

Demography of Soybean Aphid (Homoptera: Aphididae) at Summer Temperatures

B. P. MCCORNACK, D. W. RAGSDALE, AND R. C. VENETTE

University of Minnesota, Department of Entomology, 219 Hodson Hall, 1980 Folwell Avenue, St. Paul, MN 55108

J. Econ. Entomol. 97(3): 854–861 (2004)

ABSTRACT Soybean aphid, *Aphis glycines* Matsumura, is now widely established in soybean, *Glycine max* L., production areas of the northern United States and southern Canada and is becoming an important economic pest. Temperature effect on soybean aphid fecundity and survivorship is not well understood. We determined the optimal temperature for soybean aphid growth and reproduction on soybean under controlled conditions. We constructed life tables for soybean aphid at 20, 25, 30, and 35°C with a photoperiod of 16:8 (L:D) h. Population growth rates were greatest at 25°C. As temperature increased, net fecundity, gross fecundity, generation time, and life expectancy decreased. The pre-reproductive period did not differ between 20 and 30°C; however, at 30°C aphids required more degree-days (base 8.6°C) to develop. Nymphs exposed to 35°C did not complete development, and all individuals died within 11 d. Reproductive periods were significantly different at all temperatures, with aphids reproducing longer and producing more progeny at 20 and 25°C than at 30 or 35°C. Using a modification of the nonlinear Logan model, we estimated upper and optimal developmental thresholds to be 34.9 and 27.8°C, respectively. At 25°C, aphid populations doubled in 1.5 d; at 20 and 30°C, populations doubled in 1.9 d.

KEY WORDS *Aphis glycines*, temperature, life table, fecundity, survivorship

THE SOYBEAN APHID, *Aphis glycines* Matsumura, is an introduced pest of soybean, *Glycine max* L., in North America and poses a serious threat to soybean production in the United States and Canada. High soybean aphid densities damage soybean plants by reducing plant height, pod number, and total yields, and yield reductions measured from grower strip trials have ranged from 12 to 45% (Ostlie 2001). Even at low densities, feeding by soybean aphid can greatly impair photosynthetic processes in soybean (Macedo et al. 2003). Indirect damage from feeding (i.e., virus transmission and sooty mold formation from honeydew excretion) is also a concern (Quimio and Calilung 1993, Clark and Perry 2002).

Temperature is a key abiotic factor that regulates insect population dynamics, developmental rates, and seasonal occurrence (Campbell et al. 1974, Logan et al. 1976, Schowalter 2000). Intrinsic rate of increase, upper and lower developmental thresholds, fecundity, and survivorship schedules are essential for describing temperature effects on aphid population dynamics (Walgenbach et al. 1988, Aldyhim and Khalil 1993, Carey 1993, Asin and Pons 2001). However, soybean aphid biology, in general, and life table statistics, in particular, are not well understood for conditions in North America.

Few studies have focused on the importance of temperature for soybean aphid population growth

(but see Hirano et al. 1996). Hirano et al. (1996) reported a lower developmental threshold of 9.5°C and an optimal temperature of 27°C. However, the effect of high temperature (maximal lethal temperature) on soybean aphid survival and reproduction has not been well characterized. Decline in relative growth rate, respiratory rate, and honeydew production for other aphid species at high temperatures has been well documented (Dixon 1998).

Management of soybean aphid in Minnesota occurs between July and August when average daily temperatures typically range from 19 to 35°C (Climatology Working Group 2003). Decisions to treat infestations of apterous soybean aphid with foliar insecticides are typically made in Minnesota during this period (Ostlie 2001). Chemical applications are typically based on an assessment of aphid densities at a fixed point in time. The relevance of this assessment to future management decisions depends on how quickly aphid densities may change over time. Thus, we must understand the influence of temperature on soybean aphid population growth.

The objective of this study was to determine the optimal and upper developmental temperatures for apterous soybean aphid growth and reproduction under controlled conditions, focusing our effort on temperatures common during midsummer in the North Central United States.

Materials and Methods

Insects and Plant Material. Laboratory colonies of soybean aphid were started in July 2002 with field-collected apterae from soybean at the University of Minnesota Rosemount Research and Outreach Center (Rosemount, MN). Voucher specimens were placed in the insect museum at the University of Minnesota (UMSP 000083760). Colonies were maintained on soybean seedlings (cultivar M96-133151) at $25 \pm 1^\circ\text{C}$, 70–80% RH, and a photoperiod of 16:8 (L:D) h. To maintain the soybean aphid colony, 20–30 aphids were transferred from mature, heavily infested plants to young, noninfested soybean plants every 2 wk.

Soybean seedlings (cultivar M96-133151) used in the experiment were grown in square pots (9 by 9 by 8 cm) in pasteurized potting soil (Sunshine SB300 Universal Professional Growing Mix, Sun Gro Horticulture, Inc., Bellevue, WA) covered with ≈ 2 cm layer of sand to prevent erosion when watered (every 2–3 d). Soybean was grown in a growth chamber (model E15, Conviron, Winnipeg, Manitoba, Canada) at $25.0 \pm 0.5^\circ\text{C}$ and $75 \pm 5\%$ RH with a photoperiod of 16:8 (L:D) h and an approximate light intensity of $875 \mu\text{mol}/\text{m}^2/\text{s}$. Soybean at the V-0 stage (newly unfolded unifoliate leaves; Fehr and Caviness 1977) were used in the experiment.

