

Effects of High and Fluctuating Temperatures on *Myzus persicae* (Hemiptera: Aphididae)

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ABSTRACT Development of green peach aphid, *Myzus persicae* (Sulzer), was modeled under high and fluctuating temperatures to determine what effects an increase in mean summer temperatures of 2.5–3.5°C would have on green peach aphid populations in Minnesota and North Dakota. Green peach aphid developed faster and had greater fecundity under fluctuating conditions. The constant temperature model failed to predict observed development under fluctuating temperatures ($R^2 = 0.01$). Optimal temperature for green peach aphid population growth was 26.7°C. The lower and upper developmental thresholds were 6.5 and 37.3°C, respectively. Under optimal conditions, intrinsic rate of increase was 0.356, and population doubling time was 1.95 d. At optimal fluctuating temperature conditions, one female aphid produced 12.2 progeny each week while under the most favorable constant temperature conditions; each female aphid produced only 5.9 progeny. Green peach aphid was able to survive 1 h each day above its calculated lethal death point of 38.5°C. It seems that, in midwestern North America, green peach aphid would benefit from an increase in mean summer temperature (20°C) of 2.5–3.5°C.

KEY WORDS *Myzus persicae*, temperature, fluctuating, life table, fecundity

Global climate change is occurring. In Europe, mean annual temperatures are expected to increase by 3.5–5.0°C by 2050 (Carter et al. 1991). In midwestern North America, mean temperatures are predicted to increase 1.5–3.5°C by 2040 (Pan et al. 2004). Being poikilothermic animals, development in insects is strongly influenced by external temperatures. Metabolic rates increase and population doubling times decrease as temperatures rise (Gullan and Cranston 2005). Thus, an increase in temperature will affect insect pest abundance by shortening generation time, disrupting predator/prey temporal synchrony (Lawton 1995), and shifting pest distributions (Porter 1995).

Aphids are among the most important pests of temperate agricultural zones (Minks and Harrewijn 1987). Aphids damage plants directly through feeding and thus reduce yields, but their primary importance as pests is as virus vectors (Shands et al. 1972). Green peach aphid, *Myzus persicae* (Sulzer), is one of the world's most important agricultural pests, colonizing >40 different plant families (Blackman and Eastop 1984). Green peach aphid is an efficient vector of >100 plant viruses (Blackman and Eastop 1984) and resistant to almost all major insecticide classes (Devonshire et al. 1998). Harrington et al. (1995) state that in northern climatic zones, temperature increases caused by climate change will increase virus spread by

aphids. Increases in temperature from 0.4 to 1.0°C have already advanced spring migrant flights in the United Kingdom by 6–14 d (Fleming and Tatchell 1995, Harrington et al. 1995).

For many aphids, optimal fecundity and developmental rates occur between 20.0 and 30.0°C (Barlow 1962, Dean 1974, Tsitsipis and Mittler 1976). Green peach aphid is reported to have lower and upper developmental thresholds of 4.0 and 30.0°C, respectively, with optimal survival at 20°C (Whalon and Smilowitz 1979, Liu and Meng 1999). Green peach aphid was found not to reproduce above 30°C and to have a thermal death point of 38.5°C (Broadbent and Hollings 1951).

Normal insect growth occurs under optimal temperature ranges, but when an insect is exposed to extreme low or high temperatures, development rates are reduced, reproduction fails, and if exposed sufficiently long enough, death occurs (Andrewartha and Birch 1954). High temperatures affect aphids by reducing respiration, increasing water loss, and accumulating waste products (Lamb 1961). Under extreme high temperatures, cells become apoptotic because of denaturation of proteins and enzymes, which leads to altered membrane structure and function (Korsloot et al. 2004, Gullan and Cranston 2005). Accumulation of denatured protein triggers production of heat shock protein, which assists in protein folding (Gullan and Cranston 2005). As heat shock proteins are produced, normal protein synthesis is inhibited (Korsloot et al.

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2004). Extreme high temperatures lead to conformational changes to lipids in the wax layer of insect cuticle, resulting in increased dehydration (Beament 1959).

Extreme high temperatures tend to be devastating to aphids. Aphids contain intracellular bacteria (endosymbionts) that convert sugars into key amino acids that aphids need for survival (Dadd 1985). This association is obligate, because neither aphid nor symbiont can survive without the other (Houk and Griffiths 1980). Extreme high temperatures can eliminate aphid endosymbionts (aposymbiosis), impairing amino acid production (Ohtaka and Ishikawa 1991). Aposymbiotic aphids have reduced growth, development, and reproduction (Prosser and Douglas 1991). Extreme high temperatures can depress aphid populations (Asin and Pons 2001) and have been implicated in population crashes of potato aphid, *Macrosiphum euphorbiae* (Thomas), and Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Barlow 1962, Basky 1993). What is not known is how increased high temperatures will affect green peach aphid under simulated field temperatures. The purpose of this study was to model development of green peach aphid under high and fluctuating temperatures mimicking observed daily fluctuations and to determine what effects an increase in mean summer temperatures of 2.5–3.5°C would have on green peach aphid populations.

