

Are Development and Growth of Pea Aphids, *Acyrtosiphon pisum*, in North America Adapted to Local Temperatures?

Author(s): R. J. Lamb, P. A. MacKay and G. H. Gerber

Source: *Oecologia*, 1987, Vol. 72, No. 2 (1987), pp. 170-177

Published by: Springer in cooperation with International Association for Ecology

Stable URL: <http://www.jstor.com/stable/4218246>

---

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



Springer and *Oecologia* are collaborating with JSTOR to digitize, preserve and extend access to

JSTOR

# Are development and growth of pea aphids, *Acyrtosiphon pisum*, in North America adapted to local temperatures?\*

R.J. Lamb<sup>1</sup>, P.A. MacKay<sup>2</sup>, and G.H. Gerber<sup>1</sup>

<sup>1</sup> Agriculture Canada Research Station, 195 Dafoe Road, Winnipeg, Manitoba R3T 2M9, Canada

<sup>2</sup> Department of Entomology, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada

**Summary.** Developmental rate and adult weight were studied at constant temperatures from 9.8 to 27.9° C for 18 clones from each of five populations of the pea aphid, *Acyrtosiphon pisum* (Harris), from locations between 39 and 53°N latitude in central North America. The response of developmental rate to temperature for each clone was accurately described by a three parameter non-linear equation. Adult weight usually decreased with increasing rearing temperature, but the shape of the response to temperature varied among clones. Variation in the developmental parameters was greater among clones within populations than among populations. No consistent trends were observed in the developmental parameters or adult weights either with latitude or the long term average temperatures at the locations. We conclude that previously reported geographic variation in the developmental threshold of this species, which was attributed to local adaptation, occurred either because the clones tested were not representative of the populations or because rearing methods differed among studies. The results are discussed in relation to the hypothesis that life history traits which are temperature sensitive are adapted to local thermal environments.

**Key words:** Developmental rate – Adult weight – Adaptation – Temperature – *Acyrtosiphon pisum*

Developmental rate (Taylor 1981) and adult weight (Matsuki 1978) and their responses to temperature are important ecological traits for ectotherms such as insects. The response of developmental rate to temperature may affect the timing of reproduction for univoltine species and the intrinsic rate of increase and number of generations per year for multivoltine species (Tauber and Tauber 1978; Taylor 1981). Adult weight may affect fecundity (Gilbert 1984a; Llewellyn and Brown 1985) and the fitness of offspring (Carroll and Hoyt 1986b). Many authors have hypothesized that for ectotherms, such traits are adapted to local temperatures. In other words, natural selection results in differentiation among populations living under different climatic conditions, in spite of gene flow among them (Lonsdale and Levinton 1985).

Local adaptation of the responses of insects to photoper-

iod has been demonstrated frequently (Bradshaw 1976; Beck 1980; Tauber et al. 1986), and local adaptation of the developmental responses of marine invertebrates to temperature is well substantiated (Lonsdale and Levinton 1985). However, similar studies on development of terrestrial invertebrates are less convincing. One of the first studies on terrestrial insects concluded that temperature thresholds for development of some aphids and their parasites are lower for populations from locations with cool springs than those from locations with warm springs (Campbell et al. 1974). Similarly, other studies conclude that, in general, populations from higher latitudes or altitudes (cool climates) have lower thresholds for development than those from lower latitudes or altitudes (warm climates) (Tauber and Tauber 1978; Trimble and Lund 1983; Hutchison and Hogg 1984; Baldwin and Dingle 1986). However, the differences among populations are often small (Trimble and Lund 1983; Nealis et al. 1984) or not evident (Baker and Miller 1978; Ritland and Scriber 1985).

The temperature responses of developmental rate and adult weight for a population are more difficult to measure than has sometimes been realized. The difficulties include: obtaining a representative sample of organisms, controlling extraneous laboratory conditions that affect the response, and choosing an appropriate model to describe the response. For example, the response of developmental rate to temperature has been studied for pea aphids, *Acyrtosiphon pisum* (Harris), from a number of localities in North America (Campbell et al. 1974; Kilian and Nielson 1971; Siddiqui et al. 1973; Hutchison and Hogg 1984). Two of these studies concluded that the response is adapted to local climatic conditions (Campbell et al. 1974; Hutchison and Hogg 1984). This conclusion is not convincing, because the aphids tested may not have been representative of the genotypes in the populations, an especially important consideration when studying aphids which are facultative parthenogens (Blackman 1985).

The objective of our research was to test the hypothesis that local populations of *A. pisum* show temperature-dependent traits adapted to local temperatures. This species can be reared easily in the laboratory and information on its temperature responses is available. We studied developmental rate and adult weight, because they affect the rate of population increase for *A. pisum* and many other insects. We describe and compare the responses of five populations sampled between 39 and 53°N latitude in central North America.

\* Contribution No. 1257, Agriculture Canada, Research Station, Winnipeg, Manitoba, Canada

Offprint requests to: R.J. Lamb

## Materials and methods

Aphids were collected from five alfalfa, *Medicago sativa* L., fields by sweeping 25 widely-separated sites in each field. The locations of the five fields are shown in Fig. 1 and Table 1. The aphids were collected early in the spring to assure they were part of the population that had wintered locally and were not recent migrants. A single aphid from each site was used to establish a clone. For each field, 18 randomly-selected experimental clones were tested along with two control clones. The control clones were originally collected at Glenlea, Manitoba, in August and had been reproducing parthenogenetically in the laboratory for 5 years.

