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TEMPERATURE REQUIREMENTS OF SOME APHIDS AND THEIR PARASITES

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INTRODUCTION

The rate of insect development depends upon the temperature to which the insects are exposed. For each species, the temperature below which no measurable development occurs is its threshold of development. The amount of heat required over time for an insect to complete some aspect of development is considered to be a thermal constant (Andrewartha & Birch 1954; Bursell 1964). Messenger (1959, 1970) has shown that the threshold and the thermal constant may be useful indicators of an insect's potential distribution and abundance. This paper is concerned with differences between the developmental thresholds and temperature requirements of *Acyrtosiphon pisum* (Harris), *Aphis craccivora* Koch, *Brevicoryne brassicae* (L.), *Macrosiphum avenae* (F.), and *Masonaphis maxima* (Mason) (Homoptera: Aphididae); their parasites *Aphidius smithi* Sharma & Subba Rao, *A. ervi ervi* Haliday, *A. e. pulcher* Baker, *A. rubifolii* Mackauer, *Diaeretiella rapae* (M'Intosh), and *Praon pequodorum* Viereck (Hymenoptera: Aphidiidae); and hyperparasites *Dendrocercus* (= *Lygocerus*) *niger* (Howard) (Hymenoptera: Ceraphronidae) and *Asaphes lucens* (Provancher) (Hymenoptera: Pteromalidae). No attempt is made to review the extensive literature on temperature effects on insect development in general. Andrewartha & Birch (1954), Bodenheimer & Swirski (1957), Howe (1967), Messenger (1959) and Schwerdtfeger (1963) have critically reviewed methods for determining temperature coefficients.

METHODS

The relationship between the rate of development and temperature is usually of the type shown in Fig. 1. Over a range of temperatures B, the relationship can be represented by a straight line which, when extended, cuts the x -axis at the temperature threshold t . It is not practical to examine the average rate of development at temperatures in the range A close to t , because considerable mortality occurs. In effect, there is selection for those individuals which can develop at the low temperature. At high temperatures in range C, the rate of development declines from the linear relationship observed in range B. Different species and, as will be shown, different populations of the same species have different temperature ranges A, B and C and different values of t . The deleterious effect of the high temperatures in range C occurs only if the temperature is held constant in the range or fluctuates about an average value within the range. If the temperature fluctuates about a daily average in range B and the daily maximum reaches range C, no

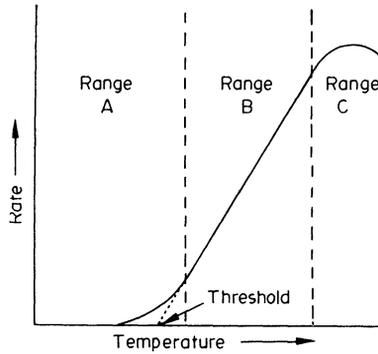


FIG. 1. The relationship between the rate of insect development and temperature, showing the non-linear portions A, C, and the linear portion B, used to estimate the threshold of development (t) by extrapolation.

deleterious temperature effect is observed. For the species examined here, the daily average temperatures in the field fell into ranges A and B. The deleterious effect of high temperature is not normally experienced. In practice, therefore, field conditions lie almost exclusively on the straight-line section of Fig. 1, or at temperatures below the threshold, when no development occurs. The straight line is best characterized biologically in terms of the threshold temperature t and a time-to-adult K , which is the number of degree-days above t required by an insect to complete its development. K is, in fact, the reciprocal of the slope b of the straight line.

Apterous aphids and parasites (Table 1) were reared in growth chambers at each of three or four constant temperatures. The number of days required to develop from the newly born nymph to adult and from egg to adult were recorded for the aphids and parasites, respectively. The reciprocals, y , i.e. the rates of development from egg to adult or birth to adult, were calculated for each individual insect and plotted against the temperature T ($^{\circ}$ C). The plot was checked for linearity. Occasionally, the value for the highest temperature had to be rejected when it did not fit the straight line through the other points. From the remaining data the regression line $y = a + bT$ was calculated; this estimates the relationship between temperature and the rate of development.