Aphid Survival, Development, and Reproduction. Development, survival, and reproduction of soybean aphid were studied at constant temperatures (20, 25, 30, and 35°C) in separate, reach-in climate-controlled growth chambers. The experiment followed a randomized complete block design with temperatures randomly assigned to a chamber. The experiment was conducted (blocked) at three points in time with chamber temperatures rerandomized in each block. An apterous adult soybean aphid from the colony was placed on each of 12 soybean plants within each chamber at the assigned temperature. Adults were allowed to reproduce for 24 h and then adults were removed. The initial cohort (F_0) was counted and allowed to develop for 2–3 d. Each late instar (third and fourth) aptera (F_0 cohort) was transferred to an individual soybean seedling and was reared singly within a chamber (Hirano et al. 1996). Each F_0 aphid was checked daily for mortality. As nymphs became adult apterae, newly deposited F_1 nymphs were counted and removed daily. Because 99.8% of nymph production occurred within the first 22 d of life at all temperatures tested, we reduced the observation time in two of the three blocks by ≈ 14 d and stopped observations after 22 d. To reduce the effects of plant age on aphid reproduction and survivorship, soybean aphids were transferred to new V-0 soybean seedlings every 3–4 d (Hirano et al. 1996). For each block, the number of aphids in a chamber varied between 34 and 83. For the entire experiment, 147 aphids were examined at 20°C , 145 at 25°C , 189 at 30°C , and 126 at 35°C .

Because insect development is dependent on temperature, insect age (d) does not realistically describe an insect's physiological maturity (Allen 1976, Hutchinson and Hogg 1984). To integrate time and tempera-

ture, we plotted survivorship and fecundity against physiological time, measured in degree-days (DD). For survivorship, we calculated the cumulative degree-days (CDD) for each aphid at time of death using the following equation:

$$\text{CDD} = (T - K_l) * t \quad [1]$$

where T is chamber temperature, K_l is lower developmental threshold, and t is number of days alive at the chamber temperature. The lower developmental threshold was estimated by regressing developmental rates, $r(T) = 1/[\text{age (d) at first reproduction}]$, at 17, 22, and 27°C reported in Hirano et al. (1996) and our observed developmental rates at 20 and 25°C against temperature. Fecundity (m_x) schedules were also developed on calendar and physiological time scales. Physiological time was estimated by substituting calendar age for t in equation 1.

From the fertility and survivorship schedules, life tables and the following population growth statistics were calculated using formulae presented in Carey (1993): intrinsic rate of increase (r), generation time, life expectancy, discrete growth rate (λ), gross fecundity, doubling time, and age-specific survivorship. Because observations of aphid survivorship and fecundity were terminated before the death of some aphids, survivorship analysis required a statistical test that accounted for censored events (Bland and Altman 1998). Life tables were calculated using PROC LIFETEST (SAS Institute 2001). We used the Kaplan-Meier (KM) estimator for survivor functions, and significant differences in survivor functions were determined using a log-rank test (Mantel-Haenszel test, Allison 1995). Effects of temperature on the prereproductive period, reproductive period, and net fecundity on calendar and physiological time scales were analyzed with one-way analysis of variance (ANOVA) (PROC GLM, SAS Institute 2001). Means were separated using the Ryan-Einot-Gabriel-Welsch (REGWQ option) multiple range test. Differences were considered significant at $\alpha = 0.05$.

Optimal and Upper Developmental Thresholds. We used the Logan model, as modified by Lactin et al. (1995), to describe the influence of temperature on aphid development. This model assumes an asymmetrical response to temperature about the optimum temperature and was used to predict the optimal and upper developmental temperatures for soybean aphid. Developmental rates, $r(T) = 1/[\text{age (d) at first reproduction}]$, were plotted against temperature (T) for all F_0 individuals that produced F_1 nymphs ($n = 336$ observations). Developmental rates for soybean aphids reared at 35°C could not be calculated, because nymphs (F_0 cohort) did not reach the adult stage. Therefore, 35°C was not used in the analysis. Data were fitted using modification one of the Logan model described by Lactin et al. (1995):

$$r(T) = e^{\rho T} - e^{\rho T_{max} - (T_{max} - T)/\Delta} \quad [2]$$

where ρ is "interpreted as a composite Q_{10} value for critical enzyme-catalyzed, biochemical reactions," T_{max} is the "temperature at which life processes can no

Table 1. Development and reproduction of soybean aphid reared at four constant temperatures on soybean

	20°C	25°C	30°C	F'	P
Prereproductive period ^b					
Days	6.6 ± 0.1a	4.9 ± 0.1a	5.1 ± 0.1a	5.45	0.07
DD ^c	74.5 ± 0.7a	80.9 ± 1.1a	109.3 ± 2.4b	241.75	<0.0001
n	115	107	114		
Reproductive period					
Days	11.7 ± 0.4a	9.5 ± 0.3b	6.3 ± 0.3c	72.46	<0.0001
DD	133.6 ± 4.1a	155.6 ± 5.4b	134.2 ± 5.8a	8.24	0.0003
n	115	107	114		
Net fecundity					
Offspring/female	63.5 ± 2.2a	61.2 ± 2.7a	20.3 ± 1.4b	45.41	0.0002
n	147	145	189		

Values are mean ± standard errors. Values within a row followed by the same letter are not significantly different ($P > 0.05$). n, number of replications.

