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The effects of temperature on aphid morphology, using a multivariate approach

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Abstract. Clonal samples of aphids were used as the groups in canonical variate (CV) analysis, in order to compare the temperature responses of single genotypes, and thus to distinguish genotypic and environmental contributions to the phenotypic response pattern. The analysis was based on a large data set obtained by measuring 19 linear variables on adult apterae reared at four temperatures (10, 15, 20 and 26.5°C). The species used were *Myzus persicae* (Sulzer) and its close relative, *M. antirrhinii* (Macchiati). Two vectors – the scores on the first two CV's – were invariably needed to describe the temperature response. In each of three *M. persicae* clones, the first CV had a close linear correlation with temperature, partly corresponding to the decrease in body size at higher temperature, whereas the temperature relationship of the second CV fitted a quadratic function, being less at both high and low temperatures, and reflecting a change of "shape", partly comprising a relative decrease in lengths of appendages at low temperature. In *M. antirrhinii* the temperature relations of these two CV's was reversed, that of CV1 being quadratic and that of CV2 linear. When different genotypes of a species were combined in the same analysis, the first and second CV's still described the "two-way" response to temperature as for clones analysed separately, but the third and fourth CV's were totally independent of rearing temperature and separated samples according to their genotype. The consistency with which temperature effects are allocated to the first two variates seems to indicate the presence of two different aspects of the phenotypic response to temperature, perhaps reflecting different metabolic pathways by which temperature affects the pattern of growth.

INTRODUCTION

It is well known that temperature affects the size of aphids, and especially that aphids, like many other insects, are smaller when they develop at higher temperatures (Dixon, 1985). One might also expect aphids to be smaller at temperatures below the optimum for development; this has now been shown for representatives of several insect orders (Burges & Cammell, 1964; Honěk, 1987; Nealls et al., 1984; Simmons & Yeargan, 1988; Vannote & Sweeney, 1980), but there seems to be no information about the effects of low temperature on the size of aphids.

Measurements of general body size, however, describe only one limited aspect of the pattern of morphological change that results from development at different temperatures. The jointed appendages of insects and other arthropods seem ideal for more detailed experimental investigation of this phenomenon, yet the effects of temperature on the shape of an insect, rather than merely on its size, seem to have received very little attention. Experimental studies on *Drosophila* (Ray, 1960) and on the aphid *Acyrthosiphon pisum* (Murdie, 1969) indicated a relative shortening of legs and antennae respectively at higher temperatures, but the statistical methods used did not distinguish between general size variation in the data and the specific effect of temperature.

In temperate climates, the successive generations of multivoltine insects are exposed to different temperatures. Considering only one quantitative trait, such as the length of an antennal segment, the extent of its variation over the range of temperatures normally experienced will depend on the phenotypic plasticity of the genotype (Gause, 1947). The particular mean value for that trait expressed at any one temperature within the range may be expected to tend towards an optimum, as a result of stabilising selection (Via & Lande, 1985; Thompson, 1991). It follows that one might expect to find a shifting pattern of temperature-dependent allometric growth, resulting in shape changes that continually adjust the phenotype to the contemporary environment.

Clearly, morphology is influenced by many other environmental variables besides temperature, and genotype-environment interactions in nature will be extremely complex. Nevertheless, a study of the phenotypic effects of temperature seems to be a good starting-point from which to examine the evolution of phenotypic plasticity. Aphids are ideal insects for such work, as single genotypes can be studied in replicated experiments, and the results may also have a more practical application to aphid taxonomy, where intraspecific seasonal and geographical variation, due in no small part to temperature, is often a problem in recognising and characterising species.

This study concentrated on the effects of temperature on the adult morphology of apterous viviparous female aphids, keeping other environmental variables as constant as possible. Our main purpose was to obtain a general picture of the phenotypic response to temperature in terms of a large number of linear variables analyzed simultaneously. For this we chose the method of canonical variates (CVA), which has proved to be a powerful discriminating tool when clones of aphids are used as the groups in the analysis (Blackman, 1992).

We investigated both intra- and interspecific variation in the temperature response of two closely-related species, *Myzus persicae* (Sulzer) and *M. antirrhinii* (Macchiati). One of our objectives was to find out whether the degree of phenotypic plasticity was related to reproductive category. *M. antirrhinii* is a permanent apomict, and might perhaps tend to compensate for lack of genetic recombination by increased phenotypic plasticity. *M. persicae* is polymorphic for reproductive category; some genotypes are holocyclic, which means that they have an obligatory annual sexual generation, while others are androcyclic, contributing males only to the sexual phase, or anholocyclic, reproducing throughout the year by apomixis (Blackman, 1974).

MATERIAL AND METHODS

Six aphid clones were used, three of *M. persicae* and three of *M. antirrhinii.* Clones were selected which represented genetically diverse forms within each species; the *persicae* clones differed from each other in insecticidal resistance, life cycle category and presence or absence of a chromosomal translocation, the *antirrhinii* clones differed in karyotype (Table 1). Stock cultures of all clones were reared on whole, excised leaves of potato (var. Majestic) in small Perspex boxes (Blackman, 1988) in a controlled-temperature room at 16h photoperiod and 15°C. Cultures were controlled and synchronised by keeping only the 25 first-born progeny of the adults of each generation, transferred to a freshly excised leaf.