Aphids were reared on excised broad bean leaves, *Vicia faba* L., on moistened paper towel in 60 × 15 mm petri dishes (MacKay and Downer 1979). Only the most recent, newly-produced, fully-expanded leaves from vegetative, green-house grown plants that had at least six expanded leaves were used. Half way through their estimated developmental time, the aphids were transferred to fresh leaves. They were transferred a second time if the leaves had senesced, although a second transfer was usually unnecessary.

First instar larvae that were <16 h old and produced by individually-reared, first-born parents which had been reproducing for 1 to 3 days, were used in the experiments. Thus, variation due to the effect of maternal age was eliminated, and few winged forms were produced (MacKay and Wellington 1977). Five aphids from the same clone were

reared in each petri dish and 20 dishes were arranged randomly on a tray, 18 with experimental clones and two with control clones. In each test, 40 trays were distributed among five differently programmed environmental chambers. For practical reasons, each population was tested at a different time, but the control clones were common to the five tests.

The environmental chambers were calibrated to give average temperatures of 11.5, 14.9, 20.6, 24.5, or 27.5 ± 0.5° C as measured in the petri dishes, a photoperiod of 18 h light:6 h dark provided by fluorescent lighting, and a relative humidity of >60%. Because of gradients in each chamber, the temperature in a petri dish varied with its position. To measure the amount of variation, the temperature inside the dishes was recorded hourly for 24 h before and after each test using thermocouple junctions connected to a 50 channel temperature recorder. The recordings indicated that temperature was uniform (±0.5° C) on a tray, but differed by <0.5 to 4° C from tray to tray. To account for variation in growth or development caused by the gradients, each tray was assigned to a specific location in a chamber and remained there for the duration of the test. The average temperature during the two, 1-day recording periods was used to estimate the temperature of the aphids on each tray. Thus, for each clone, five aphids were tested at each of 40 temperatures from 9.8 to 27.9° C.

The aphids were examined every 24 h at 9.8 to 16° C and every 12 h at 19 to 27.9° C. Records were kept of mortality, the number of non-winged and winged adults, and of the time of the moult to the adult stage. Too few winged adults were produced to permit a separate analysis for this morph (3 to 13% for the five populations) and so winged adults were excluded from the results. As non-winged adults appeared, they were placed in a vial with other adults from the same dish and frozen at -15° C. When all non-winged aphids had reached adulthood, they were dried to constant weight at 60° C and weighed using a Cahn G2 electrobalance. The average weight of the aphids in each dish was determined.

After the five tests were completed, we conducted a subsidiary test to confirm that the differences among clones tested at different times were real and not due to variation in the test conditions over time. Three clones were selected from each of the five populations and tested simultaneously in a chamber that was calibrated to give an average temperature of 17.5° C in the petri dishes. Ten replicate dishes of five aphids per dish were used for each clone, with one dish per clone on a tray. The test was conducted as described above. The developmental times for the clones in



Fig. 1. Map of North America showing collection sites for *Acyrthosiphon pisum* used in this (◊) and previously-published studies (☆)

Table 1. Mean parameter values ( $n=18$ ) ± 95% confidence intervals and ranges, in parentheses, for equations of normal curves describing the response of developmental rate to rearing temperature for five populations of *Acyrthosiphon pisum* from central North America, the latitudes where they were collected, and the long-term mean daily temperatures for July from nearby weather stations

Population	Latitude	July daily mean, °C	$R_m^a$ , %/day	$T_m$ , °C	$T_\sigma$ , °C
1. Manhattan, KS	39° 11'	25.7	19.1 ± 0.45 (16.8–20.1) <sup>a</sup> <sup>b</sup>	26.0 ± 0.31 (24.5–27.0) <sup>a</sup>	9.82 ± 0.26 (8.71–11.10) <sup>a</sup>
2. Rosemount, MA	44° 45'	22.2	17.4 ± 0.72 (15.0–20.0) <sup>b</sup>	24.7 ± 0.34 (23.3–25.8) <sup>b</sup>	8.89 ± 0.16 (8.17– 9.50) <sup>c</sup>
3. Mapleton, ND	46° 53'	21.5	18.6 ± 0.65 (15.7–19.9) <sup>a</sup>	24.6 ± 0.26 (23.8–25.6) <sup>b</sup>	8.85 ± 0.21 (8.28–10.03) <sup>c</sup>
4. Glenlea, MAN	49° 38'	19.6	18.5 ± 0.53 (15.9–19.6) <sup>a</sup>	24.5 ± 0.21 (23.7–25.3) <sup>b</sup>	8.67 ± 0.14 (8.15– 9.17) <sup>c</sup>
5. Prince Albert, SASK	53° 12'	17.4	19.5 ± 0.34 (18.5–20.9) <sup>a</sup>	25.6 ± 0.34 (24.9–27.8) <sup>a</sup>	9.40 ± 0.21 (8.86–10.46) <sup>b</sup>

<sup>a</sup>  $R_m$ , maximum developmental rate at  $T_m$ , the optimum temperature, with  $T_\sigma$  being the spread of the curve

<sup>b</sup> Parameter values in a column followed by the same letter do not differ ( $P>0.05$ ), based on Tukey's test

this test were compared with the expected developmental times estimated for the clones from the results of the five previous tests.