^a Degrees of freedom = 2,4.

^b Time from F₀ larvaponition to F₁ larvaponition.

^c Threshold temperature 8.6°C

longer be maintained for prolonged periods of time," and Δ is the "temperature range over which thermal breakdown becomes the overriding influence" (Logan et al. 1976). Parameters from Logan's model (ρ , T_{max} , and Δ) were estimated using nonlinear regression (PROC NLIN, SAS Institute 2001). The Marquardt (1963) method was used to select least-square estimates for the above-mentioned nonlinear parameters.

Aphid Size. In a separate, companion study, we examined the effects of temperature on aphid size. F₁ nymphs were kept on V-1 (one expanded trifoliolate) soybean plants and nymphs were allowed to develop and reproduce on a plant for 10 d at 20, 25, and 30°C. This was replicated four times at each temperature. After 10 d, all aphids were removed from the plants and placed in 70% ethanol. Lengths and widths of adult apterae were measured using a dissecting microscope fitted with a calibrated ocular micrometer. No alatae or alatoid nymphs were observed. Length (millimeters) was measured from the tip of the head to the tip of the cauda, and width (millimeters) was measured at the widest point of the aphid. These data were only available from a single block, so the effect of temperature was not truly replicated. Thus, only means and standard errors for all adults measured are reported.

Results and Discussion

Aphid Survival and Development. All adults from the original colony held at 25°C and placed at four constant temperatures (20, 25, 30, and 35°C) produced nymphs (F₀) within 24 h. All nymphs held at 35°C died within 11 d and never produced offspring. Successful development from F₀ to F₁ occurred at 20, 25, and 30°C. There were no significant differences in prereproductive periods at temperatures 20, 25, or 30°C ($F = 5.45$; $df = 2, 6$; $P = 0.07$) (Table 1). Because there was a significant block effect, data could not be pooled and further mean separations tests could not be calculated. However, Hirano et al. (1996) did find a significant difference in prereproductive periods;

aphids reared at 22°C matured slower than aphids reared at 27°C.

On a degree-day scale, prereproductive periods were greatly affected by temperature. The prereproductive period was significantly longer at 30°C than at 20 or 25°C ($F = 241.75$; $df = 2, 6$; $P < 0.0001$), but there was no difference between 20 and 25°C (Table 1). Soybean aphids developed ≈ 34.8 DD (1.6 d) slower at 30°C than aphids reared at 25°C. If 30°C was not adversely affecting development, we would not expect a difference in the number of degree-days accumulated before the onset of reproduction. However, the later onset of nymph production observed at 30°C could be attributed to sublethal temperature effects, and our data suggest that the optimum temperature for development is between 25 and 30°C.

The lower developmental threshold (K_l) was first estimated by Hirano et al. (1996) to be 9.5°C. From a plot of our observed developmental rates at 20 and 25°C, we predicted a K_l of 5.6°C (Fig. 1). However, we

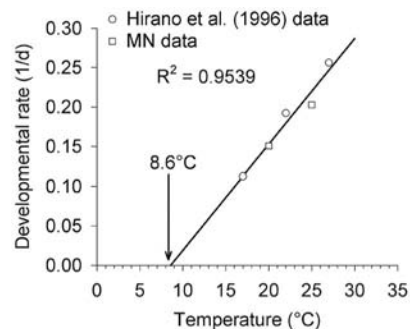


Fig. 1. Mean developmental rate, $r(T) = 1/[\text{age (d)}]$ at first reproduction], versus temperature for soybean aphid. Open squares represent developmental rates observed in this Minnesota study and open circles represent developmental rates reported by Hirano et al. (1996). Solid line is predicted based on linear regression. Calculated lower developmental threshold is 8.6°C.

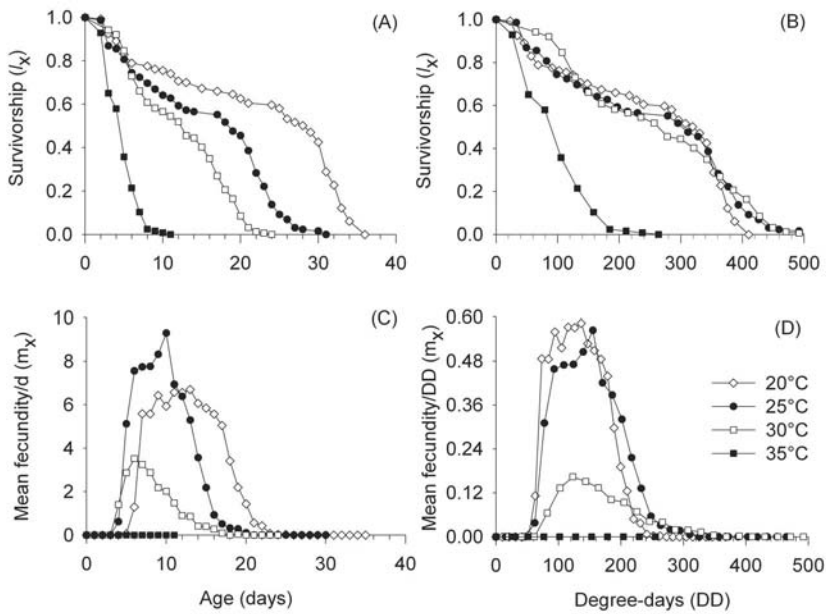


Fig. 2. Survivorship as a function of (A) calendar age and (B) physiological age (degree-days, base 8.6°C), and fecundity as a function of (C) calendar age and (D) physiological age for soybean aphid reared at four constant temperatures on soybean.