Experimental lineages were started by taking a single adult apterous vivipara of each clone and rearing through two generations at 15°C. Clones of *persicae* and *antirrhinii* were compared in pair-wise combinations. For each clone, 60 prelarviposition adult apterae (called "generation 0", and constituting the granddaughters of the original aphid) were divided between 12 excised leaf boxes, five individuals per box, and three boxes were placed in each of four Gallenkamp illuminated incubators set respectively at the

experimental temperatures (10, 15, 20 and 26.5°C). All temperatures were controlled to ±1°C. Photoperiod was 16 h, and ambient humidity was uncontrolled, but at the leaf undersurface, where the aphids were feeding in still air, it was probably close to 100%. At least 10 adult apterae of each of the next five generations (numbered 1–5) produced at the experimental temperatures were preserved for mounting and measuring. Generation 6 was transferred in the fourth larval instar back to the controlled temperature room at 15°C, and adults of the transitional generation 6 were preserved, as were adults of five further generations (7–11).

TABLE 1. Biological characteristics of the 6 aphid clones studied.

Myzus species	Name of clone	Ref. No.	Life cycle category	Karyotype (2n, female)	Insecticide resistance level
persicae	R1	3978	anholocyclic	12 normal	low
persicae	FrR	3985	holocyclic	12 normal	medium
persicae	R3	3980	androcyclic	12 (Al, 3 translocation)	high
antirrhinii	919	3241	anholocyclic	14 (A2 and A3 dissociated)	susceptible
antirrhinii	RLu	3078	anholocyclic	13 (A4 dissociated)	susceptible
antirrhinii	BMG	4010	anholocyclic	13 (A3 dissociated)	susceptible

Individual adult apterae, usually a sample of 10 from each of the three lineages of each clone, were taken from selected generations and mounted in Canada balsam using Martin's method (Martin, 1983). When the balsam was dry the specimens were measured using a Kontron Bildanalyse Videoplan interactive image analysis system coupled with a Zeiss phase contrast microscope. Measurements were taken by moving a "mouse" with an LED spotlight on the crosswires across a digitising tablet, the measuring field being superimposed on the image of the aphid by means of a drawing tube. The 19 characters measured on each aphid as linear variables are detailed in Table 2. Body length (BL) of apterae of generation 5 was also measured, to provide a separate measure of body size that was not included in the multivariate analysis.

TABLE 2. The 19 linear variables measured and their abbreviations. The 8 variables of the reduced set are marked *.

Measured variable	Abbreviation
Third antennal segment*	AS3
Fourth antennal segment	AS4
Fifth antennal segment*	AS5
Base of sixth antennal segment*	BASE6
Processus terminalis of antenna*	PT
Ultimate rostral segment	URS
Femur of foreleg	FEM1
Tibia of foreleg	TIB1
Second tarsal segment of foreleg	2TARS1
Femur of middle leg	FEM2
Tibia of middle leg	TIB2
Second tarsal segment of middle leg	2TARS2
Femur of hindleg*	FEM3
Tibia of hindleg*	TIB3
Second tarsal segment of hindleg*	2TARS3
Length of siphunculus	SIPHL
Maximum width of siphunculus*	MAXWSI
Minimum width of siphunculus	MINWSI
Length of cauda	CAUDA

The data were analysed using multivariate analysis programmes written in BASIC by Dr Ian M. White; the canonical variates analysis (CVA) is based on Blackith and Reyment (1971), and the linear discriminant analysis (LDA) is based on Davies (1971). The samples, each of 10 apterae, were the groups used in CVA. The analyses here reported were all done on untransformed data (analyses on log-transformed data were also carried out and gave essentially the same results).

RESULTS

Temperature responses of separate clones

The main features of the phenotypic response of *M. persicae* to temperature as revealed by CVA are shown in a bivariate plot of the mean scores of samples of clone FrR on the first two canonical variates (Fig. 1). The other two *persicae* clones gave similar responses. CV1 and CV2 together accounted for 71%–79% of the total variance in the data for each clone. CV1 scores, accounting for 50%, 60% and 64% of the variance respectively in the