The parameters t and K are not very satisfactory from a statistical point of view. The standard error of t is approximately:

$$\frac{\bar{y}}{b} \sqrt{\frac{s^2}{N\bar{y}^2} + \left[\frac{\text{S.E. of } b}{b} \right]^2}$$

where s^2 is the residual mean square of y and \bar{y} is the sample mean. The S.E. of K is approximately: $(\text{S.E. of } b)/b^2$. Since the threshold t is necessarily found by extrapolation of the regression line, it is very inaccurately estimated. To obtain an accurate estimate of t , at least fifty individuals must be reared at each of three or four constant temperatures, and checked twice or three times daily at temperatures between 5 and 15 $^{\circ}$ C, and every 2 or 3 h at temperatures between 16 and 30 $^{\circ}$ C. However, the estimates of time-to-adult and the threshold are highly negatively correlated. A small positive error in t is automatically corrected by a corresponding negative error in K , so that predicted rates of development are hardly affected, except at temperatures a degree or two above the threshold. This means that ten to twenty animals per temperature are adequate to estimate a physiological time-scale for use in the field.

The thermal constant of greatest interest to ecologists is that for development from

birth to final moult for aphids, and from oviposition to adult emergence from the aphid mummy for parasites and hyperparasites. This time-to-adult largely determines the rate of turnover of successive generations. It is shorter than the vague 'generation time', if only because further time usually elapses before reproduction begins. For one parasite population, the time-to-adult was not measured, and Table 1 shows the time-to-mummy formation instead.

The time-to-adult (but not the threshold) varies according to the host or diet on which the insect is feeding (Bonnemaison 1951; Gutierrez, Morgan & Havenstein 1971; Markkula 1953). Unless care is taken to ensure that the hosts used in the laboratory are similar to those in the field, the temperature coefficients may not be suitable for computing a physiological time-scale for a field study (Hughes 1963; Mackauer 1972). Nearly all the data in Table 1 refer to first-generation, or occasionally second-generation, progeny of insects collected in the field. The host plants and aphids used for rearing were of the same species and variety as those occurring in the given localities. Additional limitations may arise from the use of constant *versus* variable temperatures (Bonnemaison 1951; Howe 1967; Messenger 1964; Siddiqui, Barlow & Randolph 1973). We have not found much difference in development rates between temperatures that were constant or fluctuating about the same average value, provided that (a) the fluctuations do not extend below the threshold, and (b) the average temperature is not in range C (Fig. 1). Gilbert & Gutierrez (1973) found that, in an aphid with discrete generations, the generation times in the field with naturally fluctuating temperatures agreed perfectly with those determined at the fixed temperatures in the laboratory.

RESULTS AND DISCUSSION

Developmental thresholds

The threshold of the pea aphid, *Acyrtosiphon pisum*, in a warm summer climate such as Berkeley, California, or Kamloops, British Columbia, is higher than that in a cooler climate such as Vancouver, British Columbia (Table 1). The cabbage aphid, *Brevicoryne brassicae*, also has relatively high thresholds in warm climates, and lower thresholds in colder areas such as Finland. The four aphids studied in Vancouver had very similar threshold values. Reductions in thresholds are easily compensated by corresponding increases in developmental time, as noted earlier. The precise value of the threshold is important only when temperatures fluctuate in range A of Fig. 1, that is, only at the beginning and end of the season. We suspect, therefore, that the different thresholds are concerned with events near the start of the season. The point may be clarified by comparing parasite and host thresholds.

In general, the thresholds of parasites are higher than those of their hosts. It follows that the build-up of the parasite population will be delayed until average temperatures increase and the host has become well established in spring. It might appear initially that it is emergence from diapause, rather than rates of development, that determines an early season coincidence between host and parasite populations. But any parasite that emerges from diapause before the host does will find no hosts at all. For all practical purposes, the parasite season cannot start earlier than that of the host. These considerations are borne out by observations on *Masonaphis maxima* made in 1972. The first fundatrices emerged precisely when the first leaf buds opened on the thimbleberry, *Rubus parviflorus* Nutt., host plant. Any fundatrices that emerged before then could not have survived.

