{max}, $T_{max\ modified}$[c]	Δ	λ	T_{min}[d]	T_{max}[d]	T_{opt}[d]			
Logan[a]	138	0.1245 ± 0.0027	34.9791 ± 0.0506	7.9887 ± 0.1693	—	—[e]	—[f]	—[g]	27.0	0.977	0.030
Lactin[b]	137	0.0813 ± 0.0080	37.5759 ± 0.8036	11.8971 ± 1.0085	−0.1316 ± 0.0414	4.0	35.0	25.5	25.7	0.945	0.025

[a] Logan model: $r(T) = e^{\rho T} - e^{[\rho^{T\,max} - (^{T\,max} - {}^{T})/\Delta]}$

[b] Lactin model: $r(T) = e^{\rho T} - e^{[\rho^{T\,max} - (^{T\,max} - {}^{T})/\Delta]} + \lambda$.

[c] T_{max} in the Lactin model is not the temperature at which $r(T) = 0$ and thus does not fit the definition of T_{max} in the Logan model; we designate it here as $T_{max\ modified}$.

[d] Estimates derived by running a simulation of the model: T_{min} = lower developmental threshold; T_{opt} = optimum developmental temperature, T_{max} = upper developmental threshold.

[e] T_{min} cannot be calculated using the Logan equation, as the model asymptotically approaches zero.

[f] Equals parameter T_{max} from fitted model.

[g] Equals $T_{max} - \Delta$.

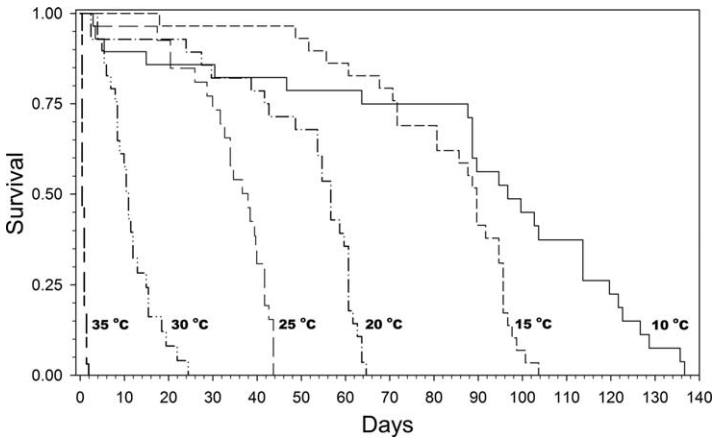

Fig. 2. Kaplan-Meier survival curves of *A. solani* reared at six different constant temperatures.

Discussion

The average developmental times for *A. solani* in this study were comparable to previous reports on other crops across a moderate temperature range (i.e., 10–25°C). However, differences occurred at high temperatures between our study and the two studies conducted in Korea. In Lee et al. (2008a), only 3.3% of the 30 aphids tested developed at 27.5°C (a temperature that is only 0.5°C above the estimated T_{opt} for our population calculated using the Logan model) and none of these produced nymphs. Similarly, Kim et al. (1991) reported that no aphids were able to develop or reproduce at 30°C. However, in our study, 12.5% of nymphs developed into adults at 30°C, and one of these aphids was able to reproduce. Using the mean developmental data given by Lee et al. (2008a) and Kim et al. (1991), we used the Logan model to estimate the T_{max} of their populations to be 28.0 and 30.0°C, respectively, with optimum temperatures of 22.6 and 24.2°C, respectively. In contrast, the T_{max} calculated for our population of *A. solani* was 35°C, a much higher estimate, but one that is similar to other aphid species in several studies (e.g., 34.2°C for green peach aphid at constant temperatures and 35.3°C for lettuce aphid [*Nasonovia ribisnigri*]) (Davis et al. 2006, Diaz et al. 2007). Thus, our *A. solani* population seems to be more heat tolerant than those tested previously in Korea and may be more likely to survive high temperatures that sometimes occur in floriculture production. Furthermore, Davis et al. (2006) showed that green peach aphid has a higher T_{max} (up to 3°C higher) when reared under fluctuating temperature regimens; therefore, our North American *A. solani* population, when reared under natural, fluctuating conditions, may be able survive in greenhouses that reach ≈37–38°C for a short periods during the day, especially if *A. solani* engage in shade-seeking behaviors, which has been reported in other aphids (Gish and Inbar 2006).