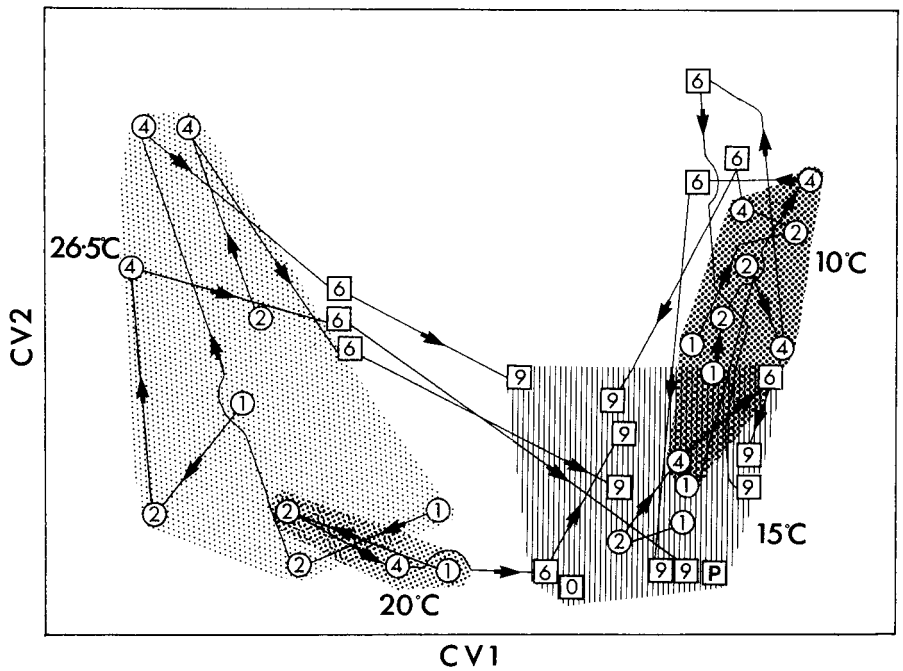


Fig. 1. Changes in the mean scores on the first two canonical variates of *Myzus persicae* clone FrR under the influence of temperature. The experiment involved rearing through 10 generations, with generations 1–5 developing at the experimental temperature (10°C, 15°C, 20°C or 26.5°C), after which all lineages were kept at 15°C for another 5 generations. The numbers in the plots are the generation numbers of the measured aphids, with 'P' and '0' respectively the grandparents and parents, reared at 15°C, of the generation 1 aphids. Thus, generations 1, 2 and 4 (encircled numbers) developed at the experimental temperatures (indicated by shading), and generations 6 and 9 (enclosed in squares) show how the phenotype changed on transfer of all lineages back to 15°C. Three replicate lineages are shown for 10°C and 26.5°C, and one each for 20°C and 15°C; the lines with arrows connect successive samples of the same lineage. (Generation 6 samples of lineages kept at 10°C and 26.5°C for the previous 5 generations were still clearly influenced by the experimental temperature although themselves developing at 15°C, so are not included in the 15°C shaded area.)

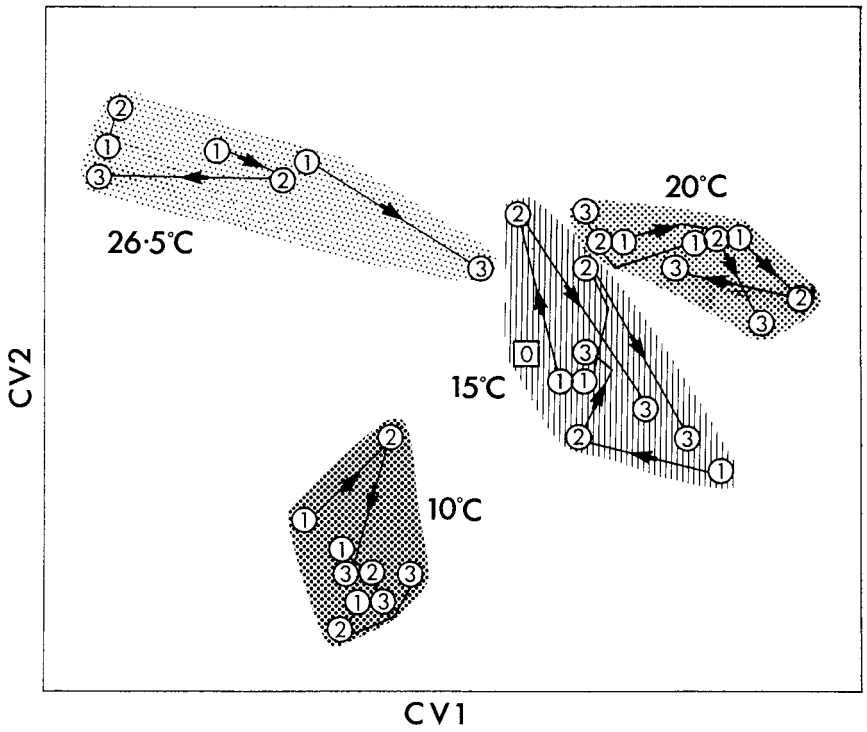


Fig. 2. Plot of the mean scores on the first two canonical variates for *Myzus antirrhinii* clone 919 reared at 4 temperatures. The encircled numbers (1–2 or 1–3) indicate 2 or 3 successive generations of 3 separate lineages maturing at each temperature, generation 0 being the grouped parents of all lineages.

three clones, showed a close linear (negative) correlation with temperature (Table 3). The highest scores were for generations reared at 10°C, the lowest for generations at 26.5°C. The effect of temperature on CV1 was immediate, especially the effect of increase in temperature, which was already apparent in the first generation wholly reared at 20–26.5°C. For two of the clones, but not for R3, CV1 scores were also highly correlated with body length, and with a "general size index" based on the sum of all parameters in the multivariate analysis (Σx).

TABLE 3. Correlations between the first two canonical variates (CV1 and CV2) and temperature (TEMP), body length (BL) and sum of 19 parameters (Σx) for all 6 clones studied.

	Myzus persicae						*Myzus persicae*					
	FrR		R3		R1		RLu		919		BMG	
	CV1	CV2	CV1	CV2	CV1	CV2	CV1	CV2	CV1	CV2	CV1	CV2
TEMP	-0.97**	0.06	-0.94**	-0.21	-0.90**	0.32	0.09	-0.92**	-0.30	-0.89**	0.61*	-0.77**
BL	0.90**	-0.15	0.17	0.46	0.86**	0.07	-0.17	0.80**	-0.17	0.62*	-0.26	0.66*
Σx	0.95**	0.28	0.53*	0.76**	0.77**	0.60	0.60*	0.82**	0.94**	0.46	0.52	0.79**