Table 1. Thresholds ($t \pm S.E.$) and times-to-adult ($K \pm S.E.$) of apterous aphids, their parasites and hyperparasites at various locations

Aphid hosts	t (°C)	K (day·°C)	Locality*	Parasites	t (°C)	K (day·°C)
<i>Acyrtosiphon pisum</i>	5.1 ± 0.22	105 ± 2.2 ^a	BER	<i>Aphidius smithi</i>	4.8 ± 0.49	172 ± 7.6 ^b
<i>A. pisum</i>	5.6 ± 0.11	104 ± 2.2 ^c	KAM	<i>A. ervi ervi</i>	6.0 ± 0.08	197 ± 1.2 ^c
				<i>A. e. pulcher</i>	6.1 ± 0.08	188 ± 1.5 ^c
				<i>A. smithi</i>	6.1 ± 0.08	180 ± 1.3 ^c
<i>A. pisum</i>	4.0 ± 0.28	118 ± 2.8 ^a	VAN	<i>Praon pequodorum</i>	6.9 ± 0.09	199 ± 1.4 ^c
<i>Aphis craccivora</i>	8.3	80 ⁱ	NSW	<i>Aphidius ervi ervi</i>	4.2 ± 0.38	230 ± 10.2 ^b
<i>Brevicoryne brassicae</i>	7.1 ± 0.48	136 ± 7.2 ^d	BER	<i>Diaeretiella rapae</i>	3.5 ± 1.43	241 ± 25.5 ^h
<i>B. brassicae</i>	5	127 ^e	CAN	<i>D. rapae</i>	7	97 ± 3 ^e
<i>B. brassicae</i>	1.7 ^f	—	TIK			
<i>B. brassicae</i>	6.5	182 ^g	WAG	<i>D. rapae</i>	6.5	188 ^g
<i>B. brassicae</i>	4.7 ± 0.80	163 ± 11.4 ^d	VAN	<i>D. rapae</i>	4.9 ± 0.94	116 ± 9.4 ^{h†}
<i>Macrosiphon avenae</i>	4.8 ± 0.61	117 ± 4.6 ^b	VAN			
<i>Masonaphis maxima</i>	3.9 ± 0.47	125 ± 5.0 ^d	VAN	<i>Aphidius rubifolii</i>	5.3 ± 0.41	176 ± 7.7 ^h
Parasite host	t (°C)	K (day·°C)	Locality*	Hyperparasites	t (°C)	K (day·°C)
<i>Aphidius smithi</i>	6.1 ± 0.08	180 ± 1.3 ^c	KAM	<i>Dendrocerus niger</i>	6.5 ± 0.11	184 ± 1.8 ^c
				<i>Asaphes lucens</i>	8.1 ± 0.22	233 ± 4.2 ^c

^a Frazer & Gilbert; ^b Frazer; ^c Campbell; ^d Gilbert & Gutierrez; ^e Hughes (1963); ^f Markkula (1953); ^g Hafez (1961); ^h Gutierrez; ⁱ Gutierrez *et al.* (1971).

* BER, Berkeley, California, U.S.A.; CAN, Canberra, Australia; KAM, Kamloops, British Columbia, Canada; NSW, New South Wales, Australia; TIK, Tikkurila, Finland; VAN, Vancouver, British Columbia, Canada; WAG, Wageningen, Holland.

† Time to mummy formation.

If these considerations are correct, Table 1 contains two anomalies. The threshold of *Diaeretiella rapae* at Berkeley is low in comparison with that at Vancouver, and the thermal constant K is correspondingly high. Similarly, *D. rapae*'s threshold at Canberra is high for the local temperatures, and its thermal constant is correspondingly low. We are inclined to suspect that these are errors of estimation.

Our observations do not agree with those of Morris (1971) or of Morris & Fulton (1970), who investigated the effects of temperature and humidity on survival and genetic quality of natural populations of the fall webworm, *Hyphantria cunea* Drury (Lepidoptera), in New Brunswick and Nova Scotia. They recognized that populations in different areas might have different thresholds, but found differences only in the thermal constants K . Since Table 1 shows threshold differences of only 1–2° C over the 1300 km difference in latitude between Berkeley and Vancouver, differences between adjoining provinces would be difficult to detect. However, Danilevsky (1957) found that three populations of *Acronycta rumicis* L. (Lepidoptera) from Leningrad, Belgorod, and Sukhumi had the same temperature threshold of 10° C, both for larval and pupal development. The difference in latitude between Sukhumi and Leningrad is one-and-a-half times that between Berkeley and Vancouver. The times-to-adult varied only from 514 (Belgorod, Leningrad) to 544 (Sukhumi) day-degrees C, but this difference was statistically significant.