A two-way analysis of variance was used to compare developmental times and weights for the control clones among the five tests, attributing variation to clone, test, and the interaction, with a separate analysis for the results from each environmental chamber. The data for adult weights were weighted by the number of aphids in each dish that contributed to the average weight. The developmental times, but not the adult weights, of the control clones differed significantly ( $P < 0.05$ ) among tests. Based on the deviation of the control clones for each test from the mean value for the control clones, the developmental times for the experimental clones were corrected for differences in rearing conditions among tests. The corrections ranged from 0 to 6% (average 2.6%) of the mean developmental time for each test and chamber. No correction was required for the adult weights.

The relationship between developmental rate or adult weight and temperature was determined for each of the 92 clones. Non-linear regression was used to fit the developmental data to the equation of a truncated normal curve:

$$R(T) = R_m \exp[-1/2((T - T_m)/T_\sigma)^2],$$

where  $R(T)$  was developmental rate (% development per day) with respect to rearing temperature,  $R_m$  was the maximum developmental rate at the temperature,  $T_m$  where the developmental rate was highest (the optimum),  $T$  was the rearing temperature, and  $T_\sigma$  was a shape parameter giving the spread of the curve (Taylor 1981). The developmental threshold and degree-day requirement for each clone was estimated by linear regression using developmental rates for temperatures from 9.8 to 25.0°C (Campbell et al. 1974). The relationship between adult weight and temperature was determined by linear regression. The mean values of  $R_m$ ,  $T_m$ ,  $T_\sigma$ , developmental threshold, and degree-day requirement for the 18 clones from each population were used to estimate the population means. These means were compared by one-way analysis of variance. Because the shape of the temperature response for adult weight varied from

clone to clone, the adult weights for the populations were compared by one way analyses of variance, conducted separately for the data from each environmental chamber. All analyses were conducted using the statistical procedures of SAS (1982).

## Results

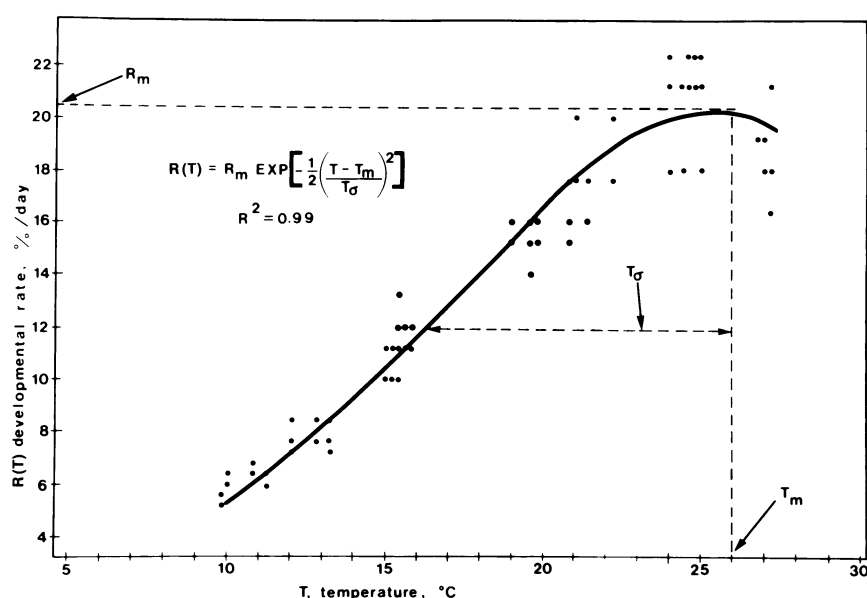
### Mortality

Less than 8% of the aphids died before reaching adulthood. Mortality was uniformly low (6.1%, SD=4.7,  $n=20$ ) at temperatures of 25.0°C or less. At 27.5°C, mortality was 21.0% (SD=16.0,  $n=5$ ) and reached 42% for one population. Nearly all mortality occurred when aphids wandered off the leaves and drowned.

### Developmental rate

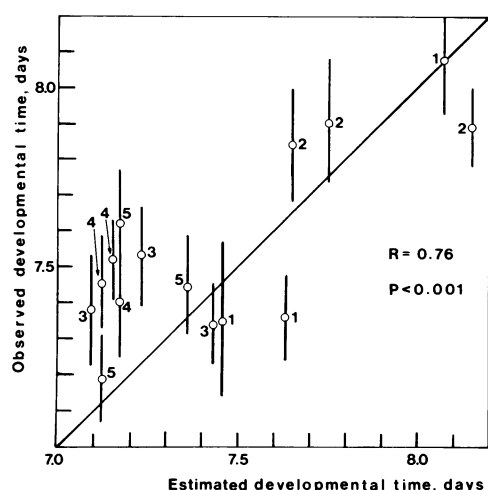
The response of developmental rate to temperature for one of the clones is shown in Fig. 2. For the 90 experimental and two control clones, the non-linear regressions were significant ( $P < 0.0001$ ) and accounted for 99% or more of the variation. The parameters of the response varied from 15.0 to 20.9% per day for  $R_m$ , 23.3 to 27.8°C for  $T_m$ , and 8.15 to 11.10°C for  $T_\sigma$  (Table 1). The results of the subsidiary test of three clones from each population reared simultaneously were consistent with the results from the five main tests (Fig. 3). This test also confirmed that there were significant differences among clones within populations (Fig. 3).