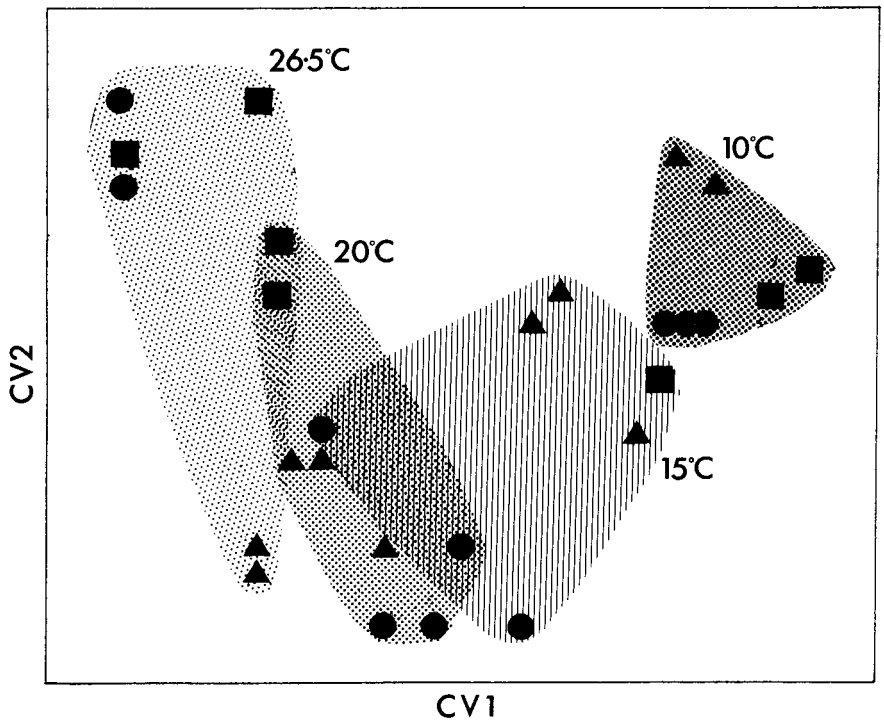


Fig. 3. Plot of the mean scores on the first two canonical variates in a combined analysis of 3 clones of *Myzus persicae* in the third generation of rearing at 4 temperatures. (Circles = R1; squares = FrR; triangles = R3.)

Scores on CV2 accounted for another 25%, 11% and 25% of variance respectively. They were uncorrelated with temperature and body length (Table 3), aphids reared at 10°C and 26.5°C having higher scores than those at intermediate temperatures (Fig. 1). In two clones there was some correlation with the "general size index" Σx (which is more an index of appendage length than body size, as most of the characters contributing to it are segments of appendages). The change in values of CV2 was slower, and generally only manifest after several generations, being especially slow at 10°C.

When returned to the original rearing environment at 15°C, all experimental lineages reverted within three generations to the original phenotype, as shown by the grouping of samples of generation 9 in Fig. 1. Scores on CV3, etc., failed to group the samples in any clearly meaningful way.

The phenotypic response of *M. antirrhinii* to temperature was similar (Fig. 2), but with the "roles" of CV1 and CV2 reversed. In this species CV1, accounting for 38%–45% of total variance, was uncorrelated with temperature in two clones and only weakly correlated in the third (BMG), and it was CV2, accounting for 26%–32% of the variance, that showed the linear response to temperature (Table 3). There was no consistent pattern of correlations between CV2 and either BL or Σx in *antirrhinii*.