obtained a more robust estimate of K_I when we combined our data with those reported by Hirano et al. (1996). Assuming a similar biotype exists between the two soybean aphid populations, regression with the joint data set produced the line $r(T) = -0.115 \pm 0.038$ (SEM) + 0.013 ± 0.002 (SEM)*T ($F = 62.01$; $df = 1, 3$; $P = 0.004$; $r^2 = 0.9539$) (Fig. 1). From this line, we estimated K_I (the temperature where no development occurs) to be 8.6°C. The 95% confidence interval from the combined analysis (2.1–15.0°C) includes both our estimate and the estimate provided by Hirano et al. (1996). Thus, all remaining degree-day calculations use the combined lower developmental estimate of 8.6°C.

Survivorship schedules on a calendar basis were significantly different from each other ($\chi^2 = 279$, $df = 3$, $P < 0.0001$) (Fig. 2A): 20 versus 25°C ($\chi^2 = 63.2$, $df = 1$, $P < 0.0001$), 20 versus 30°C ($\chi^2 = 114.5$, $df = 1$, $P < 0.0001$), 20 versus 35°C ($\chi^2 = 181.5$, $df = 1$, $P = 0.0007$), 25 versus 30°C ($\chi^2 = 49.4$, $df = 1$, $P < 0.0001$), 25 versus 35°C ($\chi^2 = 148.5$, $df = 1$, $P < 0.0001$), and 30 versus 35°C ($\chi^2 = 167.8$, $df = 1$, $P < 0.0001$). In general, as temperature increased, survivorship of aphids decreased (Fig. 2A). Complete mortality for F_0 aphids reared at 20, 25, 30, and 35°C was observed at 36, 31, 24, and 11 d, respectively. This relationship between aphid survivorship and temperature has been reported for other aphid species: *Eriosoma lanigerum* (Hausmann) (Asante et al. 1991), *Toxoptera citricida* (Kirkaldy) (Tang et al. 1999, Tsai and Wang 1999), and *Sitobion avenae* (F.) (Kieckheffer et al. 1989). In all cases, aphid mortality increased and longevity decreased with increasing temperatures.

Hirano et al. (1996) found a similar relationship when comparing nymphal survivorship to tempera-

ture. Nymphs had a greater rate of survival at lower temperatures than at higher temperatures. Hirano et al. (1996) also showed that mean adult longevity was significantly greater at 22°C compared with aphids reared at 27°C. Nymphs of *Aphis gossypii* Glover, a close relative to soybean aphid, also lived significantly longer at lower temperatures (Komazaki 1982, Aldyhim and Khalil 1993). Like soybean aphid, *A. gossypii* nymphs reared at a constant temperature of 35°C complete some development but fail to reach the third instar (Aldyhim and Khalil 1993).

When survivorship (l_x) was expressed in physiological time (degree-days), soybean aphid survivorship curves at 20, 25, and 30°C were not significantly different from each other ($\chi^2 = 5.45$, $df = 3$, $P = 0.07$) (Fig. 2B). Survivorship at 35°C was significantly different from 20, 25, and 30°C ($\chi^2 = 147$, $df = 2$, $P < 0.0001$). Complete mortality for aphids reared at 20, 25, 30, and 35°C was observed at 410, 508, 513, and 290 DD, respectively (Fig. 2B). Our data suggests that soybean aphid is not well adapted to constant 35°C.

Age-specific daily fecundity (m_x) varied greatly at different temperatures (Fig. 2C). All F_0 nymphs held at 35°C died so there are no data at this temperature. Offspring production at 20, 25, and 30°C peaked after 13, 10, and 6 d, respectively. Mean fecundity at the time of peak production at 20, 25, and 30°C was 6.5, 9.5, and 3.5 nymphs per day, respectively (Fig. 2C). Soybean aphids reared at lower temperatures produced offspring for a significantly longer period than aphids at higher temperatures ($F = 72.46$; $df = 2, 6$; $P < 0.0001$) (Table 1). Significantly more total offspring per female were produced at 20 and 25°C than at 30°C ($F = 45.41$; $df = 2, 6$; $P = 0.0002$). Our fecundity schedule coincides with other reported data. At 22°C,

Table 2. Life table parameters describing soybean aphids reared at four constant temperatures on soybean

	20°C	25°C	30°C	35°C
Intrinsic rate of increase (r ; d^{-1})	0.368	0.474	0.375	-0.383
Discrete daily growth rate (λ ; d^{-1})	1.445	1.606	1.455	0.682
Gross fecundity (offspring/female)	75.48	72.96	22.55	— ^a
Doubling time (d)	1.88	1.46	1.85	—
Generation time (d)	12.86	9.76	8.06	—
Life expectancy (d)	21.93	15.25	11.79	3.38

^a All aphids died before reproduction.

soybean aphid fecundity peaks at 11 d with a mean daily fecundity of eight nymphs per day, and aphids at 27°C peak after 8 d with a mean daily fecundity of 9.5 nymphs per day (Hirano et al. 1996). Lin and Ives (2003) report a peak in nymphal production 13 d after initial reproduction with an average production of four nymphs per day for soybean aphids reared on a 25 and 20°C, 16:8 (L:D)h schedule.