The values of  $R_m$ ,  $T_m$ , and  $T_\sigma$  differed significantly among some of the populations (Table 1). The value of  $R_m$  for the Minnesota population was significantly lower than those for the other populations. The values of  $T_m$  and  $T_\sigma$  were significantly higher for the Kansas and Saskatchewan populations than those for the others. However, the differences among populations were small compared with the differences among clones within populations; the ranges of the parameter values for the clones from the five populations showed a high degree of overlap.



**Fig. 2.** Developmental rates for individuals (●) of a Manitoba clone of *Acyrthosiphon pisum* reared at 9.8–27.0°C, to illustrate the response. The curve (—) was fitted to the data by non-linear regression





**Fig. 3.** Relationship between observed developmental times for three clones from each of five populations of *Acyrthosiphon pisum* (1–5, Table 1) reared simultaneously at  $17.5 \pm 0.5^\circ\text{C}$  and developmental times estimated from the equation relating developmental rate to temperature for each clone (Fig. 2)

The parameter values for the populations were not related to the latitudes or the long-term average temperatures of the locations. For example, the optimum temperature for rapid development,  $T_m$ , was not related to the long-term average temperature of the warmest month, July, although the latter temperature varied by  $8^\circ\text{C}$  among locations (Table 1). Similarly, neither the developmental thresholds nor the degree-day requirements were related to latitude or long-term average temperature for May, either for the populations of this study or for those of other studies (Table 2). The developmental thresholds for the clones sampled in Minnesota completely enclosed the thresholds for all North American populations studied.

#### Adult weight

Adult weight was less closely related to rearing temperature than developmental rate, and the shape of the relationship was less consistent among clones. For most clones, the relationship was linear with a negative slope (Fig. 4A, Table 3), but a linear model never accounted for more than 67%

of the variation in weight. For some clones, there was no significant ( $P > 0.05$ ) relationship between weight and temperature (Fig. 4B). For some clones, the response at  $27.5^\circ\text{C}$  was not consistent with the response for  $9.8$  to  $25.0^\circ\text{C}$ : there was either little effect or a linear relationship with a slight negative slope up to  $25.0^\circ\text{C}$  and then a substantial drop in weight at  $27.5^\circ\text{C}$  (Fig. 4C). None of the clones showed an increase in adult weight with increasing temperature.

Adult weight differed significantly among populations at all temperatures (Table 3). Adults of the Minnesota population were the lightest at all temperatures. The weights of the other populations did not differ, except that the Kansas population had a significantly higher weight at  $27.5^\circ\text{C}$ . Assuming that the relationship between adult weight and temperature was linear (the form of the response for most clones), the population parameters were estimated by averaging the linear parameters for individual clones (Table 3). Neither the slope,  $b$ , nor the intercept,  $a$ , showed a consistent trend with latitude. However, there were some noteworthy features of the relationships for the populations. The most northerly population had the highest intercept, reflecting the fact that it had the highest adult weight at  $11.5^\circ\text{C}$ . Also, this population had the second highest slope and highest  $R^2$  value, indicating that the weights of adults were more closely related to temperature than those of the other populations. In comparison, the most southerly population had the lowest slope and the lowest  $R^2$  value (Table 3).