Materials and Methods

Aphid Colony. The green peach aphid colony used in these experiments was founded from aphids field collected from potato at the University of Minnesota Outreach, Research and Education Park (UMore Park), Rosemount, MN, in 2002. This colony was maintained on Chinese cabbage [*Brassica rapa* L. ssp. *pekinensis* (Lour.) Hanelt] (Gurney's Seed and Nursery Co., Yankton, SD) planted in 10-cm-diameter plastic pots containing sterile potting mix (Sun Gro Horticulture, Elma, Canada) and 5 g Osmocote (14–14–14), a slow release fertilizer (Scotts Company, Marysville, OH). Plants were grown in GC15 EGC Plant Growth Chambers (Environmental Growth Chambers, Chagrin Falls, OH) held at 20 ± 0.2°C, 50 ± 5% RH, and a photoperiod of 16:8 (L:D).

Host Plants. Chinese cabbage was grown in Jiffy-7 peat pellets (Jiffy Products, Shippagan, Canada) placed in black 28 by 56-cm plastic plant trays (Jiffy Products) in GC15 EGC Plant Growth Chambers held at 20 ± 0.2°C, 50 ± 5% RH, and a photoperiod of 16:8 (L:D). Plants were fertilized weekly with Peters' Excel All Purpose Water Soluble Fertilizer (21–5–20; Scotts Company). Chinese cabbage plants were used in temperature experiments when they reached the second true leaf stage. Plants remained healthy for duration of each experiment and were not replaced.

Temperature Regimens. Temperature regimens used were of three types: constant, fluctuating, and pulse (Table 1). Constant temperatures ranged from 5 to 35°C, typical of most published aphid developmental temperature experiments. Constant tempera-

Table 1. Temperature regimens

Regimen	Mean temperature (°C)	Temperature range (°C)	Hours at maximum
Constant	5.0	Constant	—
	10.0	Constant	—
	15.0	Constant	—
	20.0	Constant	—
	25.0	Constant	—
	30.0	Constant	—
	32.0	Constant	—
	35.0	Constant	—
Pulse	30.0	30.0–35.0	3 ^a
	30.0	30.0–35.0	6 ^a
	30.0	30.0–35.0	8 ^a
	30.0	30.0–35.0	24 ^a
	30.0	30.0–35.0	48 ^b
Fluctuating	15.0	7.4–18.2	1 ^c
	18.6	13.3–23.4	1 ^c
	19.0	14.8–25.0	1 ^c
	20.1	13.9–25.5	2 ^c
	23.1	20.0–35.0	1 ^c
	27.2	25.0–35.0	1 ^c
	30.0	29.0–37.0	1 ^c
	32.3	30.0–39.0	1 ^c

^a In the first 24-h cycle.
^b In the first and second 24-h cycles.
^c Every 24-h cycle.

ture regimens interrupted by short pulses at 35°C were conducted to determine sensitivity of first-instar nymphs to this extreme high temperature. Fluctuating temperature regimens were chosen to yield daily mean temperatures similar to the constant temperature regimens used. To simulate potential field conditions, we chose temperatures typical of midsummer in the Minnesota and North Dakota Red River Valley of the North by averaging 15-yr hourly temperatures for the months of May, June, July, and August recorded by the North Dakota Agricultural Weather Network (NDSU 2006) for Grand Forks, ND, site of the Northern Plains Potato Growers Association Potato Research Farm. The average summer mean temperature (May to August) for this area is 20°C, with a mean high of 27°C and a mean low of 12°C (NDSU 2006). It is not infrequent for summer temperatures in Minnesota and North Dakota to go above 30°C, the reported upper developmental threshold for green peach aphid (Weed 1927, Barlow 1962, DeLoach 1974, El Din 1976, Whalon and Smilowitz 1979, Liu and Meng 1999), and yet green peach aphid populations do not collapse. With this in mind, fluctuating temperature regimens also included short-term exposure to extreme high temperatures (≥35°C) and recovery periods that resulted in mean temperatures for these test regimens equal to mean temperatures in corresponding constant temperature regimens. Mean fluctuating temperature regimens ranged from 15.0 to 32.3°C. This resulted in 24 h of constant or fluctuating temperature regimens that were programmed into GC15 EGC Plant Growth Chambers held at 20 ± 0.2°C, 50 ± 5% RH, and a photoperiod of 16:8 (L:D). As an example, the fluctuating regimens for the mean temperatures of 15.0, 19.0, 27.2, and 32.3°C are shown in Fig. 1. Each fluctuating regimen has a somewhat

