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The influence of temperature and photoperiod on the development, survival and reproduction of the sowthistle aphid, *Hyperomyzus lactucae*

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Abstract

The development time, survivorship and age-specific fecundity of apterous and alate virginoparae of the sowthistle aphid, *Hyperomyzus lactucae* (L.) (Homoptera: Aphididae), reared on *Sonchus oleraceus* L., were measured under various temperature and light regimes. Within the temperature range of daily means of 12.5–24 °C, speed of development and reproductive rate increased, while life span and total fecundity decreased, with an increase in temperature. The relationship between temperature and rate of development was nearly linear, with a notional development threshold estimated at about 2 °C. The intrinsic rate of increase (r_m) was positively correlated with temperature when calculated on a daily basis, but was inversely related to temperature when measured on a physiological time scale. Alatae generally had a longer development time, and achieved a lower reproductive rate and life-time fecundity, than apterae reared under identical conditions.

Comparison of aphid performance under constant and alternating temperature regimes, and between successive generations under the same regime, showed that (1) the conditions experienced by the aphid as an embryo within its mother are important in determining survival and development and (2) tolerable temperature limits vary with the pattern and amplitude of the fluctuations of temperature.

At 22 °C, changes of photoperiod within the range of 12D:12L to 8D:16L had little effect on aphid performance.

Introduction

The sowthistle aphid, *Hyperomyzus lactucae*, originally a palaearctic species, is now cosmopolitan (Eastop, 1966). Its main host plant is the common sowthistle, *Sonchus oleraceus*, which is a cosmopolitan weed of virtually no economic importance, except as the principal reservoir of several viruses, which *H. lactucae*, particularly, transmits to lettuce and other crops sometimes causing severe crop losses (Duffus, 1963, 1973; Stubbs & Grogan, 1963).

Despite its pest status as a virus vector, and the occasional damage it does to its primary host plants, *Ribes* spp., little quantitative information has yet been published on the responses of *H. lactucae* to climatic conditions. In this paper, we report our laboratory studies of the effect of constant and alternating temperatures and of photoperiod on its development, survival and reproduction.

Materials and methods

Sowthistle plants were grown in 'compost' soil flats in a glasshouse maintained at 23 ± 2 °C, 60–90% R.H. with photoperiod augmented to 13 h a day.

A stock culture of *H. lactucae* was established from 60 apterous adults collected from the field in Canberra in September 1980 and maintained on young sowthistle seedlings in a glasshouse insectary at 22 ± 2 °C, 70–80% R.H. with photoperiod augmented to 14 h a day.

Aphids for experiments were reared individually or in groups on either detached flower shoots or detached young leaves of the host plant. Detached flower shoots were cut from large solitary plants in the glasshouse, stood in a modified Hoagland-Snyder culture solution (see Hughes & Woolcock, 1965) and were enclosed in a clear cylindrical cage (63 mm diameter × 120 mm high; Liu, 1983).

Detached young leaves were cut from the young seedlings in the glasshouse and placed flat on nutrient agar set at the bottom of 25 × 50 mm clear plastic vials (Hughes & Bryce, 1984). When such vials were inverted the aphids could feed in their natural position on the undersurface of the leaf. A 10 mm diameter (gauzed) hole on the top half of the vial ensured ventilation. Whenever the leaves appeared discoloured they were replaced with fresh ones.

A preliminary experiment showed that, with both young flower shoots and young leaves, the performance of the aphids on the excised plant material was not significantly different from that on whole plants, as far as development, survival and reproductive rates are concerned.

Experimental conditions for rearing test aphids. Various temperature and light regimes were set up and maintained in small environmental cabinets in which temperature was controlled within ± 0.5 °C of the set value. The cabinets could be set so that temperatures were higher during the photophase than during the scotophase. The time taken for a cabinet to change from one temperature to the other varied with the amplitude of alternation, e.g. approximately 1 h was required for a 15 °C change. The required photoperiods were provided by two 20 watt fluorescent tubes set vertically on the back wall inside each cabinet. Thermoperiods and photoperiods were controlled by timeclocks. No attempt was made to control humidity in the cabinets.

Basic procedures of experiments and analysis. Except for the experiments to test deleterious effects of high constant temperatures, experimental cohorts to be reared under the various temperature and light regimes were initiated with first instar (0–24 h old) nymphs produced by apterous adults born and reared under the same conditions. The test nymphs were transferred onto the flower shoots or young leaves and then examined at 24 h intervals to record and remove exuviae and progeny, until each individual female died. The immature development time, the total life span and the number of progeny for each aphid under each regime were recorded and age-specific life (l_x), tables and fertility (m_x) tables for the cohort were developed on a daily basis. Where required, the intrinsic rate of increase (r_m), the net reproductive rate (R_o) and the mean generation time (T) were calculated following the procedures of Andrewartha & Birch (1954).