With regard to low temperatures, at 10°C, we observed extremely long survival of some *A. solani* individuals (up to 136 d from birth to death). However, this is probably not biologically relevant in nature. Older aphids (those past their reproductive period) were more often observed on the sides of the petri dish than on the embedded leaf. In nature, they likely would have left the plant at this point and perished.

On comparing the lower developmental thresholds of *A. solani* populations, we noted that our adjusted t_{min} value of 3.7°C was 1°C higher than that calculated by Kim et al. (1991) (at 2.7°C), but was much higher than the extremely low value calculated by Lee et al. (2008a) (0.08°C). The value obtained by Lee et al. (2008a) is surprising considering that Pozarowska (1987) provided empirical evidence that a selected population of *A. solani* did not develop at a temperature as low as even 2°C. Because this estimate seemed biologically unrealistic, and because of the relatively low R^2 value of their linear regression ($R^2 = 0.75$), we suspected that Lee et al. (2008a) used their entire data set in their linear model in obtaining this t_{min}. For the proper calculation of t_{min} and K, however, only those data that fit a straight line should be used (Kontodimas et al. 2004). To confirm this possible miscalculation, we conducted a linear regression of the mean data given in Lee et al. (2008a) using the Campbell method described earlier. Using their entire data set (12.5–25°C), we obtained an extremely low t_{min} as well (=0.15°C). Using the approximately linear portion of the data set (i.e., 12.5–22.5°C, as estimated by visual inspection of the developmental rate graph provided in their paper) yielded a t_{min} of 4.8°C (with an R^2 of 0.94), a value that is much more realistic, although higher than our estimated t_{min} of 3.7°C.

Table 6. Median survival times (ST_{50}) of *A. solani* at six temperatures (Kaplan-Meier estimates)

Temperature (°C)	ST_{50} (95% CI) (d)
10	96.66 (88.67–113.67)
15	89.67 (80.67–94.67)
20	56.67 (53.67–60.67)
25	37.92 (32.67–39.92)
30	10.92 (8.42–11.92)
35	0.42 (0.42–0.92)

Table 7. Mean ± SE prelarviposition period, larviposition period, total fecundity, daily fecundity, and longevity of adult *A. solani* females reared at constant temperatures

Temperature (°C)	n^a	Prelarviposition period[b]	Larviposition period[b]	Total fecundity[b]	Daily fecundity[b,c]	Adult longevity[b]
10	22	4.37 ± 0.22 a	53.31 ± 2.01 a	74.38 ± 4.05 a	0.91 ± 0.12 a	82.98 ± 4.64 a
15	29	2.62 ± 0.16 b	32.70 ± 1.46 b	74.89 ± 2.94 a	1.11 ± 0.08 ac	70.08 ± 3.37 a
20	26	1.93 ± 0.18 c	25.89 ± 1.66 c	68.35 ± 3.34 a	1.58 ± 0.10 b	45.47 ± 3.82 b
25	25	2.48 ± 0.18 bc	18.77 ± 1.63 d	39.07 ± 3.28 b	1.48 ± 0.09 bc	28.16 ± 3.75 c
30	4	—[d]	—	—	—	11.39 ± 10.63 d
35	0	—[d]	—	—	—	—

[a] *n* represents the no. of aphids that reached adulthood (of 32 original replicates per temperature).
[b] Means within columns followed by same letter are not significantly different (Tukey-Kramer test, $\alpha = 0.05$).
[c] Daily lifetime fecundity = total fecundity/adult longevity.
[d] Parameters could not be estimated because only one aphid reproduced at 30°C and no aphids reached adulthood at 35°C.