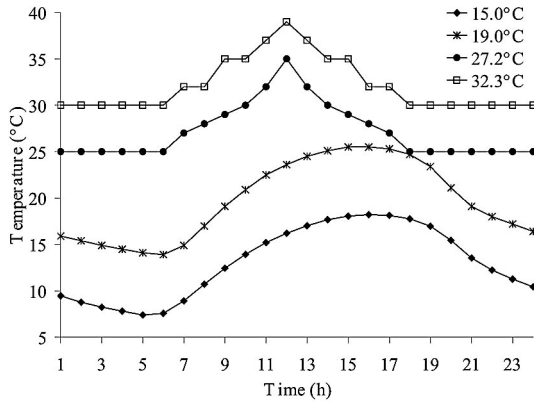


Fig. 1. Daily fluctuating regimens for mean temperatures of 15.0, 19.0, 27.2, and 32.3°C.

different shaped curve. The 15-yr average temperatures tended to have a sinusoidal appearance, whereas the extreme temperature regimens tended to have a more trapezoidal shaped curve (Fig. 1). The amount of time each fluctuating regimen was above the mean temperature for that regimen was 9–11 h.

Experimental Protocol. Host plants were placed in black 28 by 56-cm plastic plant trays in GC15 EGC Plant Growth Chambers at appropriate temperature regimens. A single apterous, green peach aphid adult was placed on each Chinese cabbage plant and allowed to larviposit for 12 h. The adult and all but one

first instar were removed. All single first instars were the cohort for that temperature regimen for the duration of the experiment. Cohort numbers varied among temperature regimens because of host plant availability.

Life Table Studies, Model Development, and Data Analysis. Life table studies were conducted for each temperature regimen. Age (x), age-specific survival (l_x), and number of progeny per female per day (m_x) were recorded until death. Age-specific fecundity ($l_x m_x$), net reproductive rate (R_0), mean generation time (T_C), and intrinsic rate of increase (r_m) were calculated as described by Birch (1948). Intrinsic rate of increase was calculated using the equation $\sum e^{-rx} l_x m_x = 1$. Net reproductive rate was calculated as $R_0 = \sum l_x m_x$, mean generation time was calculated as $T_C = \ln(R_0) / r_m$, finite rate of increase (λ_F) was calculated as $\lambda_F = e^{r_m}$, and doubling time (DT) as $DT = \ln(2) / r_m$.

Temperature-dependent developmental thresholds under constant and fluctuating temperature regimens were estimated using a Logan model (Logan et al. 1976) as modified by Lactin et al. (1995), i.e., $r(T) = e^{\rho T} - e^{\rho T_{max} - (T_{max} - T)/\Delta} + \lambda$, where $r(T)$ is the mean developmental rate at temperature T (°C). Fitted parameters, ρ (rate of increase at optimal temperature), T_{max} (upper developmental threshold), Δ (difference between optimal and upper developmental threshold), and λ (which allows curve to intercept x-axis), were estimated using Marquardt's method in PROC NLIN (SAS Institute 2001). For each model, R^2

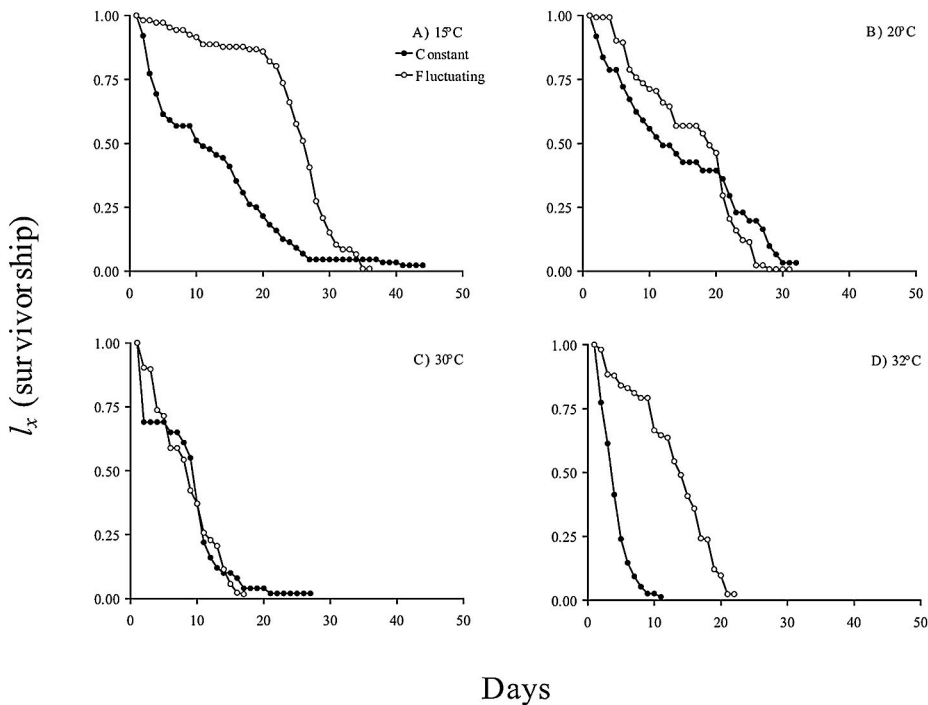


Fig. 2. Survivorship (l_x) under constant and fluctuating regimens with mean temperatures of (A) 15, (B) 20, (C) 30, and (D) 32°C.

was calculated using the equation of Medeiros et al. (2004), $R^2 = 1 - (S_r/S_m)$, where S_r is variance of the model residuals and S_m is mean squared error of developmental rates. SEs for r_m and 95% CIs were calculated using a Jackknife procedure as described in Meyer et al. (1986).