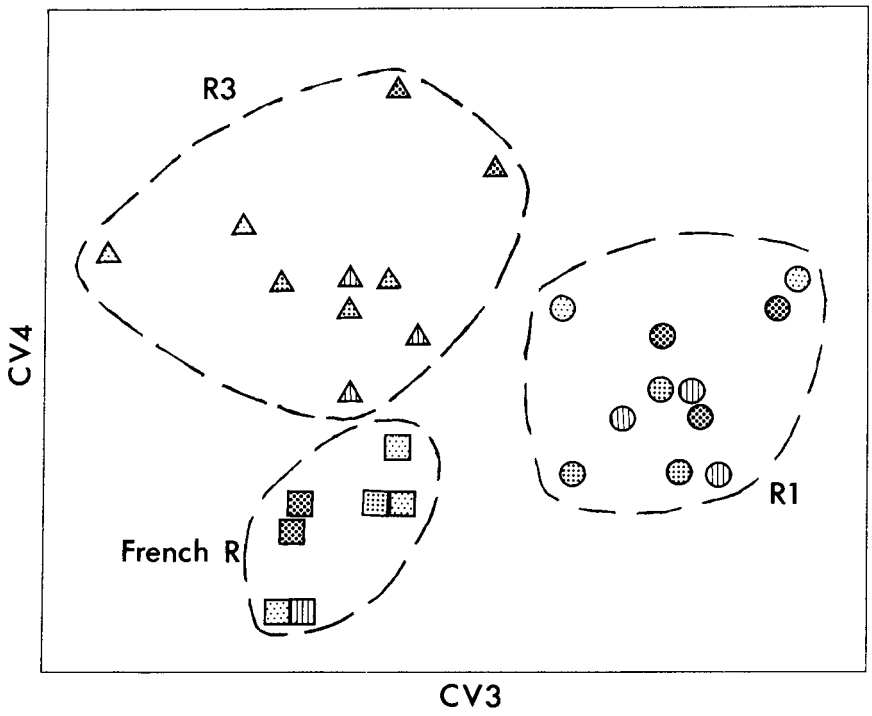


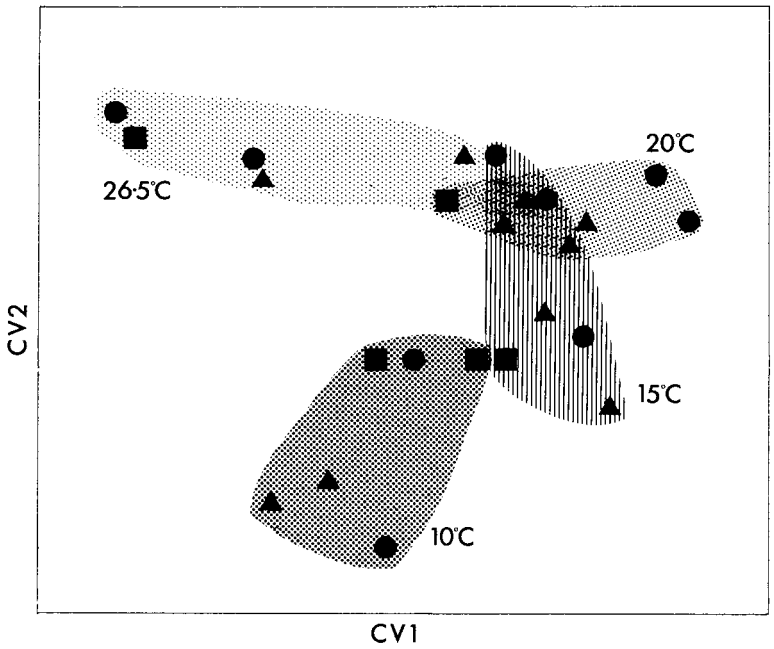
Fig. 4. Plot of the mean scores for CV3 and CV4 from the same combined analysis of *M. persicae* clones as illustrated in Fig. 3, showing the samples now grouped according to genotype and independently of the rearing temperature (the latter is indicated by the pattern of shading inside the symbols, which corresponds to that in Fig. 1).

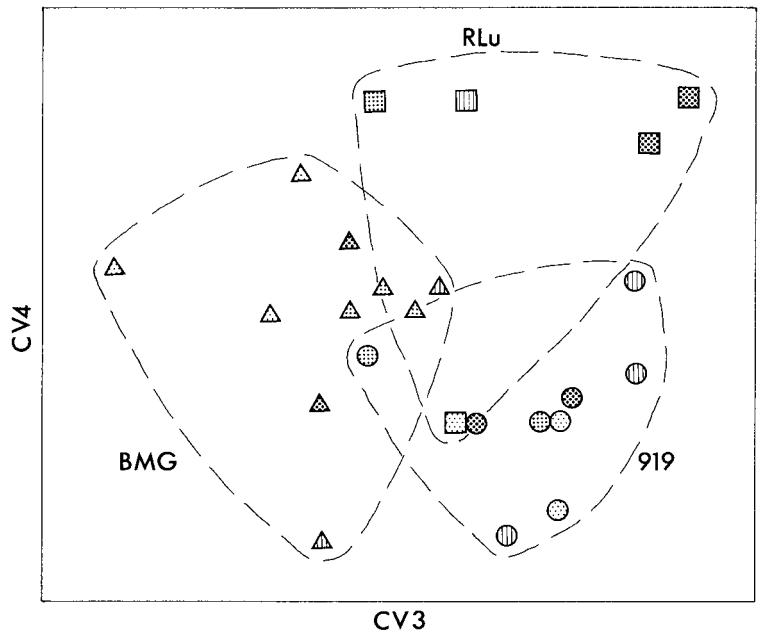
Combined CVA of *Myzus persicae* clones

Data for the adult apterae of generation 3 at the four experimental temperatures for all three *M. persicae* clones were analyzed together by CVA to examine genotype-environment interactions. CV1 and CV2 for the combined data described the response to temperature in exactly the same way as when clones were analysed separately (Fig. 3, cf. Fig. 1). CV3 and CV4, however, could now be interpreted in a biologically meaningful way, being concerned with the maximisation of genotypic differences. CV3 separated clone R1 from the other two clones, and CV4 separated out clone FrR, so that a plot of CV3 against CV4 provided a totally different picture from that given by CV1 and CV2, grouping the samples according to genotype, irrespective of rearing temperature (Fig. 4). CV3 and CV4 together accounted for 17.7% of total variance (Table 4).

Combined CVA of *Myzus antirrhinii* clones

The result of pooling data for adult apterae of generation 3 of the three *antirrhinii* clones was analogous to that obtained with *M. persicae*. CV1 and CV2 were concerned with the effect of temperature, exactly as in the separate clones (Fig. 5a, cf. Fig. 2),