Because of the higher t_{min} estimate in this study versus Kim et al. (1991), our thermal constant estimate is slightly lower. Using the method described by Campbell et al. (1974), we calculated K (for development from nymph to adult) to be 141 DD and adjusted it to 133 by taking the estimate of T_{min} from the nonlinear model into account; Kim et al. (1991) calculated K as 142 DD. Lee et al. (2008a) originally calculated K to be 165 DD, but this was based on their application of a linear regression to an inappropriate data set.

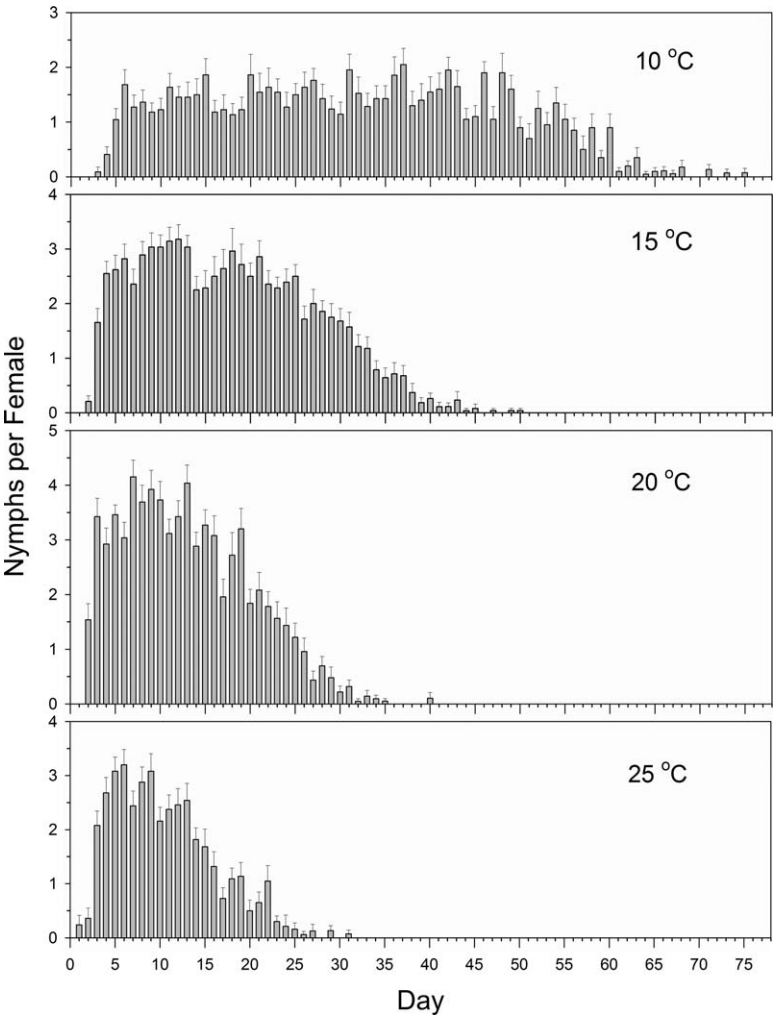

Fig. 3. Age-specific daily fecundity of *A. solani* reared at constant temperatures (*x*-axis is not indicative of longevity). Error bars show +SE only.

Table 8. Life table statistics of *A. solani* reared at differing temperatures

Temperature (°C)	r_m	R_o	GT	DT
10	0.0964	61.6507	42.7540	7.1903
15	0.3045	75.4190	14.1970	2.2763
20	0.4098	64.4600	10.1660	1.6914
25	0.4435	37.6770	8.1827	1.5629
30	—[a]	—	—	—
35	—[a]	—	—	—

r_m, intrinsic rate of increase; R_o, net reproductive rate; GT, mean generation time; DT, doubling time.

[a] Values could not be calculated because only a single individual reproduced at 30°C and no aphids developed at 35°C.