Experimental design. All the experiments were carried out from December 1980 to June 1981. The comparisons of the effects of constant and alternating temperatures with same daily mean (e.g. 12.5 °C and 5–20 °C) were initiated at the same time.

Ten cohorts of apterous aphids were reared as individuals on flower shoots under temperature and light regimes, from high temperatures with long days to low temperatures with short days, chosen to encompass the normal range of the factors encountered in the field (Table 1). The effects of high temperature were observed by rearing cohorts of the aphids on flower shoots at 26 °C and 28 °C for a few generations (Table 2). To test the effect of photoperiod, 4 cohorts were reared on flower shoots and young leaves at 22 °C, with the photophase varying from 12 h to 16 h each day (Table 3).

For the experiments with alatae, test nymphs were first reared in groups of 20 per flower shoot. When winged forms became apparent in the third instar, they were transferred to new shoots and reared singly until death. In all, five cohorts were reared and observed under various temperature-light regimes (Table 4).

Results and analysis

Performance of apterae

Rate of development. At each temperature tested up to 24 °C, the duration of nymphal development decreased significantly with an increase in temperature (Table 1). Except at 12.5 °C, where a morph 'switch' to sexuparae occurred in the test aphids (see below), no significant differences were found between durations at each of the other two pairs of constant and alternating temperatures with the same daily mean.

For constant temperatures, the relationship between percent of nymphal development per day (Y), and temperature (X) for *H. lactucae* was approximately linear from above 12.5 °C to below 26 °C ($r^2 = 0.9996$, d.f. = 2). The data obtained at 26 °C were excluded from the linear analysis because the reversal in trend of development rate at this temperature was obvious. Similarly, the data obtained at 12.5 °C was not included because of the morph switch to sexuparae at this temperature. The regression line was $Y = 0.6962X - 1.2892$, with a notional threshold temperature at 1.9 °C. The thermal constant for the whole nymphal development was then calculated as $K = 143.7\ D°_{1.9}C$.

For the alternating temperature regimes tested the relationship between percent development per day and daily mean temperature ($\bar{x}$) was also nearly linear ($r^2 = 0.9985$, d.f. = 3), and the regression line $Y = 0.6965\bar{x} - 1.3775$ virtually identical to the one derived from constant temperature data.

Examination of the data on development times of the separate instars showed that each of the first three instars were of approximately equal duration. The fourth instar lasted 1.25 times longer. Thus, the thermal constant of total nymphal development can be partitioned into instars with a 1:1:1:1.25 ratio.

Life span and age-specific survival. At each temperature tested up to 24 °C, the mean life span of the aphids decreased significantly with increased temperature in both constant and alternating regimes (Table 1). At a constant temperature of 28 °C, all nymphs died in the first instar soon after birth but over the middle temperature range, no mortality occurred during the immature stages. Except for the sexuparae at constant 12.5 °C, no significant differences were found between the mean life spans of the aphids under each of the constant and the corresponding alternating temperature regimes (t-test, $P > 0.05$).

The patterns of survival during adult life under each of the temperature/light regimes was very similar. Deaths were few at first and then gradually became more and more numerous. The similar spread about the mean life spans may be judged from the coefficients of variation, i.e. 100 × S.D./Mean, given in Table 1.

Fecundity and age-schedule of births. At each temperature tested above 12.5 °C up to 22 °C, the mean total number of young per female decreased significantly with an increase in temperature (Table 1). At 26 °C constant temperature, about half of the adults died without producing any young, a circumstance showing the apparent deleterious effect of this temperature on aphid reproduction. At 22 °C and at 17 °C, the mean number of young produced under constant temperature was similar to that at the corresponding alternating temperature regime (t-test, $P > 0.05$). At all temperatures, the age schedule of births (m_x) reached a peak early in adult life, then fluctuated around the same level for a period, before declining slowly. At 22 °C and at 17 °C, aphids showed very similar patterns of reproduction under constant and alternating regimes.

Intrinsic rate of increase. Values of intrinsic rate of increase (r_m, and mean generation time (T) listed in Table 1 were computed on a daily basis from the l_x and m_x data. Over the temperature range tested, r_m values increased with an increase in temperatures up to 24 °C. A constant temperature of 26 °C gave rise to deleterious effects which caused the value of r_m to drop to a very low level. In fact, at this temperature the r_m value is meaningless, as the aphids became extinct at the third generation (see below).