Results

Survival from first instar to adult occurred at all temperature regimens except constant 35°C. At constant 32°C, only 1 of 75 nymphs reached adult stage. Age-specific survivorship and m_x between constant and fluctuating temperature regimens are shown in Figs. 2 and 3. Fluctuating temperatures enhanced survivorship at the lowest and highest temperature regimens (Fig. 2A and D). The 15°C survivorship graph for the fluctuating regimens tended to follow a type I curve, whereas those at 20, 30, and 32°C fluctuating regimens tended to closely follow a type II curve (relatively constant death rate throughout life span). This indicates that, at the 15°C fluctuating regimen, green peach aphid nymphs had a high rate of survival and those adults lived out their expected life span. At fluctuating regimens of 20, 30, and 32°C, green peach aphid had a relatively constant death rate caused by the negative impacts of higher temperatures. The constant temperature regimens, 15, 20, and 30°C, tended to a type II curve and 32°C to a type III curve. This indicated that, at 15, 20, and 30°C, green peach aphid death rate was constant while a constant 32°C increased the death rate. Number of progeny per female

per day was similar under constant and fluctuating temperature regimens (Fig. 3A, C, and D), except at 20°C (Fig. 3B). Under constant temperature regimens, survivorship increased to a maximum at 25°C and decreased as temperatures increased. Under constant temperatures, greatest r_m occurred at constant 20°C and at fluctuating 27°C (Table 2). Negative reproductive rates were observed at constant temperatures 5 and 32°C, at a pulse of 35°C for 48 h, and at fluctuating 32.3°C (Table 2). Net reproductive rates were highest at constant 25°C and at fluctuating 20.1°C (Table 2). The longest mean generation times occurred at the lowest constant and fluctuating temperature regimens (Table 2). The shortest population doubling time occurred at fluctuating 27°C (1.95 d) and at constant 20°C (2.70) (Table 2). Highest finite rates of increase were 1.29 at constant 20°C and 1.43 at fluctuating 27°C (Table 2). Under fluctuating 27°C, each female aphid had, at the end of 1 wk, produced 12.2 progeny, whereas under the most favorable constant temperature condition, each female aphid had produced only 5.9 progeny (Table 2).

Lactin models of development rates under constant or fluctuating temperature regimens are depicted in Fig. 4. Lactin models indicated development to be fastest at fluctuating 26.7°C or constant 23.2°C (Table 3). Upper developmental thresholds were fluctuating 37.3°C and constant 34.2°C (Table 3). Lower developmental thresholds were fluctuating 6.5°C and constant 2.5°C (Table 3). Observed development rate values for fluctuating temperature means were compared with predicted values from Lactin models for

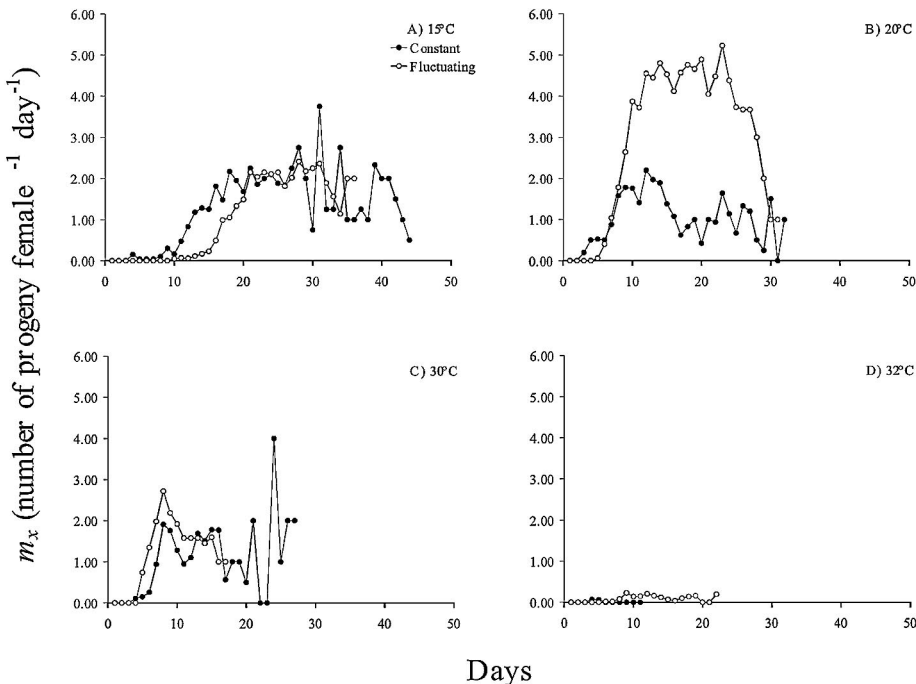


Fig. 3. Number of progeny per female per day (m_x) under constant and fluctuating regimens with mean temperatures of (A) 15, (B) 20, (C) 30, and (D) 32°C.