As defined by Logan et al. (1976), T_{max} is the upper temperature point at which the line describing development intersects the *x*-axis (temperature). This point, at which $r(T)$ equals zero, is most precisely referred to as the upper development threshold (UDT). In fitting data to the Lactin model, one finds that the parameter T_{max} clearly does not fit this definition. The T_{max} generated by fitting the Lactin equation to our data, for example, corresponds to a negative developmental rate, which translates to an overestimation of UDT. Although not always the case, this overestimation does appear consistently in the literature of insect developmental times. For example, in their original paper, Lactin et al. (1995) noted that their modifications of the Logan model produced estimates of T_{max} that were sometimes as much as 5°C higher than those from the original Logan model. With respect to aphids, Diaz et al. (2007) obtained a T_{max} parameter from the Lactin equation that was 1.4°C higher than their estimate of UDT. A proper estimate of UDT is obtainable from the Lactin model only via simulation (substituting values into the equation to identify the point of intersection). Given that T_{max} in the Lactin model does not actually represent UDT, we would argue that researchers fitting a Lactin model should refrain from referring to this parameter as an estimate of UDT. Furthermore, to avoid confusion in the literature when using nonlinear models for developmental rates, it is important to clearly define true T_{min} and T_{max} as the temperatures at which $r(T) = 0$. These lower and upper development thresholds could be identified as T_{LDT} and T_{UDT}, respectively. A more fitting alternative, however, would be to rename the parameter T_{max} in the Lactin model; in Table 2, we refer to it as $T_{max\ modified}$. Finally, it should also be noted that with the Lactin-2 model, the estimate of optimum developmental temperature (T_{opt}) obtained from simulation also differs slightly from the calculation of $T_{max} - \Delta$.

In our study, *A. solani* reared at constant 25°C had significantly lower fecundity than aphids reared at 10–20°C. Studies with other aphid species show that a higher fecundity and a higher r_m may be achieved at more natural, fluctuating temperatures versus constant temperatures (Siddiqui et al. 1973, Elliott and Kieckhefer 1989, Kieckhefer and Elliott 1989, Davis et al. 2006). Thus, under greenhouse conditions, *A. solani* may possibly have a higher r_m and doubling time than indicated by our study.

The important differences in life table characteristics observed between our population and other populations of *A. solani* support the hypothesis of multiple biotypes. For example, the *A. solani* in Lee et al. (2008a, b) were originally collected from a commercial organic lettuce producer and developed more slowly at 25°C than at 20°C, which contrasts with both our study and that of Kim et al. (1991), who used a population collected from soybean in Korea. Also, our population developed and reproduced at warmer temperatures than those used by either Lee et al. (2008b) or Kim et al. (1991). These life history differences may have resulted from selection under different environmental conditions such as temperature (lettuce is typically grown at cooler temperatures of ≈15.5–18.3°C, Sanders 2001). However, these differences (Table 2) may also be attributable to the various host plants used among these studies. The much higher r_m value observed in our study versus that reported by Lee et al. (2008b) (0.44 versus 0.26 at 25°C) could simply be the result of pansy being a more nutritious food source than lettuce. This would seem to be supported by the higher nymphal mortality rates reported by Lee et al. (2008a) (13.3–30.0% at 15–25°C versus 0.0–7.1% in our study at the same temperatures).

This paper provides the first report of multi-temperature life table statistics and developmental time modeling for a North American population of *A. solani.* Intrinsic rates of increase are highest and doubling times are shortest for this species at 20–25°C, which is consistent with the observation that this species is most abundant in northeastern U.S. greenhouses on spring bedding crops during the cooler spring crop production temperatures. The poor survival/nearly complete lack of reproduction at 30°C and the upper development threshold of 35°C are also consistent with the observed decline of these aphids during greenhouse production temperatures of the summer months (J.P.S., personal observations). The information gathered in this study increases our knowledge of the biology of this pest and may lead to better predictions of *A. solani* outbreaks and improvements in the timing of greenhouse pest management practices.

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References Cited

Allison, P.D. 1995. Survival analysis using the SAS system: a practical guide. SAS Institute, Cary, NC.

Birch, L. C. 1948. The intrinsic rate of natural increase of an insect population. J. Anim. Ecol. 17: 15–26.

Blackman, R. L., and V. F. Eastop. 1984. Aphids on the world's crops: an identification and information guide. Wiley, New York.