When the timings of the life cycle are expressed on a physiological time scale, the intrinsic rate of increase (♀/♀/22D°_{2}C) showed a decreasing trend with an increase in temperature (Table 1) as a result of lowered survival and birth rates.

Performance at 12.5 °C. As has been mentioned, the aphids reared at constant 12.5 °C, became sexuparae which showed characteristics different from aphids reared under the corresponding alternating temperature regime. They took longer to develop, lived longer, and produced fewer young, of which 29% were males (Table 1). These male individuals were reddish instead of greenish at birth; their sex was confirmed by rearing them to the adult stage.

Note that the aphids which produced male offspring were females from the second generation

Table 1. Population parameters (Mean ± s.e.) of apterous *H. lactucae* reared on flower shoots of *S. oleraceus* under various experimental conditions.

Rearing conditions			N[b]	Devel. time (birth-adult)	% mortality in immature stages	Life span		Young/♀[d]	Intrinsic rate of increase, r_m		Mean gen. time, T
Temp. (°C)	Light	R.H.		(days)		(days)	$\frac{100 \times S.D.}{Mean}$		(♀/♀/day)	(♀/♀/22D°C)	(days)
1 – 16 (8.5)[a]	12D:12L	70 – 90%	73	21.7 ± 0.2	8.8	–[c]	–	–	–	–	–
12.5	12D:12L	60 – 90%	39	17.3 ± 0.1	0.0	55.2 ± 2.0	18.8	43.7 ± 3.2	–	–	–
5 – 20 (12.5)[a]	12D:12L	55 – 95%	44	14.0 ± 0.1	0.0	48.7 ± 2.2	24.2	65.7 ± 3.5	0.188	0.394	22.3
17	11D:13L	60 – 80%	80	9.5 ± 0.1	0.0	32.7 ± 1.8	29.3	57.2 ± 4.3	0.263	0.386	15.4
9.5 – 23.5 (17)[a]	11D:13L	50 – 80%	45	9.4 ± 0.1	0.0	29.3 ± 1.4	24.9	58.0 ± 3.8	0.260	0.381	15.6
22	10D:14L	60 – 80%	77	7.1 ± 0.1	0.0	21.9 ± 1.3	31.0	44.8 ± 4.2	0.301	0.332	12.6
13.5 – 28 (22)[a]	10D:14L	40 – 90%	38	7.2 ± 0.1	0.0	21.8 ± 1.1	25.6	48.3 ± 3.9	0.315	0.347	12.3
24	10D:14L	60 – 80%	48	6.7 ± 0.1	4.0	18.1 ± 1.0	29.0	41.3 ± 3.9	0.332	0.332	11.1
26	10D:14L	40 – 60%	40	12.0 ± 0.2	12.5	17.1 ± 1.0	27.2	1.6	0.001	0.002	15.9
28	10D:14L	40 – 60%	100	–	100.0	< 1.0	–	0.0	< 0.000	–	–

[a] Higher temperature coincides with light period in each 24 h; daily mean in brackets.
[b] Under each temperature regime, only 28 individuals chosen randomly observed from birth to death, remaining aphids discarded upon becoming adult.
[c] Observations under this temperature regime discontinued after first 5 days of adult life, during which each adult had produced on average 7.2 ± 1.5 young.
[d] Where no immature mortality occurred, mean young/♀ = net reproductive rate R_o.

Table 2. Population parameters (Mean ± s.e.) for different generation of apterous *H. lactucae* population exposed continuously to high constant temperatures.

Temp.* (°C)	Gen.	N	Devel. time (birth-adult) (days)	% mortality in immature stages	Life span (days)	Young/♀
26	1	40	6.6 ± 0.1	4.2	–	–
	2	40	12.0 ± 0.2	12.5	17.1 ± 0.9	1.6
	3	20	12.5	95.0	7.5 ± 1.9	0.0
28	1	54	6.1 ± 0.1	4.0	14.6 ± 1.0	14.5 ± 2.0
	2	100	–	100.0	< 1.0	0.0

* For photoperiod and R.H., see corresponding temperature in Table 1.

(see Methods), i.e. they had spent all their embryonic and nymphal development at a constant 12.5 °C.

Performance at high constant temperatures. Table 1 shows that constant temperatures of 26 °C and 28 °C were deleterious to the development, survival and reproduction of the aphid. When the aphids were reared at these temperatures, marked differences in the results between the first and later generations were revealed (Table 2). In the pre-experimental first generation (see methods), the aphids were not greatly affected at either temperature. The mean development time continued to decrease as temperature increased. Survival and reproduction were not seriously affected either, even the aphids at 28 °C lived on average 8.5 days after reaching maturity and produced young through most of their adult life. However, at 28 °C all nymphs produced by the first generation died on the day they were born, while at 26 °C the aphid cohort became extinct in the third generation.