Table 2. Life table statistics for differing temperature regimens

Regimen	n	Intrinsic rate of increase		Net reproductive rate	Mean generation time	Doubling time	Finite rate of increase
		r_m	SE				
Constant							
5.0	56	-0.040	±0.021	0.27	33.4	∞	0.96
10.0	58	0.082	±0.011	5.06	19.8	8.45	1.09
15.0	88	0.125	±0.012	7.92	16.6	5.55	1.13
20.0	61	0.256	±0.017	12.80	10.0	2.71	1.29
25.0	51	0.225	±0.014	21.42	13.6	3.08	1.25
30.0	69	0.217	±0.014	7.95	9.6	3.19	1.24
32.0	75	-0.711	±0.458	0.04	4.4	∞	0.49
35.0	46	—	—	—	—	—	—
Pulse							
3	34	0.217	±0.029	5.85	8.1	3.19	1.24
6	55	0.199	±0.037	6.51	9.4	3.48	1.22
8	47	0.104	±0.022	2.49	8.8	6.66	1.11
24	26	0.027	±0.018	1.39	12.1	25.67	1.03
48	42	-0.084	±0.029	0.24	17.2	∞	0.92
Fluctuating							
15.0	106	0.132	±0.003	16.71	21.3	5.25	1.14
18.6	132	0.293	±0.006	37.23	12.3	2.37	1.34
19.0	129	0.285	±0.010	29.76	11.9	2.43	1.33
20.1	116	0.294	±0.006	40.45	12.6	2.36	1.34
23.1	133	0.304	±0.012	30.79	10.5	2.28	1.36
27.2	131	0.356	±0.011	25.88	9.1	1.95	1.43
30.0	175	0.243	±0.015	6.99	8.0	2.85	1.28
32.3	206	-0.012	±0.036	0.87	11.4	∞	0.99

the corresponding constant temperatures using Pearson's correlation. Under linear conditions (20, 23, and 27°C), the constant model accurately predicted development rates under fluctuating temperature regimens ($R^2 = 0.90$). However, when development becomes curvilinear (15, 30, and 32°C), the constant model failed to predict observed development under fluctuating temperatures ($R^2 = 0.18$). Pulse temperature regimens indicate green peach aphid can survive 25.8 h at constant 35°C before recovery is no longer possible (Fig. 5).

Discussion

Under constant temperatures, our results were consistent with published literature reporting optimal survival and development of green peach aphid from 20 to 25°C, with an upper developmental threshold of

30°C (Weed 1927, Barlow 1962, DeLoach 1974, El Din 1976, Whalon and Smilowitz 1979, Liu and Meng 1999). However, under fluctuating temperature regimens, we found that green peach aphid had higher optimal and upper developmental thresholds. One explanation for why our results differ in optimal and upper developmental thresholds from previous reported values could be aphid biotypes, but for green peach aphid, this seems unlikely. Whalon and Smilowitz (1979) studied green peach aphid from Pennsylvania, Maine, and Washington; all populations responded similarly when subjected to the same temperatures. Clearly, the reason our optimal and upper developmental thresholds differ under fluctuating temperatures is because these temperature regimens more closely model what occurs in nature.

Green peach aphid was able to survive high temperatures under fluctuating temperature regimens. As temperatures went above upper developmental thresholds, development slowed, but the aphid was able to recover once temperatures returned to below threshold. The m_x graphs indicate very similar numbers of progeny per day per female except at 20°C. At this temperature, the fluctuating regimens resulted in significantly more progeny per aphid per day. At mean 20°C, the effects of increased high temperatures under a fluctuating regimen are beginning to become apparent. Our data indicate that, at constant temperatures, optimal development is at 23°C. Under fluctuating conditions, optimal development occurs at a mean temperature of 26.7°C. The increased high temperatures coupled with low temperature recoveries allowed green peach aphid to increase more rapidly with better survivorship and higher fecundity. Why this occurs is only speculation, but it is possible that the endosymbionts are favored by higher tempera-

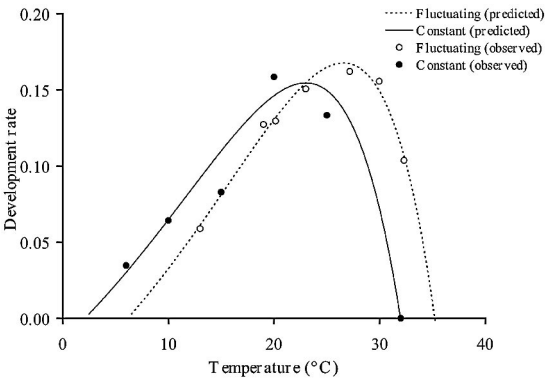


Fig. 4. Constant and fluctuating temperature dependent development rate Lactin models.