Blackman, R. L., and V. F. Eastop. 1994. Aphids on the world's trees: an identification and information guide. CAB International, Wallingford, United Kingdom.

Blackman, R. L., and V. F. Eastop. 2006. Aphids on the world's herbaceous plants and shrubs, vol. 1&2. Wiley, Chichester, United Kingdom.

Campbell, A., B. D. Frazer, N. Gilbert, A. P. Guiterrez, and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. J. Appl. Ecol. 11: 431–438.

Conover, W. J. 1999. Practical nonparametric statistics, 3rd ed. Wiley, New York.

Crawley, M. J. 2007. The R book. Wiley, New York.

Damsteegt, V. D., and D. J. Voegtlin. 1990. Morphological and biological variation among populations of *Aulacorthum solani* (Homoptera: Aphididae), the vector of soybean dwarf virus. Ann. Entomol. Soc. Am. 83: 949–955.

Davis, J. A., E. B. Radcliffe, and D. W. Ragsdale. 2006. Effects of high and fluctuating temperatures on *Myzus persicae* (Hemiptera: Aphididae). Environ. Entomol. 35: 1461–1468.

Diaz, B. M., M. Muniz, L. Barrios, and A. Fereres. 2007. Temperature thresholds and thermal requirements for development of *Nasonovia ribisnigri* (Hemiptera: Aphididae). Environ. Entomol. 36: 681–688.

Down, R. E., A.M.R. Gatehouse, W.D.O. Hamilton, and J. A. Gatehouse. 1996. Snowdrop lectin inhibits development and decreases fecundity of the glasshouse potato aphid (*Aulacorthum solani*) when administered *in vitro* and via transgenic plants both in laboratory and glasshouse trials. J. Insect. Physiol. 42: 1035–1045.

Elliott, N. C., and R. W. Kieckhefer. 1989. Effects of constant and fluctuating temperatures on immature development and age-specific life tables of *Rhopalosiphum padi* (L.) (Homoptera: Aphididae). Can. Entomol. 121: 131–140.

Gish, M., and M. Inbar. 2006. Host location by apterous aphids after escape dropping from the plant. J. Insect. Behav. 19: 143–153.

Govier, D. A. 1957. The properties of tomato aspermy virus and its relationship with cucumber mosaic virus. Ann. Appl. Biol. 45: 62–73.

Heinz, K. M. 1998. Dispersal and dispersion of aphids (Homoptera: Aphididae) and selected natural enemies in spatially subdivided greenhouse environments. Environ. Entomol. 27: 1029–1038.

Kieckhefer, R. W., and N. C. Elliott. 1989. Effect of fluctuating temperatures on development of immature Russian wheat aphid (Homoptera: Aphididae) and demographic statistics. J. Econ. Entomol. 82: 119–122.

Kim, D-H., G-H. Lee, J-W. Park, and C-Y. Hwang. 1991. Occurrence aspects and ecological characteristics of foxglove aphid *Aulacorthum solani* Kaltenbach Homoptera Aphididae in soybean. Res. Rept. RDA (Crop. Prot.) 33: 28–32 (in Korean).

Kontodimas, D. C., P. A. Eliopoulos, G. J. Stathas, and L. P. Economou. 2004. Comparative temperature-dependent development of *Nephus includens* (Kirsch) and *Nephus bisignatus* (Bohenman) (Coleoptera: Coccinellidae) preying on *Planococcus citri* (Risso) (Homoptera: Pseudococcidae): evaluation of a linear and various nonlinear models using specific criteria. Environ. Entomol. 33: 1–11.

Lactin, D. J., N. J. Holliday, D. L. Johnson, and R. Craigen. 1995. Improved rate model of temperature-dependent development by arthropods. Environ. Entomol. 24: 68–75.

Lamb, R. J. 1992. Developmental rate of *Acyrthosiphon pisum* (Homoptera: Aphididae) at low temperatures: implication for estimating rate parameters in insects. Environ. Entomol. 21: 10–19.