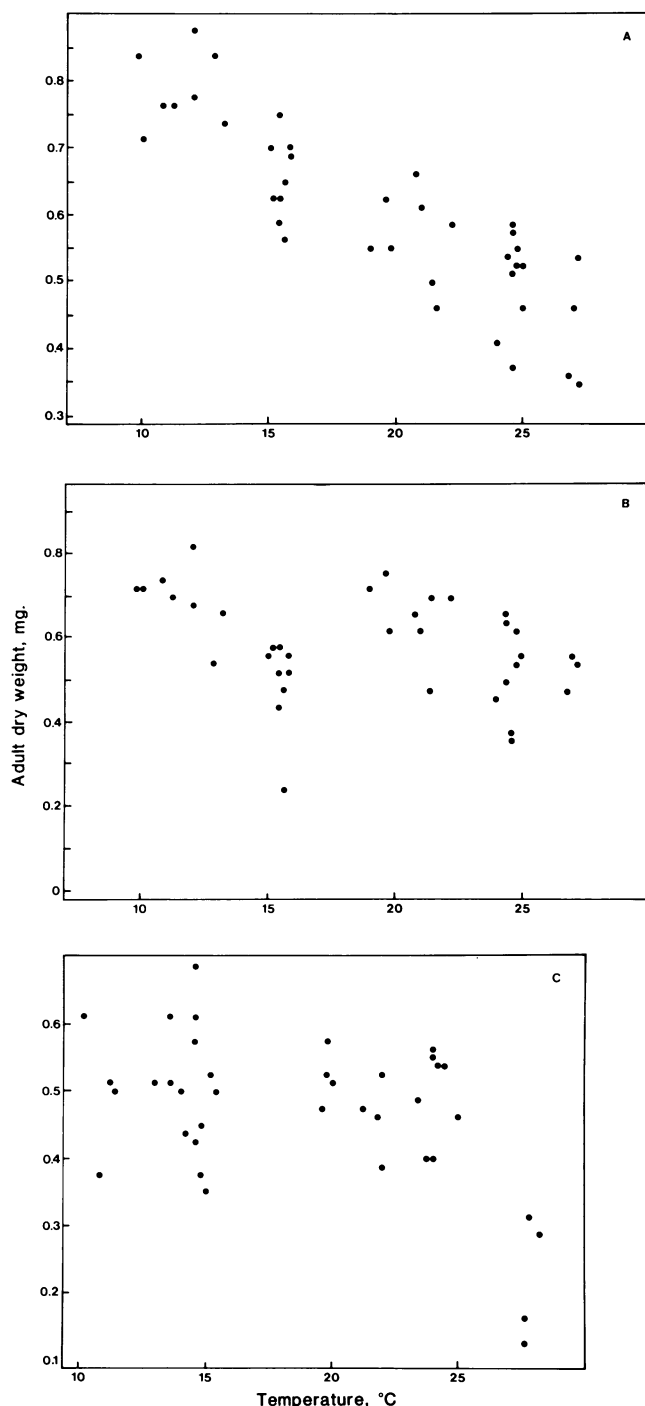
#### Discussion

The shape of the curve relating developmental rate to temperature for *A. pisum* was similar to that observed for many insects (Campbell et al. 1974; Taylor 1981). Developmental rate increased with temperature to a maximum and then declined at high temperatures. The response was described accurately by the equation of a truncated normal curve (Taylor 1981; Lamb et al. 1984). *A. pisum* is unusual in that it has the highest maximum developmental rate,  $R_m$ , so far observed for an insect (Taylor 1981), with rates of 15.0 to 20.9% per day for the clones of this study.  $T_m$ , the optimum temperature for rapid development, ranged from  $23.3$  to  $27.8^\circ\text{C}$ . The Kansas population had an optimum of  $26.0^\circ\text{C}$ , which is close to the average monthly air temper-

**Table 2.** Developmental thresholds  $\pm 95\%$  confidence intervals and ranges, in parentheses, for populations or clones of *Acyrthosiphon pisum* from 10 North American locations, their latitudes, and long-term mean daily temperatures for May from nearby weather stations. The thresholds and degree-day requirements from this study are mean values for 18 clones per population

Location	Latitude	May daily mean, $^\circ\text{C}$	Developmental threshold, $^\circ\text{C}$	Degree days	Source
Berkeley, CA	$38^\circ$	14.9	5.1	105	Campbell et al. (1974)
Manhattan, KS	$39^\circ$	18.1	$4.2 \pm 0.37$ (2.5–5.2)a *	$105 \pm 5$ (96–128)ab	this study
Madison, WI	$43^\circ$	13.3	2.6	140	Hutchison et al. (1984)
Rosemount, MA	$45^\circ$	13.9	$4.3 \pm 0.40$ (2.5–5.8)ab	$113 \pm 6$ (96–136)a	this study
Ottawa, ONT	$45^\circ$	12.8	2.5	150	Hutchison et al. (1984)
Mapleton, ND	$47^\circ$	12.6	$4.8 \pm 0.31$ (3.2–5.7)b	$100 \pm 5$ (90–127)b	this study
Vancouver, BC	$49^\circ$	11.8	4.0	118	Campbell et al. (1974)
Glenlea, MAN	$50^\circ$	11.4	$4.7 \pm 0.19$ (4.2–5.6)ab	$103 \pm 4$ (96–122)b	this study
Kamloops, BC	$51^\circ$	14.7	5.6	104	Campbell et al. (1974)
Prince Albert, SASK	$53^\circ$	10.0	$4.9 \pm 0.16$ (4.1–5.6)b	$99 \pm 2$ (94–105)b	this study

\* The means in a column do not differ ( $P > 0.05$ ) if followed by the same letter, based on Tukey's test



**Fig. 4A–C.** The average adult dry weight for 1–5 aphids reared at 9.8–27.8° C for three clones of *Acyrthosiphon pisum*, illustrating the types of responses observed: **A** negative linear response; **B** no response; **C** no response up to 25° C and a drop in weight at 27.5° C

ature of 25.7° C that it normally experiences in July. Therefore, this population would usually be exposed to average temperatures, above the optimum for one or two generations per year. In contrast, the beetle, *Entomoscelis americana* Brown, has a  $T_m$  of 33.4° C for egg hatching and 32.5° C for larval and pupal development in an environ-

ment where the average air temperatures are close to 10° C (Gerber and Lamb 1982; Lamb et al. 1984; Lamb and Gerber 1985). Four of the five aphid species that Taylor (1981) considered, including *A. pisum*, have low values for  $T_m$ . These values ranged from 26.0 to 27.5° C compared with 30° C or higher for 70% of the 47 insect species he examined. Our data for *A. pisum* were consistent with his findings, as were those for *Acyrthosiphon kondoi* (Summers et al. 1984) and *Aphis pomi* (Carroll and Hoyt 1986a). Another aphid that Taylor considered, *Macrosiphum euphorbiae*, had a  $T_m$  of 30.6° C, but this result is suspect, because it was based on extrapolation and no aphids survived to adulthood at 30° C in the study from which the data were taken (Barlow 1962). Thus, aphids as a group appear to have low optimum temperatures compared with other insects.

Based on the data for the five populations of the present study, we conclude that the temperature response of developmental rate for *A. pisum* is not related to the temperatures populations experience locally or to latitude. Although there were small significant differences among the values for  $R_m$ ,  $T_m$ ,  $T_o$ , the threshold, and degree-day requirements for the populations, there were no patterns among the differences that could be related to long-term average temperatures at the locations.