The reproductive period in physiological time (degree-day scale) was also affected by temperature (Fig. 2D; Table 1). Aphids reared at 25°C spent significantly more physiological time reproducing than aphids reared at 20 or 30°C ($F = 6.21$; $df = 2, 6$; $P = 0.002$); however, there was no significant difference in the number of degree-days spent reproducing at 20 or 30°C (Table 1). This result is different from what we observed for age-specific reproductive periods at 20 and 30°C (Fig. 2C). On a calendar basis, soybean aphids spent more time (5.5 d) producing offspring at 20°C than at 30°C. However, when we compare reproductive periods in physiological time, aphids spent an equal amount of degree-days reproducing at 20 and 30°C (Fig. 2D; Table 1). Even though there is no difference in physiological time spent reproducing, net fecundity is greatly reduced when soybean aphids are reared at constant 30°C (Table 1). Although aphids spent the most physiological time reproducing at 25°C, there seems to be some advantage for aphids to reproduce at 20°C. Specifically, soybean aphids reared at 20°C can produce more nymphs in a shorter amount of time than aphids reared at 25°C. Conversely, more physiological time is spent producing offspring at 25°C than 20°C, but the net number of offspring produced at these temperatures is the same. Even though aphids at 30°C are spending as much physiological time reproducing as aphids at 20°C, reproduction at 30°C is significantly reduced (Table 1).

Net fecundity at higher temperatures is greatly reduced in many aphid species (Dixon 1998, Aldyhim and Khalil 1993, Hirano et al. 1996, Asante et al. 1991, Tsai and Wang 1999). In our experiment, exposing soybean aphids to 30°C caused a 30–33% reduction in net offspring production compared with aphids reared at 20 or 25°C. Hirano et al. (1996) showed a similar relationship; at 27°C, soybean aphids produced 15% fewer offspring than aphids exposed to 22°C. For *A. gossypii*, the greatest reproduction occurs at a constant 25°C, and total fecundity is reduced by ≈85% when aphids are exposed to a constant 30°C (Aldyhim and Khalil 1993). For *E. lanigerum*, net fecundity is reduced by 89% when reared at 5°C above its optimal

temperature (Asante et al. 1991). When *Rhopalosiphum padi* (L.) is reared at 27.5°C, total fecundity is 96% greater than when reared at 30°C. Tsai and Wang (1999) reared *T. citricida* at 32°C and found that fecundity was reduced by 83% compared with aphids reared at 28°C.

Population Statistics. Summary life table statistics for the soybean aphid are presented in Table 2. The negative r value at 35°C indicates that population size is decreasing due to high mortality and no reproduction. Intrinsic rate of increase was higher at 25°C than 30 or 20°C (Table 2). Aphids reared at 25 and 30°C are developing faster than aphids at 20°C and are producing more offspring sooner (Fig. 2C). Intrinsic rate of increase is also higher at 25°C because nymphs that were deposited are becoming reproductive adults sooner than nymphs reared at 20°C. However, net offspring production is the same at 20 and 25°C. Other life table parameters describing soybean aphid development at different temperatures show similar trends. Discrete daily growth rates for soybean aphid peaked at 25°C ($\lambda = 1.606$) and were smallest when exposed to 35°C ($\lambda = 0.682$); $\lambda < 1$ indicates that the population is decreasing (Table 2). Gross fecundity (the total number of offspring that a female could produce if lived to her absolute age) was also higher at 20 and 25°C than aphids reared at 30°C. Doubling time was lowest at 25°C (1.46 d) and higher at 20 and 30°C (1.88 and 1.85 d, respectively). Soybean aphid generation time decreased as temperature increased toward an optimal temperature. Generation time is defined as “the time required for a population to increase by a factor equal to the net reproductive rate” (Carey 1993). As temperatures increase the developmental rate defined by the prereproductive period decreases and aphids are producing offspring at a faster rate. Life expectancy was also negatively affected by increasing temperature. Soybean aphids reared at 30°C would live about one-half as long as individuals at 20°C.