Table 3. Estimated parameters of Lactin models for constant and fluctuating temperature regimens

Model	ρ	SE	T_{max}	SE	Δ	SE	λ	SE	R^2
Constant	0.088	± 0.069	34.206	± 5.633	10.993	± 7.390	-0.123	± 0.305	0.76
Fluctuating	0.092	± 0.022	37.282	± 2.142	10.580	± 2.309	-0.122	± 0.101	0.91

tures and that the green peach aphid is benefiting from more endosymbionts resulting in more amino acid production while the intervening cool intervals allow green peach aphid to feed more efficiently and recover from high temperature exposure. At fluctuating 32.3°C, high temperatures were at or above the reported upper developmental threshold and for 1 h above the reported point of lethality for this species. Green peach aphid was still able to recover and reproduce, although populations declined. Siddiqui et al. (1973) studied pea aphid under constant and fluctuating temperatures. Alternating temperatures resulted in higher r_m than occurred at constant temperatures because of quicker larviposition and reproduction. For Russian wheat aphid and bird cherry-oat aphid, *Rhopalosiphum padi* L., Kieckhefer and Elliott (1989) and Elliott and Kieckhefer (1989) found the highest r_m under a fluctuating temperature regimen of 20.0–33.4°C (mean, 26.7°C). Our results were similar for green peach aphid. Andrewartha (1971) stated that the range of temperatures suitable for an animal is related to where that animal is found. Clearly, this is true for green peach aphid, which is of cosmopolitan distribution and, as indicated by our results, able to survive under extreme conditions.

Constant temperature studies do not predict what occurs at typical, fluctuating temperatures (Lamb 1961, Messenger 1964). Constant temperature studies underestimate thresholds because fluctuating temperatures extend threshold limits (Messenger 1964). Degree-day models are accurate when temperatures fall within the lower and optimal developmental thresholds, i.e., the linear portion of a development curve. When temperatures go beyond the optimal temperature, degree-day models do not work, and are in fact, unsuitable for predicting insect development. Degree

day models tend to underestimate development of populations at high temperatures (Elliott and Kieckhefer 1989) and simple heat unit summations are not well correlated with population growth at high temperatures (Tamaki et al. 1982). Likewise, results from our constant temperature development model failed to predict development under fluctuating temperatures.

High temperatures have negative impacts on aphid populations by slowing development and reducing fecundity (Nowierski et al. 1983). High temperatures can be harmful to developing embryos, and thus, population growth can be slowed in subsequent generations (Harrison and Barlow 1973). Insects can, to some extent, control their body temperatures by movement to microclimates that suit their needs, e.g., moving to lower canopies or transpiring surfaces (Broadbent and Hollings 1951). Typically, green peach aphid is found on lower leaves in the plant canopy, but our results indicate that even when it is exposed to short intervals of high temperatures in the field, the effect is likely to be beneficial, increasing development and reproduction rates.

High upper development thresholds similar to our results for the green peach aphid are not unusual and have been reported in other aphid species. Walnut aphid, *Chromaphis juglandicola* (Kaltenbach), suffered adverse effects only when exposed to temperatures >37.8°C (Nowierski et al. 1983). Yellow pecan aphid, *Monelliopsis pecanis* Bissell, and black pecan aphid, *Melanocallis caryaefoliae* (Davis), were able to withstand exposure to 34°C for 5 h with little deleterious effects (Kaakeh and Dutcher 1993). Spotted alfalfa aphid, *Therioaphis maculata* (Buckton), had maximum r_m (0.410) at 29°C and an upper developmental threshold of 33°C (Messenger 1964).

Effects of climate change on aphids are likely to be complex. Cocu et al. (2005) have shown that an increase in green peach aphid abundance in Europe is positively correlated with temperature and changes in the crop species cultivated, e.g., expansion of canola production. Newman (2005) speculates that cereal aphids in southern Britain will decline in pest status because of increased CO₂ emissions, increased temperature, and decreased rainfall. Cereal aphids, in general, have low upper developmental thresholds (e.g., 25°C), and as temperatures increase above upper developmental thresholds, development slows and fecundity and longevity are reduced. Skirvin et al. (1997) predict that as hot summers become more frequent in Britain, coccinellids will have greater impacts on grain aphids because their populations will increase faster at higher temperatures. In European cereal aphid development models, high temperature

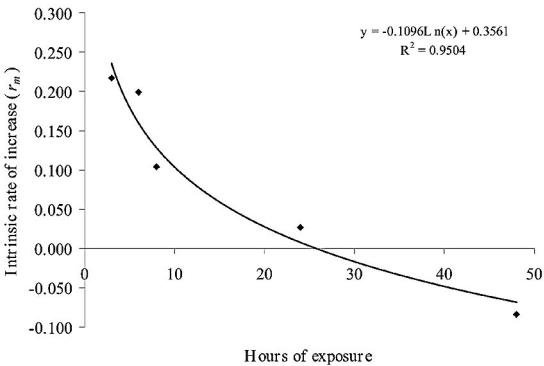


Fig. 5. Effects of duration of exposure at 35°C on first-instar green peach aphid intrinsic rate of increase under a constant 30°C temperature regimen.