The response of adult weight to rearing temperature has not been studied for as many insects as that of developmental rate, and is not as well defined or consistent. Most species show a negative linear response (McLaren 1963; Baker 1969; Dixon et al. 1982; Gilbert 1984a), but for some, adult weight increases with rearing temperature (Orcutt and Porter 1983; Lamb and Gerber 1985). The response of most *A. pisum* clones was similar to that of the majority of insects, but for some clones there was no effect of temperature on weight. On average, there was a 45% reduction in adult dry weight from 0.61 mg at 11.5° C to 0.33 mg at 27.5° C.

As with developmental rate, there was no consistent relationship between the response of adult weight to rearing temperature and the environmental temperature or latitude of the populations. However, the most southerly population had the highest adult weight at 27.5° C and the weakest response to rearing temperature while the most northerly population had the highest adult weight at 10° C and a stronger response to rearing temperature than the most southerly. More populations must be studied to confirm that these suggestive differences truly reflect adaptation to local environments.

Our results lead to conclusions which contradict those of Campbell et al. (1974) and Hutchison and Hogg (1984), who concluded that the developmental threshold of *A. pisum* varies with the climatic conditions at the collection sites. The difference in conclusions may reflect differences in the way the response of development to temperature was measured. To estimate the response of a population adequately, a representative sample of the population must be tested and the rearing method must provide reasonably-sized samples of aphids fed on a suitable diet.

Because *A. pisum* is capable of continuous parthenogenetic reproduction under long day conditions (MacKay et al. 1983), the response of many genetically uniform individuals from the same clone can be measured (Blackman 1985). The results from such a study measure the response of a clone, not necessarily the average response of the popula-

**Table 3.** Mean adult dry weights ( $n=18$ ) at five rearing temperatures for five populations of *Acyrtosiphon pisum* from central North America and mean linear regression coefficients  $\pm 95\%$  confidence intervals for the relationship between adult dry weight ( $w$ ) and rearing temperature ( $T$ )

Population	Adult dry weight, mg					Regression coefficients, $w = a + bT$		
	Rearing temperature, °C					$a$	$b$	$R^2$
	11.5	14.9	20.6	24.5	27.5			
1. Manhattan, KS	0.622b*	0.565b	0.559b	0.486b	0.451c	0.733 ( $\pm 0.050$ )	-0.0097 ( $\pm 0.00197$ )	0.29
2. Rosemount, MA	0.559a	0.497a	0.500a	0.375a	0.246a	0.741 ( $\pm 0.067$ )	-0.0147 ( $\pm 0.00265$ )	0.49
3. Mapleton, ND	0.615ab	0.565b	0.526ab	0.491b	0.316b	0.747 ( $\pm 0.066$ )	-0.0114 ( $\pm 0.00203$ )	0.31
4. Glenlea, MAN	0.598ab	0.589b	0.516ab	0.481b	0.317b	0.711 ( $\pm 0.112$ )	-0.0128 ( $\pm 0.00249$ )	0.43
5. Prince Albert, SASK	0.645b	0.577b	0.514ab	0.492b	0.329b	0.804 ( $\pm 0.043$ )	-0.0141 ( $\pm 0.00180$ )	0.53

\* Means in a column followed by the same letter do not differ ( $P > 0.05$ ), based on Tukey's test

tion from which the clone was taken. Our results show that the responses of clones from one population can vary more than the average responses of populations from widely different locations. To estimate the response of a population, a random sample of clones from the population must be tested. Moreover, it is not sufficient to test a sample from a population which is reared as a mixed colony prior to the test, because competition among clones takes place and the sample size of clones tested is unknown. Most studies of *A. pisum* development were based on results from one clone or a mixed sample of an unknown number of clones (e.g. Kilian and Nielson 1971; Siddiqui et al. 1973; Campbell et al. 1974). It is not possible to determine whether the differences in developmental responses among these studies reflect differences among clones or differences among populations. Only the latter could show local adaptations of populations.

The rearing conditions are also critical for accurately assessing the developmental response of a population, because they affect the sample size and observed developmental time. Poor conditions may cause mortality that results in a sample size inadequate for non-linear regression or for an accurate estimate of a developmental threshold from linear regression (e.g. Hutchison and Hogg 1984). Poor survival of the test aphids can also cause differential survival among clones, resulting in biased estimates for the response of the population. If the host plants are of poor nutritional quality, the developmental rate at all temperatures may be reduced. In this case, the developmental threshold is higher than when the nutritional quality of the diet is high (Lamb and Loschiavo 1981; Dixon et al. 1982; Ritland and Scriber 1985). The developmental rates and survivals from our study were higher than those at equivalent temperatures from other North American studies, indicating that our results were less affected by rearing conditions than those previously reported. They were similar to those reported for aphids reared on intact, growing plants (Bieri et al. 1983).