In the aphids studied here, all instars had the same thresholds, within the limits of experimental error. However, in the cabbage white butterfly, *Pieris rapae* (L.), the threshold at Vancouver (Table 2) is remarkably high in first and second instars, but declines

Table 2. *Thresholds ($t \pm S.E.$) of *Pieris rapae* (L.)*

Vancouver*		England†	
Stage (instar)	t (° C)	Stage	t (° C)
I+II	10.9 ± 0.32	Egg	8.3
III	7.1 ± 0.99	Instars I–V	7.7
IV	5.6 ± 0.73	Pupa	2.8

* Gilbert.

† Baker (1968), Richards (1940).

as the larva grows older. We have no data for egg hatch at Vancouver, but estimates made from data in the literature for *P. rapae* in southern England show the same effect. These declining thresholds will, once again, affect timing. The high temperatures required for egg and early larval development will ensure that the host plant is sufficiently well grown to support the larvae by the time the larvae enter their voracious fourth and fifth instars. The reduction in the threshold that follows ensures that cool weather cannot prevent completion of the generation.

Developmental time

Table 3 gives the developmental time at a constant temperature of 10° C of pea aphid and of cabbage aphid and its parasite, *Diaeretiella rapae*, at Berkeley and Vancouver. The data show that the temperature requirements of the three Berkeley stocks are higher than those of the corresponding Vancouver stocks. This means that the temperature requirements have been adjusted to suit local climatic conditions. In particular, the Berkeley insects take longer to develop than they might; that is, Vancouver insects maintained under Berkeley conditions would develop faster than their local counterparts.

Table 3. *Developmental time (days) of Berkeley and Vancouver races of three insects reared at 10° C*

Species	Vancouver	Berkeley
<i>Diaerietrella rapae</i> *	22.1 ± 1.08	28.4 ± 1.23
<i>Brevicoryne brassicae</i> †	33.7 ± 0.88	42.0 ± 0.84
<i>Acyrtosiphon pisum</i> †	19.5 ± 0.26	20.9 ± 0.25

* Time to mummy formation.

† Time to adult.

The pea and cabbage aphids at Berkeley differ markedly in their thermal characteristics from those at Vancouver and, presumably, from other biotypes adapted to different climatic conditions. Although these biotypes may be ephemeral, existing only through the summer period (Frazer 1972), our findings do not support applicability of Johnson's (1969) suggestion that aphids form vast, uniform continental populations. Kilian & Nielson (1971) in reporting data which evidently refer to range C of Fig. 1, confirm that strains of pea aphid from hot regions of the U.S.A. can withstand high temperatures better than strains from cooler regions.

In addition to populations of a given species varying in their thermal constants from place to place, there are differences in the reaction of a different species to similar climatic conditions. For example, *Aphis craccivora*, a very opportunistic and ephemeral species in New South Wales, develops much faster than *Brevicoryne brassicae* at Canberra. The cabbage aphid has a much longer developmental period than the pea aphid in Vancouver and Berkeley, but not at Canberra. This may be connected with the fact that the favourable season is short at Canberra (Hughes 1963); however, we do not have enough comparisons to investigate this point further.

A long time-to-adult for the parasite has the effect of making the parasite's generation time longer than that of its host, regardless of the ambient temperature. The predicted effect is confirmed by field observations, but we cannot generalize about the underlying reasons (Gilbert & Gutierrez 1973). However, by developing more slowly than their hosts, some parasites ensure the continued availability of a minimum host supply and thus their own survival. Such a situation would be expected to occur in established and presumably well-adapted host-parasite relationships. It would not necessarily occur in emerging and initially unstable relationships, such as may arise when natural enemies are introduced and released for biological pest control.

Perhaps these observations may explain why a relatively large proportion of introduced parasites become established in the release areas, but fail to contribute in any significant way to the control of the host (DeBach 1964; Munroe 1971). Current biological control practice is to import natural enemies, if possible, from areas having a climate similar to the intended release area (Messenger 1970; Messenger & van den Bosch 1971). While pre-adaptedness to climate indeed may be essential for a species to become established, at the same time this adaptedness may limit a parasite's ability to achieve satisfactory host control early in the season.

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SUMMARY

- (1) The temperature requirements of some aphids differ from place to place for the same species and from species to species.
- (2) The temperature requirements of the parasites and hyperparasites associated with these aphids differ in a similar manner but, as a rule, are higher than those of their hosts.
- (3) It is suggested that a thermal constant higher for the parasite than for the host is advantageous to the parasite.

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