Lee, S. G., H. H. Kim, T. H. Kim, G-J. Park, K. H. Kim, and J. S. Kim. 2008a. Development model of the foxglove aphid, *Aulacorthum solani* (Kaltenbach) on lettuce. Kor. J. Appl. Entomol. 47: 359–364.

Lee, S. G., H. H. Kim, T. H. Kim, G-J. Park, K. H. Kim, and J. S. Kim. 2008b. Longevity and life table of the foxglove aphid (*Aulacorthum solani K.*) adults on lettuce (*Lactuca sativa* L.). Kor. J. Appl. Entomol. 47: 365–368.

Logan, J. A., D. J. Walkind, S. C. Hoyt, and L. K. Tanigoshi. 1976. An analysis model for description of temperature dependent rate phenomena in arthropods. Environ. Entomol. 5: 1133–1140.

Mansouri, H. 1999. Multifactor analysis of variance based on the aligned rank transform technique. Comput. Stat. Data Anal. 29: 177–189.

MacGillivray, M. E., and G. B. Anderson. 1958. Development of four species of aphids (Homoptera) on potato. Can. Entomol. 90: 148–155.

Medeiros, R., F. S. Ramalho, J. E. Serrao, and J. C. Zanuncio. 2004. Estimative of *Podisus nigrispinus* (Dallas) (Heteroptera: Pentatomidae) development time with non linear models. Neotrop. Entomol. 33: 141–148.

Miles, P.W. 1990. Aphid salivary secretions and their involvement in plant toxicoses, pp. 131–147. *In* R. K. Campbell and R. D. Eikenbary (eds.), Aphid-plant genotype interactions. Elsevier, Amsterdam, The Netherlands.

Miller, G. L., and M. B. Stoetzel. 1997. Aphids associated with chrysanthemums in the United States. Fla. Entomol. 80: 218–239.

Miller, G. L., C. Favret, A. Carmichael, and D. J. Voegtlin. 2009. Is there a cryptic species within *Aulacorthum solani* (Hemiptera: Aphididae)? J. Econ. Entomol. 102: 398–400.

Mittler, T. E., and L. Wilhoit. 1990. Sexual morph production by two regional biotypes of *Myzus persicae* (Homoptera: Aphididae) in relation to photoperiod. Environ. Entomol. 19: 32–35.

Müller, F. P. 1970. Zucht und übertregungsversuche mit populationen and klonen der grünfleckigen kartoffelblattlaus *Aulacorthum solani* (Kalthenbach, 1843) (Homoptera: Aphididae). Dtsch. Entomol. Z. 17: 259–270 (in German).

Müller, F. P. 1976. Hosts and non-hosts in subspecies of *Aulacorthum solani* (Kalthenbach) and intraspecific hybridizations (Homoptera: Aphididae). Symp. Biol. Hung. 16: 187–190.

Nagano, T., Y. Umetsu, N. Hoshi, and T. Kidokoro. 2001. Outbreak of the foxglove aphid, *Aulacorthum solani* (Kalthenbach), in soybean fields of Miyagi Prefecture. II. Effect on soybean yield. Ann. Rep. Plant Prot. North Japan 52: 168–171 (in Japanese).

Okubu, T. 2001. Suppression of reproduction of the foxglove aphid (*Aulacorthum solani*) by high temperature—a thought on the outbreak of the foxglove aphid in Tohoku District in 2000. Ann. Rept. Plant Prot. North Japan 52: 168–171 (in Japanese).

Palumbo, J. C. 2003. The emergence of the foxglove aphid, *Aulacorthum solani*, as an economic pest of lettuce in the desert southwest. *In* D. N. Byrne and P. Baciewicz (eds.),

2003 vegetable report. (http://ag.arizona.edu/pubs/crops/az1323).

Patch, E. M. 1928. The foxglove aphid on potato and other plants. Maine Agric. Exp. Stn. Bull. 346: 49–60.