26·5°C
20°C
15°C
10°C
CV2
CV1


RLu
BMG
919
CV4
CV3

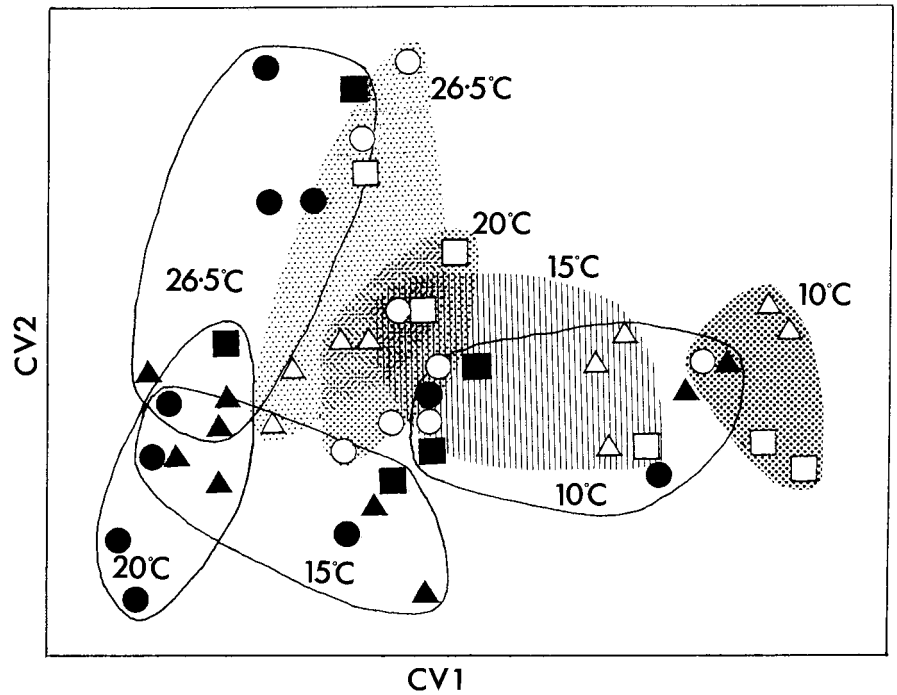


Fig. 6. Plot of mean scores on CV1 and CV2 in a combined analysis of all 6 clones (3 *persicae*, 3 *antirrhinii*), in the third generation of rearing at 4 temperatures. (Solid symbols are *antirrhinii* samples, open symbols are *persicae* samples; shapes of symbols correspond to clones as in Figs 3 and 5a.)

whereas CV3 and CV4 (together accounting for only 10.7% of the total variance) clearly grouped samples according to their genotype and without respect for temperature (Fig. 5b).

TABLE 4. Percentage of total variance between samples accounted for by the first 6 canonical variates in combined analyses.

	CV1	CV2	CV3	CV4	CV5	CV6
M. persicae (all clones)	46.5	24.4	11.5	6.2	2.4	2.1
M. antirrhinii (all clones)	39.7	36.4	6.7	4.0	2.7	2.2
Both species, all clones	40.0	28.2	8.3	4.9	4.5	3.3

Combined CVA for both species

Data for generation 3 of all clones of both species were combined for further analysis. Again, CV1 and CV2 accounted for the phenotypic effects of temperature, the two species

Fig. 5a (upper): Plot of mean scores for CV1 and CV2 in a combined analysis of 3 clones of *Myzus antirrhinii* in the third generation of rearing at 4 temperatures (circles = 919, squares = RLu, triangles = BMG). Fig. 5b (lower): Plot of CV3 against CV4 from the same data set, showing grouping of samples according to genotype (with shape of symbol indicating clone as in Fig. 5a, and pattern of shading inside symbols indicating rearing temperature as in Fig. 1).

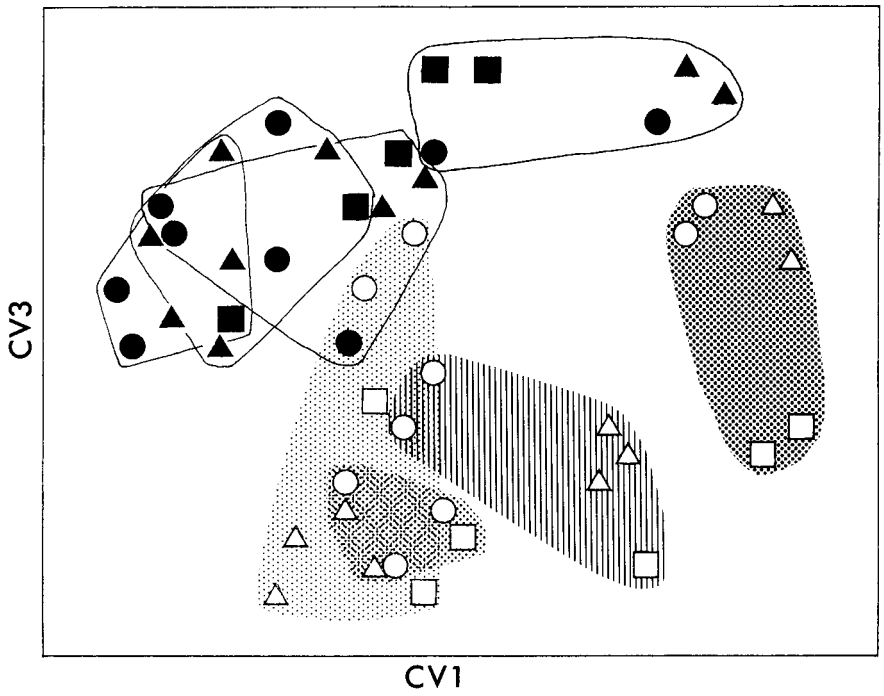


Fig. 7. Plot of CV1 against CV3 from the same analysis as Fig. 6, and using the same symbols, showing almost complete separation of the two species.

responding in parallel with only slight differences in their response patterns (Fig. 6). In *antirrhinii*, the axes seem to have rotated so that they conform nearly, but not exactly, to a common pattern with those of *persicae*.

CV3, accounting for 8.3% of the total variance, tended to group samples according to species with minimal effect of temperature; it failed only in that scores for clone R3 at 10°C, and for samples of R1 at both temperature extremes, overlapped with those for *antirrhinii* (Fig. 7). CV4 found correlations among the remaining variance to discriminate partially between the 3 *persicae* clones (Fig. 8). The *antirrhinii* clones had "neutral" scores on CV4, but showed some tendency to group into their respective genotypes in their scores on CV5 and CV6 (Fig. 9, cf. Fig. 5b).