Daily survivorship, fecundity schedules, and developmental rates dictate intrinsic rates of increase in aphids (Dixon 1998). Even though net fecundity is 30% lower at 30°C than at 20°C, the population is increasing at a faster rate than a population at 20°C. There is little difference between soybean aphid survivorship curves at 20 and 30°C within the first 8–9 d of life. During this time, aphids at 30°C produce more offspring faster at an earlier age than aphids at 20°C, which explains the higher r observed at 30°C. Hirano et al. (1996) also found a greater r at 27°C (0.533) versus 22°C (0.445) and the values reported at these

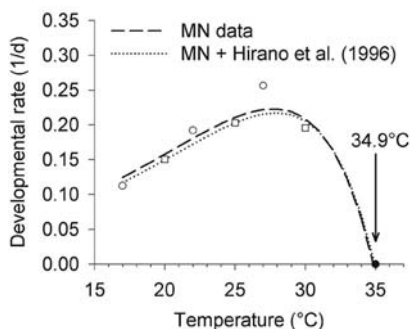


Fig. 3. Plot of developmental rate versus temperature for individual soybean aphids exposed to constant temperatures. Open squares represent the Minnesota mean developmental rate for individuals within a given temperature, open circles represent data reported by Hirano et al. (1996), and the solid circle represents data excluded from the analysis. Long dash line represents the fitted Logan model to our data and dotted line represents our data combined with Hirano et al. (1996). Calculated upper developmental threshold is 34.9°C.

temperatures are consistent with our data (Table 2). A rapid generation time is offset by lower net fecundity and shorter life span when aphids are held at a constant 30 versus 20°C. As soybean aphid developmental rates increase past the optimum developmental threshold, net fecundity of an individual is reduced, demonstrating that this species performs best in cooler temperatures. *A. gossypii* has a growth rate similar to soybean aphid at 25°C ($r = 0.496$, Aldyhim and Khalil 1993), yet *A. gossypii* persists in warmer climates (Blackman and Eastop 2000). In general, longevity, generation time, and population doubling time for *A. gossypii* Glover decrease as temperature increases (Aldyhim and Khalil 1993). All life table statistics reported for soybean aphids reared at 25°C coincide with values reported for *A. gossypii* (Aldyhim and Khalil 1993).

Upper Developmental Thresholds. A fundamental component to ectotherm development is the nonlinear relationship between temperature and development. This is especially true for aphids, which are viewed as temperate insect pests (Dixon 1998). Once temperatures exceed the developmental optimum, the results are prolonged development and premature death (Lactin et al. 1995). Many models have been used to predict developmental thresholds in insects (Logan et al. 1976, Sharpe and DeMichele 1977, Taylor 1981, Wagner et al. 1984). We used modification one of the Logan model (Lactin et al. 1995) to fit our observed developmental rates (1/d) against temperature (Fig. 3). A good fit ($r^2 = 0.997$) was achieved using all aphid developmental rates within the temperature range of 20–30°C. The upper developmental threshold (maximal lethal temperature), Δ (range of thermal breakdown), and ρ were estimated at $34.9 \pm 0.5^\circ\text{C}$ (95% CI, 33.9–35.9°C), $7.1 \pm 0.4^\circ\text{C}$ (95% CI, 6.4–7.9°C), and 0.14 ± 0.01 (95% CI, 0.12–0.15), respectively ($F = 117.5$; $df = 3, 334$; $P < 0.0001$). Hirano

et al. (1996) observed some soybean aphid development from nymphs to adults at 32°C, but survival of immature stages was greatly reduced. In our experiment, soybean aphids reared at 35°C failed to develop to adults and thus never produced F_1 offspring. This observation is independent confirmation that our calculation of an upper developmental threshold of 34.9°C is accurate; recall that data for 35°C were not used to fit the Logan model.

Optimal temperature for soybean aphid development was estimated from our data to be 27.8°C, at which time from birth to first reproduction was predicted to be 4.5 d (Fig. 3). The optimal temperature was calculated by subtracting Δ (7.1°C) from the upper developmental threshold (34.9°C). The developmental rate (1/d) at the optimal temperature was calculated by substituting 27.8°C for T in equation 2 and solving for $r(T)$. In Hirano et al. (1996), the number of days to first reproduction was shortest at 27°C and was 3.9 d. When the Logan model is applied to our developmental rates alone at temperatures ranging from 20 to 30°C, it overestimates the number of days to develop at 27°C by only 0.6 d.

To evaluate the sensitivity of our result to the amount of data that were available, we recalculated the optimal temperature by applying the Logan model to a data set that included our mean developmental rates and the rates reported in Hirano et al. (1996) (Fig. 3). This analysis also assumes that biotypes from both populations are not different from each other. The upper developmental threshold, Δ , and ρ from the combined data set were estimated at $35.0 \pm 0.2^\circ\text{C}$ (95% CI, 34.3–35.6°C), $7.0 \pm 0.6^\circ\text{C}$ (95% CI, 5.4–8.6°C), and 0.14 ± 0.01 (95% CI, 0.11–0.18), respectively ($F = 167.3$; $df = 3, 4$; $P < 0.0001$). Optimal developmental threshold was calculated as in the previous model and was estimated at 28.0°C with a developmental rate of 0.217 (1/d) (Fig. 3). Upper developmental threshold and Δ estimates that include data from Hirano et al. (1996) are well within the 95% CL derived from our original prediction model.