Peccoud, J., C. C. Figueroa, A. X. Silva, C. C. Ramirez, L. Mieuzet, J. Bonhomme, S. Stoeckel, M. Plantegenest, and J. C. Simon. 2008. Host range expansion of an introduced insect pest though multiple colonizations of specialized clones. Mol. Ecol. 17: 4608–4618.

Pozarowska, B. J. 1987. Studies on low temperature survival, reproduction and development in Scottish clones of *Myzus persicae* (Sulzer) and *Aulacorthum solani* (Kaltenbach) (Hemiptera: Aphididae) susceptible and resistant to organophosphates. Bull. Entomol. Res. 77: 123–134.

Roy, M., J. Brodeur, and C. Cloutier. 2002. Relationship between temperature and developmental rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *Tetranychus mcdanieli* (Acarina: Tetranychidae). Environ. Entomol. 31: 177–187.

Sanders, D. C. 2001. NC State University horticulture information leaflets: lettuce production. (http://www.ces.ncsu.edu/depts/hort/hil/hil-11.html).

Sanchez, J. A., F. Canovas, and A. Lacasa. 2007. Thresholds and management strategies for *Aulacorthum solani* (Hemiptera: Aphididae) in greenhouse pepper. J. Econ. Entomol. 100: 123–130.

SAS Institute. 2003. SAS/STAT user's guide. SAS Institute, Cary, NC.

Siddiqui, W. H., C. A. Barlow, and P. A. Randolph. 1973. Effects of some constant and alternating temperatures on population growth of the pea aphid, *Acyrthosiphon pisum* (Homoptera: Aphididae). Can. Entomol. 105: 145–156.

Southwood, T.R.E. 1978. The construction, description and analysis of age-specific life-tables, p. 367. *In* T.R.E. Southwood (ed.), Ecological methods: with particular reference to the study of insect populations, 2nd ed. Chapman & Hall, London, United Kingdom.

Stokes, M. E., C. S. Davis, and G. G. Koch. 2001. Categorical data analysis using the SAS system, 2nd ed. SAS Institute, Cary, NC.

Takada, H., T. Ono, H. Torikura, and T. Enokiya. 2006. Geographic variation in esterase allozymes of *Aulacorthum solani* (Homoptera: Aphididae) in Japan, in relation to its outbreaks on soybean. Appl. Entomol. Zool. 41: 595–605.

Tamada, T. 1970. Aphid transmission and host range of soybean dwarf virus. Ann. Phytopathol. Soc. Japan 36: 266–274.

Valenzuela, I., A. A. Hoffmann, M. B. Malipatil, P. M. Ridland, and A. R. Weeks. 2007. Identification of aphid species (Hemiptera: Aphididae: Aphidinae) using a rapid polymerase chain reaction restriction fragment length polymorphism method based on the cytochrome oxidase sub-unit I gene. Aust. J. Entomol. 46: 305–312.

Van Driesche, R. G., S. Lyon, J. P. Sanderson, K. C. Bennett, E. J. Stanek III, and R. Zhang. 2008. Greenhouse trials of *Aphidius colemani* (Hymenoptera: Braconidae) banker plants for control of aphids (Hemiptera: Aphididae) in greenhouse spring floral crops. Fla. Entomol. 94: 583–590.

Vasicek, A., F. De La Rossa, and A. Paglioni. 2001. Aspectos biológicos y poblacionales de *Aulacorthum solani*, *Myzus persicae* y *Macrosiphum euphorbiae* (Homoptera: Aphidoidea) en Pimiento (*Capsicum annum* L.). Bol. San. Veg. Plagas 27: 439:446 (in Spanish).

Vasicek, A., F. La Rossa, A. Paglioni, and P. Mendy. 2003. Biological and populational functionality of *Aulacorthum solani* (Kalthenbach) (Homoptera: Aphididae) on vegetable hosts under laboratory conditions. Bol. San. Veg. Plagas 29: 359–365 (in Spanish).

Wave, H. E., W. A. Shands, and G. W. Simpson. 1965. Biology of the foxglove aphid in the northeastern United States. Tech Bull. U.S. Dep. Agric. 1338: 1–40.

Zar, J. H. 1999. Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, NJ.

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