regimens for Britain ranged from 13 to 14°C (model of Skirvin et al. 1997) and as high as 18°C (Newman 2005). These temperature ranges are below mean summer temperatures in Minnesota and North Dakota. The European models used optimal, lower, and upper developmental thresholds based on constant temperatures. Our data suggest that models predicting outcomes at high temperatures from development at constant temperatures are inherently inaccurate. Our results show that *M. persicae* develops faster and has greater fecundity under fluctuating temperatures.

Based on our results, we conclude that green peach aphid would benefit from an increase in temperature of 2.5–3.5°C. Based on our fluctuating temperature regimen data, the optimal temperature for green peach aphid population growth is 26.7°C and lower and upper developmental thresholds are 6.5 and 37.3°C, respectively.

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References Cited

- Andrewartha, H. G. 1971. Introduction to the study of animal populations. University of Chicago Press, Chicago, IL.
- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, IL.
- 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.
- Barlow, C. A. 1962. The influence of temperature on the growth of experimental populations of *Myzus persicae* (Sulzer) and *Macrosiphum euphorbiae* (Thomas) (Aphididae). *Can. J. Zool.* 40: 145–156.
- Basky, Z. 1993. Incidence and population fluctuation of *Diuraphis noxia* in Hungary. *Crop Protect.* 12: 605–609.
- Beament, J. W. L. 1959. The waterproofing mechanism of arthropods. 1. The effect of temperature on cuticle permeability in terrestrial insects and ticks. *J. Exp. Biol.* 36: 391–422.
- 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 guide. Wiley, New York.
- Broadbent, L., and M. Hollings. 1951. The influence of heat on some aphids. *Ann. Appl. Biol.* 38: 577–581.
- Carter, T. R., M. L. Parry, and J. H. Porter. 1991. Climate change and future agroclimatic potential in Europe. *Int. J. Climatol.* 11: 251–269.
- Cocu, N., R. Harrington, M. D. A. Rounsevell, S. P. Worner, M. Hulle, and the EXAMINE project participants. 2005. Geographical location, climate and land use influences on the phenology and numbers of aphid, *Myzus persicae*, in Europe. *J. Biogeogr.* 32: 615–632.
- Dadd, R. H. 1985. Nutrition: organisms, pp. 313–389. In G. A. Kerkut and L. I. Gilbert (eds.), *Comprehensive insect physiology, biochemistry and pharmacology*. Pergamon, New York.
- Dean, G. J. 1974. Effect of temperature on the cereal aphids *Metopolophium dirhodum* (Wilk.), *Rhopalosiphum padi* (L.), and *Macrosiphum avenae* (F.) (Hem., Aphididae). *Bull. Entomol. Res.* 63: 401–409.
- DeLoach, C. J. 1974. Rate of increase of populations of cabbage, green peach, and turnip aphids at constant temperatures. *Ann. Entomol. Soc. Am.* 67: 332–340.
- Devonshire, A. L., L. M. Field, S. P. Foster, G. D. Moores, M. S. Williamson, and R. L. Blackman. 1998. The evolution of insecticide resistance in the peach-potato aphid, *Myzus persicae*. *Phil. Trans. R. Soc. Lond. B* 353: 1677–1684.
- El Din, N. S. 1976. Effects of temperature on the aphid, *Myzus persicae* (Sulz.) with special reference to critically low and high temperature. *Z. Ang. Entomol.* 80: 7–14.
- 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.
- Fleming, R. A., and G. M. Tatchell. 1995. Shifts in the flight periods of British aphids: a response to climate warning?, pp. 505–508. In R. Harrington and N. E. Stork (eds.), *Insects in a changing environment*. Academic, San Diego, CA.
- Gullan, P. J., and P. S. Cranston. 2005. The insects: an outline of entomology. Blackwell Publishing, Malden, MA.
- Harrington, R., J. S. Bale, and G. M. Tatchell. 1995. Aphids in a changing climate, pp. 125–155. In R. Harrington and N. E. Stork (eds.), *Insects in a changing environment*. Academic, San Diego, CA.
- Harrison, J. R., and C. A. Barlow. 1973. Survival of the pea aphid, *Acyrtosiphon pisum* (Homoptera: Aphididae), at extreme temperatures. *Can. Entomol.* 105: 1513–1518.
- Houk, E. J., and G. W. Griffiths. 1980. Intracellular symbionts of the Homoptera. *Annu. Rev. Entomol.* 25: 161–187.
- Kaakeh, W., and J. D. Dutcher. 1993. Survival of yellow pecan aphids and black pecan aphids (Homoptera: Aphididae) at different temperature regimens. *Environ. Entomol.* 22: 810–817.
- 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.
- Korsloot, A., C. A. M. van Gestel, and N. M. van Straalen. 2004. Environmental stress and cellular response in arthropods. CRC, Boca Raton, FL.
- 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, K. P. 1961. Some effects of fluctuating temperatures on metabolism, development, and rate of population growth in the cabbage aphid, *Brevicoryne brassicae*. *Ecology* 42: 740–745.
- Lawton, J. H. 1995. The response of insects to environmental change, pp. 3–26. In R. Harrington and N. E. Stork (eds.), *Insects in a changing environment*. Academic, San Diego, CA.
- Liu, S., and X. Meng. 1999. Modelling development time of *Myzus persicae* (Hemiptera: Aphididae) at constant and natural temperatures. *Bull. Entomol. Res.* 89: 53–63.
- 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.
- Medeiros, R., F. S. Ramalho, J. E. Serrao, and J. C. Zanuncio. 2004. Estimative of *Podisus nigrispinus* (Dallas) (Het-