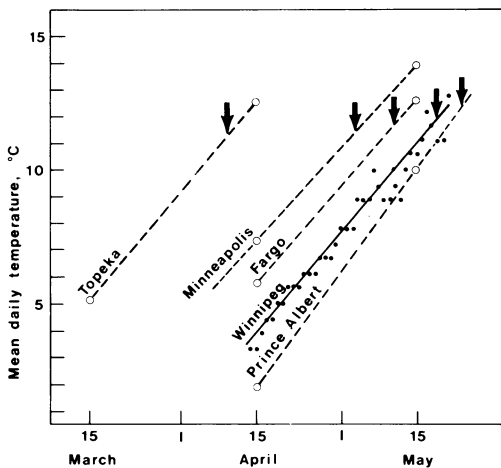
We conclude that the variation in developmental threshold among populations reported in previous studies of *A. pisum* (Table 2) can be attributed either to differences among clones (not differences among populations), or to differences in rearing conditions among studies. Based on all the data collected for North American *A. pisum*, there is no convincing evidence that the developmental response to temperature is adapted to local temperature conditions or varies with latitude. This conclusion applies both to com-

parisons based on the developmental threshold and degree-day requirements which assume the response is linear, and to comparisons based on the parameters of a more realistic non-linear representation of the developmental response to temperature.

Why have local populations of *A. pisum* not adapted their developmental response to local temperature? We might argue that there have been too few sexual generations for adaptation to be detectable, because the species was introduced to North America from Europe about 100 years ago (Harper et al. 1978). However, local differentiation of migratory tendency (Lamb and MacKay 1979, MacKay unpublished) and photoperiodic control of reproduction (Smith and MacKay unpublished) have been observed.

Based on his examination of the developmental response of many insects to temperature, Taylor (1981) suggested that aphids have evolved to maximize developmental rate, an hypothesis first proposed by Kennedy and Stroyan (1959). It is possible that strong selection for a high rate of development constrains the shape of the developmental response and prevents its adaptation to local conditions. Genetic variation in developmental rate still exists as shown by the variation in the developmental parameters among clones, but this variation might be maintained by a mechanism similar to the one proposed by Gilbert (1984b). For cabbage white butterflies, *Pieris rapae*, he found that very high selection against the heaviest individuals constrained selection for an increase in size and yet variability was maintained. Alternatively, Campbell et al. (1974) proposed that temperature in spring acts as a strong selection force for the developmental response. If the shape of the response is constrained by the response at low temperature, we would expect the five populations to have similar developmental parameters, as we observed, because they experience similar temperatures in spring, although there is a latitudinal gradient in the timing of the onset of temperatures above the threshold (Fig. 5). The hypotheses of Gilbert (1984b) and Campbell et al. (1974) cannot be tested for *A. pisum* with the data presently available.

We do not know why the responses of developmental rate and adult weight to rearing temperature do not show the same degree of adaptation to local conditions as photoperiodic response and migratory tendency. Studies of clones under field conditions might provide a clearer picture of the adaptive significance of the temperature responses of developmental time and adult weight. Our study provides another example supporting the view that developmental



**Fig. 5.** Long-term (30 years) average temperatures in spring for the weather stations closest to the locations where *Acyrtosiphon pisum* was sampled (Table 1). The open circles are monthly averages and the closed circles are the daily averages for Winnipeg. The arrows indicate the estimated average temperature and date when the first generation would reach adulthood at each location based on degree days accumulated above the developmental threshold (Table 2)

rate, and possibly adult weight, of terrestrial insects may not be as well adapted to local conditions as other life history traits.