Aphid Size. Aphid size seemed to vary greatly between the temperatures. Results must be interpreted carefully because statistical analysis was not appropriate; size differences could be due to a chamber effect and not temperature. However, there seems to be a trend between higher temperature and aphid size (Fig. 4). Aphids under high temperature spend more energy on catabolic processes and less energy on development (Dixon 1998). Aphids reared at 30°C were smaller in length and width than aphids reared at 20°C. This relationship has been reported for other aphid species (Dixon 1998). In *A. gossypii*, aphid body length is negatively correlated with temperature (Aldyhim and Khalil 1993). As temperature increases, body length for this species decreases to <1 mm where normal apterae length is between 0.9 and 1.8 mm (Blackman and Eastop 2000). *Myzus persicae* (Sulzer) is also affected by high temperature, and reduction in aphid size is directly linked to adverse effects on aphid symbionts (Dixon 1998). Aphid size can affect population dynamics by changing predator/parasitoid and

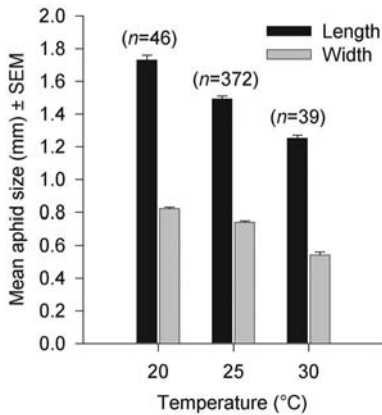


Fig. 4. Length and width (millimeters) of apterous adult soybean aphid reared at 20, 25, and 30°C on soybean. n, number of adults measured.

prey relationships. Lin and Ives (2003) were able to show size preference of an aphid parasitoid, *Aphidius colemani* (Viereck), to large, reproductive soybean aphids. Handling rates decreased and search time increased for the sevenspotted ladybeetle, *Coccinella septempunctata* L., in response to increasing size of *A. gossypii* (Xia et al. 2003).

In all 3 yr that soybean aphid has been present in Minnesota, soybean aphid has never been exposed to 35°C for more than a few hours per day (Climatology Working Group 2003). Clearly, rearing aphids at a constant 35°C is beyond the normal range experienced in southern Minnesota soybean fields. However, results from this research provide a starting point for developing a model that could be applied to soybean aphid population growth. In the field, aphid demographics also may be influenced by predators (Rutledge et al. 2004), parasitoids (Heimpel et al. 2004), pathogens (Ragsdale et al. 2004), plant growth (B.P.M., unpublished data), and aphid density, each of which may respond to temperatures differently. Our studies establish the biotic potential of soybean aphid in the absence of antagonists on young hosts under strictly defined climatic conditions. Our studies clearly demonstrate that soybean aphid populations have the potential to change very quickly. Under suitable conditions, populations may double in <2 d. Consequently, growers may have to react to estimates of aphid densities quickly, having to decide whether to treat or resample. Conversely, under inclement temperature conditions, aphid populations may change very little in time, affording growers more time to make a management decision. Thus, simply understanding the potential for populations to change has some utility for management decisions. Our goal is to provide guidance to crop professionals about the potential population dynamics that could be expected given a particular set of temperatures. Future research efforts should focus on the effects of fluctuating temperatures on soybean aphid population growth.

Acknowledgments

We thank Adriano Pereira (University of Minnesota) for help in data collection and Erin Hodgson (University of Minnesota) and two anonymous reviewers for helpful comments on the manuscript. This study was supported by the North Central Soybean Research Program and the University of Minnesota Rapid Agricultural Response Fund.

References Cited

- Aldyhim, Y. N., and A. F. Khalil. 1993. Influence of temperature and daylength on population development of *Aphis gossypii* on *Cucurbita pepo*. *Entomol. Exp. Appl.* 67: 167–172.
- Allen, J. C. 1976. A modified sine wave method for calculating degree days. *Environ. Entomol.* 5: 388–396.
- Allison, P. D. 1995. *Survival analysis using SAS: a practical guide*. SAS Institute, Cary, NC.
- Asante, S. K., W. Danthararayanan, and H. Heatwole. 1991. Bionomics and population growth statistics of apterous virginoparae of woolly apple aphid, *Eriosoma lanigerum*, at constant temperatures. *Entomol. Exp. Appl.* 60: 261–270.
- Asin, L., and X. Pons. 2001. Effect of high temperature on the growth and reproduction of corn aphids (Homoptera: Aphididae) and implications for their population dynamics on the Northeastern Iberian Peninsula. *Environ. Entomol.* 30: 1127–1134.
- Blackman, R. L., and V. F. Eastop. 2000. *Aphids on the world's crops: an identification guide*, 2nd ed. Wiley, New York.
- Bland, J. M., and D. G. Altman. 1998. Survival probabilities (the Kaplan-Meier method). *Br. Med. J.* 317: 1572.
- Campbell, A., B. D. Frazer, N. Gilbert, A. P. Gutierrez, and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. *J. Appl. Ecol.* 11: 431–438.
- Carey, J. R. 1993. *Applied demography for biologists with special emphasis on insects*. Oxford University Press, New York.
- Clark, A. J., and K. L. Perry. 2002. Transmissibility of field isolates of soybean viruses by *Aphis glycines*. *Plant Dis.* 86: 1219–1222.
- Climatology Working Group. 2003. Historical climate data retrieval. University of Minnesota, St. Paul, MN. <http://climate.umn.edu/doc/historical.hm>.
- Dixon, A.F.G. 1998. *Aphid ecology: an optimization approach*. 2nd ed. Chapman & Hall, London, England.
- Fehr, W. R., and C. E. Caviness. 1977. *Stages of soybean development*. Iowa State University Coop. Ext. Serv. Special Rep. 80. Ames, IA.
- Heimpel, G. E., D. W. Ragsdale, R. Venette, K. R. Hopper, R. J. O'Neil, C. E. Rutledge, and Z. Wu. 2004. Prospects for importation biological control of the soybean aphid: anticipating potential costs and benefits. *Ann. Entomol. Soc. Amer.* 97: 249–258.
- Hirano, K., K. Honda, and S. Miyai. 1996. Effects of temperature on development, longevity, and reproduction of the soybean aphid, *Aphis glycines* (Homoptera: Aphididae). *Appl. Entomol. Zool.* 31: 178–180.
- Hutchison, W. D., and D. B. Hogg. 1984. Demographic statistics for the pea aphid (Homoptera: Aphididae) in Wisconsin and a comparison with other populations. *Environ. Entomol.* 13: 1173–1181.
- Kieckheffer, R. W., N. C. Elliott, and D. D. Walgenbach. 1989. Effects of constant and fluctuating temperatures on developmental rates and demographic statistics of the