- eroptera: Pentatomidae) development time with non linear models. *Neotropical Entomol.* 33: 141–148.
- Messenger, P. S. 1964. The influence of rhythmically fluctuating temperatures on the development and reproduction of the spotted alfalfa aphid, *Therioaphis maculata*. *Econ. Entomol.* 57: 71–79.
- Meyer, J. S., C. G. Ingersoll, L. L. McDonald, and M. S. Boyce. 1986. Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. *Ecology* 67: 1156–1166.
- Minks, A. K., and P. Harrewijn. 1987. Preface, pp. v–vi. In A. K. Minks and P. Harrewijn (eds.), *Aphids: their biology, natural enemies and control*. World crop pests. Elsevier, Amsterdam, The Netherlands.
- Newman, J. A. 2005. Climate change and the fate of cereal aphids in Southern Britain. *Glob. Chang. Biol.* 11: 940–944.
- North Dakota State University [NDSU]. 2006. North Dakota agricultural weather network (<http://ndawn.ndsu.nodak.edu/>).
- Nowierski, R. M., A. P. Gutierrez, and J. S. Yaninek. 1983. Estimation of thermal thresholds and age-specific life table parameters for the walnut aphid (Homoptera: Aphididae) under field conditions. *Environ. Entomol.* 12: 680–686.
- Ohtaka, C., and H. Ishikawa. 1991. Effects of heat treatment on the symbiotic system of an aphid mycetocyte. *Symbiosis* 11: 19–30.
- Pan, Z., R. W. Arriott, E. S. Takle, W. J. Gutowski Jr., C. J. Anderson, and M. Segal. 2004. Altered hydrologic feedback in a warming climate introduces a “warming hole.” *Geophysical Res. Lett.* 31: 1–4.
- Porter, J. 1995. The effects of climate change on the agricultural environment for crop insect pests with particular reference to the European corn borer and grain maize, pp. 94–113. In R. Harrington and N. E. Stork (eds.), *Insects in a changing environment*. Academic, San Diego, CA.
- Prosser, W. A., and A. E. Douglas. 1991. The aposymbiotic aphid: an analysis of chlortetracycline-treated pea aphid, *Acyrtosiphon pisum*. *J. Insect Phys.* 37: 713–719.
- SAS Institute. 2001. PROC user's manual, version 6. SAS Institute, Cary, NC.
- Shands, W. A., G. W. Simpson, B. A. Seaman, F. S. Roberts, and C. M. Flynn. 1972. Effects of differing abundance levels of aphids and of certain virus diseases upon yield and virus disease spread in potatoes. *Life Sci. Agric. Exp. Stn. Univ. Maine Tech. Bull.* 56. 40 pp.
- 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, *Acyrtosiphon pisum* (Homoptera: Aphididae). *Can. Entomol.* 105: 145–156.
- Skirvin, D. J., J. N. Perry, and R. Harrington. 1997. A model describing the population dynamics of *Sitobion avenae* and *Coccinella septempunctata*. *Ecol. Model.* 96: 29–39.
- Tamaki, G., M. A. Weiss, and G. E. Long. 1982. Effective growth units in population dynamics of the green peach aphid (Homoptera: Aphididae). *Environ. Entomol.* 11: 1134–1136.
- Tsitsipis, J. A., and T. E. Mittler. 1976. Development, growth, reproduction, and survival of apterous virginoparae of *Aphis fabae* at different temperatures. *Entomol. Exp. Appl.* 19: 1–10.
- Weed, A. 1927. Metamorphosis and reproduction in apterous forms of *Myzus persicae* Sulzer as influenced by temperature and humidity. *Econ. Entomol.* 20: 150–157.
- Whalon, M. E., and Z. Smilowitz. 1979. Temperature-dependent model for predicting field populations of green peach aphid, *Myzus persicae* (Homoptera: Aphididae). *Can. Entomol.* 111: 1025–1032.

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