**Acknowledgements.** We are grateful to C. Shearer, J. Walkof, and D. Wright for their technical assistance.

## References

- Baker CRB, Miller GW (1978) The effect of temperature on the post-diapause development of four geographical populations of the European cherry fruit fly (*Rhagoletis cerasi*). *Ent Exp Appl* 23:1–13
- Baker RR (1969) The evolution of the migratory habit in butterflies. *J Anim Ecol* 38:703–746
- Baldwin JD, Dingle H (1986) Geographic variation in the effects of temperature on life-history traits in the large milkweed bug *Oncopeltus fasciatus*. *Oecologia* (Berlin) 69:64–71
- Barlow CA (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
- Beck SD (1980) *Insect Photoperiodism*. Academic Press, New York
- Bieri M, Baumgaertner J, Bianchi G, Delucchi V, von Arx R (1983) Development and fecundity of pea aphid (*Acyrtosiphon pisum* Harris) as affected by constant temperatures and by pea varieties. *Bull Soc Entomol Suisse* 56:163–171
- Blackman RL (1985) Aphid cytology and genetics. In: *Evolution and Biosystematics of Aphids*. Proc Int Aphidological Symp at Jablonna, April 1981. pp. 171–237. Polish Academy of Science, Warsaw
- Bradshaw WE (1976) Geography of photoperiodic response in a diapausing mosquito. *Nature* (London) 262:384–385
- Campbell A, Frazer BD, Gilbert N, Gutierrez AP, Mackauer M (1974) Temperature requirements of some aphids and their parasites. *J Appl Ecol* 11:431–438
- Carroll DP, Hoyt SC (1986a) Developmental rate, weight, and ovarian parameters of apple aphids, *Aphis pomi* (Homoptera: Aphididae), reared at one or two constant temperatures, with evidence of residual effects. *Environ Entomol* 15:607–613
- Carroll DP, Hoyt SC (1986b) Some effects of parental rearing conditions and age on progeny birth weight, growth, development, and reproduction in the apple aphid, *Aphis pomi* (Homoptera: Aphididae). *Environ Entomol* 15:614–619
- Dixon AFG, Chambers RJ, Dharma TR (1982) Factors affecting size in aphids with particular reference to the black bean aphid, *Aphis fabae*. *Ent Exp Appl* 32:123–128
- Gerber GH, Lamb RJ (1982) Phenology of egg hatching for the red turnip beetle, *Entomoscelis americana* (Coleoptera: Chrysomelidae). *Environ Entomol* 11:1258–1263
- Gilbert N (1984a) Control of fecundity in *Pieris rapae* I. The problem. *J Anim Ecology* 53:581–588
- Gilbert N (1984b) Control of fecundity in *Pieris rapae* III. Synthesis. *J Anim Ecology* 53:599–609
- Harper AM, Miska JP, Manglitz GR, Irwin BJ, Armbrust EJ (1978) The literature of arthropods associated with alfalfa. III. A bibliography of the pea aphid *Acyrtosiphon pisum* (Harris) (Homoptera: Aphididae). Special Publication 50. Agricultural Exp. Station, University of Illinois at Urbana-Champaign
- Hutchison WD, Hogg DB (1984) Demographic statistics for the pea aphid (Homoptera: Aphididae) in Wisconsin and a comparison with other populations. *Environ Entomol* 13:1173–1181
- Kennedy JS, Stroyan HLG (1959) Biology of aphids. *Annu Rev Entomol* 4:139–169
- Kilian L, Nielsen MW (1971) Differential effects of temperature on the biological activity of four biotypes of the pea aphid. *J Econ Entomol* 64:153–155
- Lamb RJ, Gerber GH (1985) Effects of temperature on the development, growth, and survival of larvae and pupae of a north-temperate chrysomelid beetle. *Oecologia* (Berlin) 67:8–18
- Lamb RJ, Loschiavo SR (1981) Diet, temperature, and the logistic model of developmental rate for *Tribolium confusum* (Coleoptera: Tenebrionidae). *Can Entomol* 113:813–818
- Lamb RJ, MacKay PA (1979) Variability in migratory tendency within and among natural populations of the pea aphid, *Acyrtosiphon pisum*. *Oecologia* (Berlin) 39:289–299
- Lamb RJ, Gerber GH, Atkinson GF (1984) Comparison of developmental rate curves applied to egg hatching data of *Entomoscelis americana* Brown (Coleoptera: Chrysomelidae). *Environ Entomol* 13:868–872
- Llewellyn M, Brown VK (1985) A general relationship between adult weight and the reproductive potential of aphids. *J Anim Ecology* 54:663–673
- Lonsdale DJ, Levinton JS (1985) Latitudinal differentiation in copepod growth: an adaptation to temperature. *Ecology* 66:1397–1407
- MacKay PA, Downer RGH (1979) Water content, weight change, and activity of apterous and alate virginoparous *Acyrtosiphon pisum* (Harris) (Homoptera: Aphididae). *Can J Zool* 57:363–367
- MacKay PA, Wellington WG (1977) Maternal age as a source of variation in the ability of an aphid to produce dispersing forms. *Res Popul Ecology* 18:195–209
- MacKay PA, Reeleder DJ, Lamb RJ (1983) Sexual morph production by apterous and alate viviparous *Acyrtosiphon pisum* (Harris) (Homoptera: Aphididae). *Can J Zool* 61:952–957
- Masaki S (1978) Climatic adaptation and species status in the lawn cricket II. Body size. *Oecologia* (Berlin) 35:343–356
- McLaren IA (1963) Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. *J Fish Res Bd Can* 20:685–727
- Nealis VG, Jones RE, Wellington WG (1984) Temperature and development in host-parasite relationships. *Oecologia* (Berlin) 61:224–229
- Orcutt JD, Porter KG (1983) Diel vertical migration by zooplankton: Constant and fluctuating temperature effects on life history parameters of *Daphnia*. *Limnol Oceanogr* 27:720–730
- Ritland DB, Scriber JM (1985) Larval developmental rates of three putative subspecies of tiger swallowtail butterflies, *Papilio glaucus*, and their hybrids in relation to temperature. *Oecologia* (Berlin) 65:185–193



- SAS Institute Inc (1982) SAS User's Guide Statistics. SAS Inst Inc, Cary NC, USA
- Siddiqui WH, Barlow CA, Randolph PA (1973) Effects of some constant and alternating temperatures on population growth of the pea aphid, *Acyrtosiphon pisum* (Homoptera: Aphididae). *Can Entomol* 105:145–156
- Summers CG, Coviello RL, Gutierrez AP (1984) Influence of constant temperatures on the development and reproduction of *Acyrtosiphon kondoi* (Homoptera: Aphididae). *Environ Entomol* 13:236–242
- Tauber MJ, Tauber CA (1978) Evolution of phenological strategies in insects: a comparative approach with eco-physiological and genetic considerations. In: Dingle H (ed) *Evolution of Insect Migration and Diapause*. Springer, New York
- Tauber MJ, Tauber CA, Masaki S (1985) *Seasonal Adaptations of Insects*. Oxford University Press, New York
- Taylor F (1981) Ecology and evolution of physiological time in insects. *Am Nat* 117:1–23
- Trimble RM, Lund CT (1983) Intra- and interpopulation variation in the thermal characteristics of preadult development of two latitudinally diverse populations of *Toxorhynchites rutilus septentrionalis* (Diptera: Culicidae). *Can Entomol* 115:659–662

Received November 6, 1986