Performance at various photoperiods. The data in Table 3 show that varying the length of the photophase within the range of 12 h to 16 h a day had no significant effect on the development rate, survival and fecundity of the aphid.

Performance of alatae

As with apterae, the mean development time of alatae decreased with an increase in temperature, although in every case alatae took longer to reach the adult stage (cf. Tables 4 and 1). A linear regression of percent development per day (Y) in the four alternating regimes on mean daily temperature resulted in the equation $Y = 0.649\bar{x} - 1.0526$ ($r^2 = 0.9989$). The notional development threshold (t) was estimated to be 1.6 °C, which is close to that estimated for apterae. The thermal constant (K) for the nymphal development of alatae was then calculated as $154.0D°_{1.6}C$. The development times of the separate instars indicated that the thermal constant can be partitioned into K_i for instars 1–4 according to a 1:1:1:1.5 ratio.

Detailed data on survival and reproduction of alatae were obtained under 17 °C, 11D:13L (Table 4). Compared with apterae, alatae showed similar survival rates, but produced fewer young through most of their reproductive life.

Table 3. Population parameters (Mean ± s.e.) of apterous *H. lactucae* reared on flower shoots or young leaves of *S. oleraceus* at 22 °C with different photoperiods.

Substrate	Light	N	Devel. time[a] (birth-adult) (days)	Life span[b] (days)	Young/♀[b]
Flower shoots	10D:14L	47	7.1 ± 0.1	21.2 ± 1.2	43.8 ± 4.1
	12D:12L	46	6.9 ± 0.1	20.8 ± 1.0	44.5 ± 3.0
Young leaves	8D:16L	57	6.6 ± 0.1	26.5 ± 1.8	55.2 ± 3.0
	12D:12L	49	6.6 ± 0.1	27.8 ± 1.3	61.9 ± 3.0

[a] No mortality during immature stages.
[b] Means of life span and young/♀ were not significantly different at the 5% level (by t-test).

Table 4. Population parameters of alate *H. lactucae* reared on flower shoots of *S. oleraceus* under various experimental conditions.

Rearing regime[a] (Temp. °C)	N	Devel. time (days)	% mortality in immature stages	Life span (days)	Young/♀[b] Mean ± S.E.	Mean Gen. time, T (days)	Intrinsic rate of increases r_m (♀/♀/day)
1 − 16 (8.5)	13	21.8 ± 0.3	7.6	-	-	-	-
5 − 20 (12.5)	20	14.4 ± 0.2	5.0	-	-	-	-
17	44	10.1 ± 0.2	0.0	31.5 ± 1.1	45.8 ± 5.1	16.8	0.227
9.5 − 23.5 (17)	44	9.8 ± 0.1	4.5	-	-	-	-
13.5 − 28 (22)	30	7.5 ± 0.1	3.3	-	-	-	-

[a] For details of each rearing regime, see Table 1.
[b] Because no mortality occurred during immature stages, mean number young/♀ = net reproductive rate R_0.

Discussion

In the experiments, photoperiods were set longer for the higher temperatures to give more realistic regimes. However, the results of the experiment on the effect of light regimes (Table 3) indicate that varying photophase within the range employed in the experiments at higher temperatures did not significantly affect the basic population parameters measured. Variation in relative humidity was not tested, but was unlikely to have much effect either, since the aphids were reared on very succulent plant material itself cultured directly on nutrient solution. Thus, it seems valid to assume that the differences in aphid performance under various rearing conditions were mainly caused by variation in temperature.

Within the favourable range, speed of development and reproductive rate increased with an increase in temperature, while both life span and total fecundity declined at higher temperatures. Temperature thus affects virtually every aspect of the life history of the aphid. The effects of temperature on the potential for population increase are most appropriately summarized by the statistic r_m, the intrinsic rate of increase. The value of r_m computed on a daily basis increased with an increase in temperature, whereas, on a physiological time scale, the aphid exhibited relatively greater potential for population increase at lower temperatures. The significance of this reversal of relationship to temperature to (say) biological control by predators, can be shown more dramatically by comparing the potential increase in numbers on this time scale. Thus, starting with 10 females, the population at 12.5 °C (5 − 20 °C) would reach a size of 18450 individuals after 420D°$_2$C, while at 22 °C (13.5 − 28 °C) they would increase to only 7460 with the same temperature accumulation. The comparison of r_m between apterae and alatae (at 17 °C) suggests that the latter has a lower reproductive potential.