Temperature responses of individual parameters

Body length (BL) was always significantly less at 26.5°C than at other temperatures, and significantly less at 20°C than at 15°C in all clones except *M. persicae* R3. However, in none of the clones was there any significant difference between BL at 15°C and BL at 10°C. Thus the relationship of body length with temperature is clearly non-linear, but there was no evidence of any reduction at a temperature below the optimum for development.

Examining the contributions of particular characters to CV1 and CV2 in terms of their vector coefficients, some fairly consistent contrasts in value were seen in CV1 for

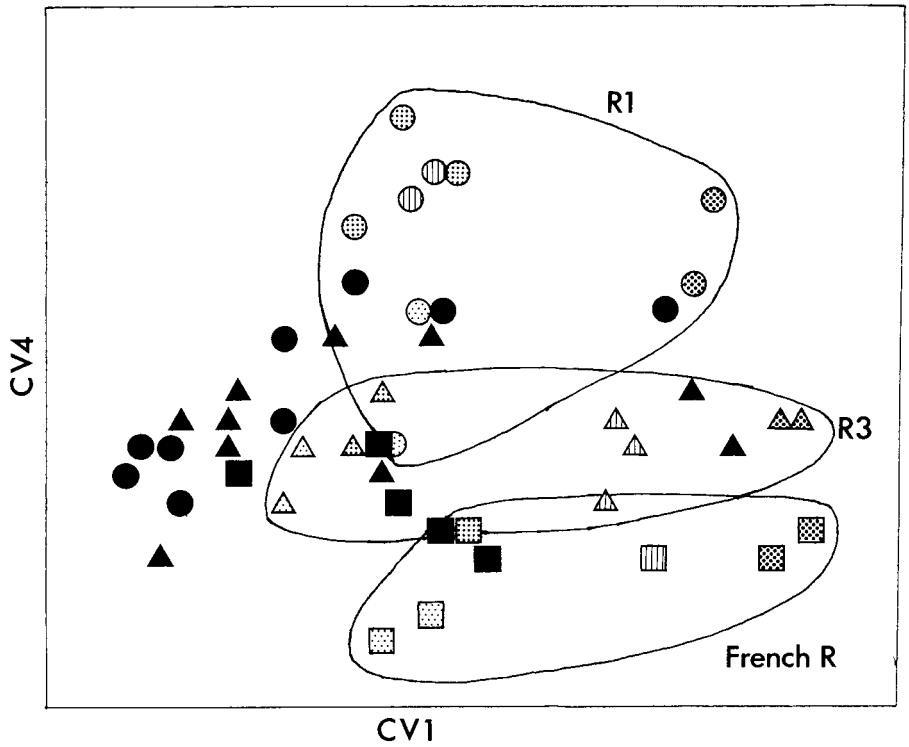


Fig. 8. Plot of CV1 against CV4 from the same analysis as Fig. 6, showing separation of the 3 *persicae* clones by their scores on CV4. (Black symbols are *antirrhinii*; shaded symbols are *persicae*, with patterns of shading corresponding to rearing temperature as in Fig. 1, and symbol shape indicating the clone, as in Fig. 3.)

persicae (AS3 and PT versus AS5 in the antenna and, less consistently, TIB 1–3 versus FEM 1–3 and 2TARS 1–3 in the legs). These same contrasts tend to occur in the vector coefficients for the equivalent (temperature-related) variate, CV2, in *antirrhinii* clones. Another consistent feature of the temperature-related CV in both species was the large positive contribution of MAXWSI, which was inversely related to temperature. When data for the *persicae* clone FrR reared at the two extreme temperatures 10 and 26.5°C were grouped according to temperature and subjected to LDA, the LD coefficients showed a similar pattern of contrasts to the CV1 coefficients.

Plots of the individual parameter values against temperature, using aphids of generation 4, showed some of these response differences. For example, in the antennae, ANT3 and PT show a greater tendency to decrease than ANT5 and ANT6BASE at lower temperature, although there were significant differences in the response patterns between clones within a species (e.g. Fig. 10). Overall, as might be expected, the parameters making the largest positive contributions to the CV with the linear relation to temperature (i.e., CV1 in *M. persicae* and CV2 in *M. antirrhinii*) tended to be those with a flatter response curve, with less or no reduction in length at low temperature, and especially those tending to an inverse linear relationship with temperature, e.g. MAXWSI. Conversely, those parameters