- English grain aphid (Homoptera: Aphididae). *Ann. Entomol. Soc. Am.* 82: 701–706.
- Komazaki, S. 1982. Effects of constant temperatures on population growth of three aphid species, *Toxoptera citricidus* (Kirkclady), *Aphis citricola* Van der Goot and *Aphis gossypii* Glover (Homoptera: Aphididae) on citrus. *Appl. Entomol. Zool.* 17: 75–81.
- 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.
- Lin, L. A., and A. R. Ives. 2003. The effect of parasitoid host-size preference on host population growth rates: an example of *Aphidius colemani* and *Aphis glycines*. *Ecol. Entomol.* 28: 542–550.
- Logan, J. A., D. J. Wollkind, S. C. Hoyt, and L. K. Tanigoshi. 1976. An analytic model for description of temperature dependent rate phenomena in arthropods. *Environ. Entomol.* 5: 1133–1140.
- Macedo, T. B., C. S. Bastos, L. G. Higley, K. R. Ostlie, and S. Madhavan. 2003. Photosynthetic responses of soybean to soybean aphid (Homoptera: Aphididae) injury. *J. Econ. Entomol.* 96: 188–193.
- Marquardt, D. W. 1963. An algorithm for least squares estimation of nonlinear parameters. *J. Soc. Ind. Math.* 11: 431–441.
- Ostlie, K. (ed.) 2001. Soybean aphid reduces yields: harvest results from insecticide strip trials. University of Minnesota, St. Paul, MN. <http://www.soybeans.umn.edu/crop/insects/aphid/studyresults.htm>.
- Quimio, G. M., and V. J. Calilung. 1993. Survey of flying viruliferous aphid species and population build up of *Aphis glycines* Matsumura in soybean fields. *Phillipp. Entomol.* 9: 52–100.
- Ragsdale, D. W., D. J. Voegtlin, and R. J. O'Neil. 2004. Soybean Aphid Biology in North America. *Ann. Entomol. Soc. Am.* 97: 204–208.
- Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004. Soybean aphid predators and their use in Integrated Pest Management. *Ann. Entomol. Soc. Amer.* 97: 240–248.
- SAS Institute. 2001. PROC user's manual, version 6th ed. SAS Institute, Cary, NC.
- Schowalter, T. D. 2000. Insect ecology: an ecosystem approach. Academic, San Diego, CA.
- Sharpe, P.J.H., and D. W. DeMichele. 1977. Reaction kinetics of poikilotherm development. *J. Theor. Biol.* 64: 649–670.
- Tang, Y. Q., S. L. Lapointe, L. G. Brown, and W. B. Hunter. 1999. Effects of host plant and temperature on the biology of *Toxoptera citricada* (Homoptera: Aphididae). *Environ. Entomol.* 28: 895–900.
- Taylor, F. 1981. Ecology and evolution of physiological time in insects. *Am. Nat.* 117: 1–23.
- Tsai, J. H., and K. Wang. 1999. Life table study of brown citrus aphid (Homoptera: Aphididae) at different temperatures. *Environ. Entomol.* 28: 412–419.
- Wagner, T. L., H. Wu, P.J.H. Sharpe, R. M. Schoolfield, and R. N. Coulson. 1984. Modeling insect development rates: a literature review and application of a biophysical model. *Ann. Entomol. Soc. Am.* 77: 208–225.
- Walgenbach, D. D., N. C. Elliott, and R. W. Kieckhefer. 1988. Constant and fluctuating temperature effects on developmental rates and life table statistics of the greenbug (Homoptera: Aphididae). *J. Econ. Entomol.* 81: 501–507.
- Xia, J. Y., R. Rabbinge, and W. Wan der Werf. 2003. Multistage functional responses in a ladybeetle-aphid system: scaling up from the laboratory to the field. *Environ. Entomol.* 32: 151–162.

Received 24 November 2003; accepted 19 January 2004.