The temperature coefficients for the development of the aphid derived from constant and alternating temperature data were nearly identical. In theory, if there is no developmental acceleration or deceleration resulting from temperature alternation, the two sets of coefficients are unlikely to be so similar unless the relationship between temperature and rate of development over the whole temperature range under consideration is nearly linear. While the limited data obtained under constant temperature in this study do not allow an analysis of the effect of temperature alternation (cf. Liu & Hughes, 1984), the similarity between the two sets of coefficients suggests that in field studies of this aphid the relationship between temperature and rate of development can, as usual, be assumed linear over the temperature range favourable to the survival and reproduction of *H. lactucae* on *S. oleraceus.*

The performance of the aphid under alternating temperature regimes demonstrates the ability of the aphid to survive through relatively low mean temperatures without recourse to sexual reproduction. Exposure for around 12 h a day to temperatures as low as 1 °C or as high as 28 °C, did not seem to have any adverse effect on the normal development and reproduction of virginoparae when temperature was alternated, whereas at constant temperatures the aphid exhibited 'normal' patterns of survival and reproduction only within much narrower limits. These differences in aphid performance between constant or alternating temperature regimes show that the effects of duration of temperature extremes are profound, and that the favourable range and the lethal low and high limits for the insect will vary with the pattern and amplitude of temperature fluctuations. The differences in development time and survival of the aphid between the first and later generations at 26 °C and 28 °C (Table 2), together with the fact that at 12.5 °C sexuparae developed in the second generation, indicate that the conditions experienced during embryonic life are as important to the aphid as those when it is free-living. This sort of complexity calls for careful qualification of laboratory-estimated temperature limits when they are used to interpret field data.

The influence of temperature on development, survival and reproduction has been examined in many other aphid species, e.g. *Myzus persicae* (Sulzer), *Macrosiphum euphorbiae* (Thomas), *Brevicoryne brassicae* (L.), *Hyadaphis pseudobrassicae* (Davis), *acyrthosiphon pisum* (Harris) and *Aphis craccivora* Koch (Barlow, 1962; Deloach, 1974; Campbell & Mackauer, 1977; Siddiqui & Barlow, 1973; Radke *et al.*, 1973). In general, the patterns of performance induced by temperature variation are similar to those observed in *H. lactucae*, although details differ between species.

Results of bioclimatic studies obtained under highly artificial environments such as described in this paper, have frequently been shown to be useful in the understanding of population events in the field. For example, thermal constants determined under laboratory conditions have proved realistic and are suitable for computing physiological time scales for practical use in the field (Hughes, 1963; Campbell *et al.*, 1974). In addition, detailed life-table and fertility-table data are frequently used to formulate the basic survival and fecundity functions of simulation models which can be made to demonstrate effects on population dynamics of various modifying factors (Gutierrez *et al.*, 1972; Frazer & Gilbert, 1976; Huffaker, 1980).

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Résumé

Influences de la température et de la photopériode sur le développement, la survie et la reproduction du puceron: Hyperomyzus lactucae

La durée du développement, le taux de survie et la fécondité en fonction de l'âge ont été suivis chez les virginipares aptères et ailés du puceron: *Hyperomyzus lactucae* L., élevé sur *Sonchus oleraceus* L., et soumis à différentes conditions de température et de lumière. A l'intérieur de la gamme de températures moyennes de 12,5 à 24 °C, la vitesse de développement et le rythme de reproduction augmentent, tandis que la longévité et la fécondité totale diminuent. La relation entre la température et la durée du développement est presque linéaire, avec un seuil théorique de développement évalué à environ 2 °C. Le taux intrinsèque d'accroissement est lié positivement à la température calculée sur une base quotidienne, mais la relation est inversée quand la température est mesurée sur une échelle physiologique. Pour des conditions d'élevage identiques, les ailés ont eu, dans l'ensemble, une durée de développement plus longue, un taux de reproduction et une fécondité totale plus faibles que les aptères.

La comparaison des performances des pucerons sous thermopériodes ou températures constantes, ou entre les générations en conditions identiques, a montré (1) que les conditions subies par l'embryon dans la mère conditionnent la survie et le développement; (2) que les limites des températures tolérables changent en fonction du type et de l'amplitude des fluctuations de température.

A 22 °C, des modifications de la photopériode, dans la gamme; 12D:12L à 8D:16L, ont eu peu d'effet sur les performances des pucerons.

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