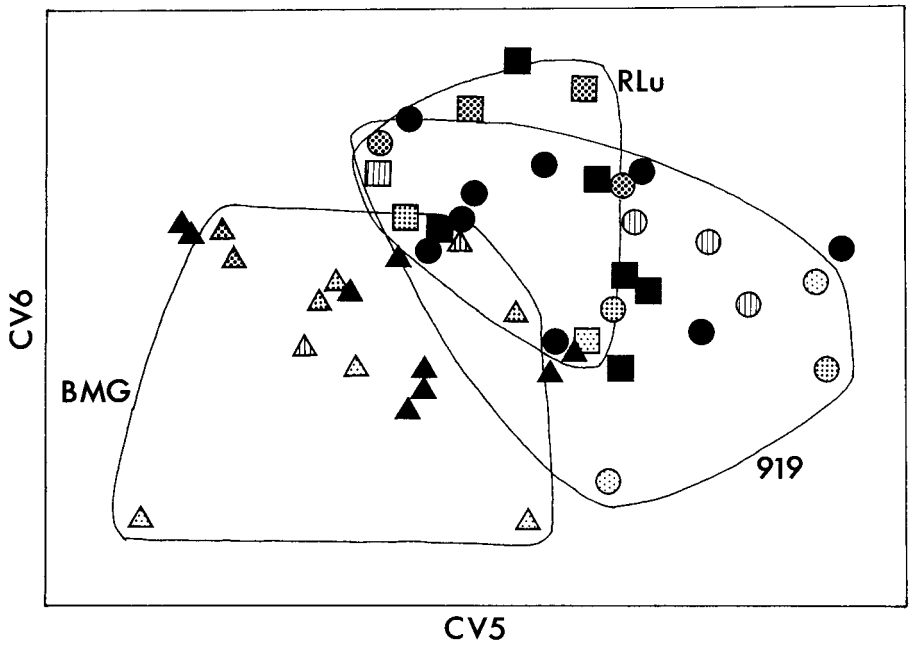


Fig. 9. Plot of CV5 against CV6, showing partial clustering of *antirrhinii* samples according to genotype. (Black symbols are *persicae*; shaded symbols are *antirrhinii*, with pattern of shading indicating the rearing temperature as in Fig. 1, and symbol shape indicating the clone, as in Fig. 5a.)

most strongly correlated with CV2 of *M. persicae* (and CV1 of *M. antirrhinii*) were usually those which had low values at both low and high temperatures, although this was not necessarily reflected in their vector coefficients. The temperature range used was not the most appropriate for all genotypes; for example, the range could usefully have been extended downwards for clone FrR, and upwards for clone R3.

DISCUSSION

It is important to note that the groups used for CVA in this work simply comprised the samples of 10 apterae. No information about rearing temperature or genotype of samples was involved in the analysis.

In experimental work on the effects of an environmental variable, there is always the problem of standardising all other environmental factors and, in the case of phytophagous insects, host plant variation can have a large effect on phenotype. Rearing on artificial diet would standardise nutritional factors but this method yields abnormally small aphids with poor fecundity, even at optimal temperatures (Van Emden, 1988). At the other extreme, aphids reared on whole plants would be affected by the feeding site chosen, and by the age and physiological condition of the plant, which would be impossible to standardise effectively across such a wide range of temperatures.

In the field, *M. persicae* preferentially colonises old, senescing leaves of potatoes and crucifers (Van Emden et al., 1969), so that whole, freshly excised mature leaves of potato,

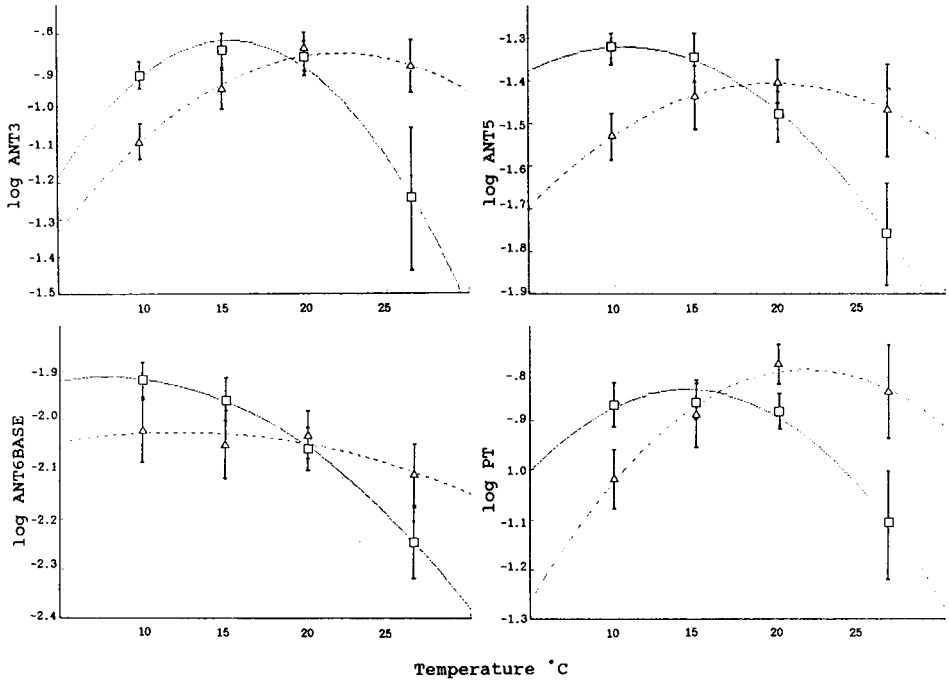


Fig. 10. Comparative temperature responses of 4 different parameters of the antenna in 2 clones of *Myzus persicae*, FrR (squares) and R3 (triangles), in the fourth generation reared at the experimental temperature. Vertical bars show standard errors, and the lines describe the best-fit quadratic functions for each response.

which gradually senesce throughout the larval development of the aphid, would seem to be as close as possible to a standardised approximation of the natural food. Replicates of the same clone at any one temperature gave consistent results and, although the rate of leaf senescence increased with temperature, so also did the rate of larval development. However, the probability that part of the aphid's temperature response was mediated through the host plant clearly cannot be ruled out.

In CVA, scores on the first CV are evaluated as a linear combination of the measured variables, selected so as to maximise the differences between samples, relative to the differences among individuals within samples. For *M. persicae* at four temperatures, the mean scores on CV1 formed clusters along a temperature gradient, and showed some high correlations with body length. Scores on CV2 are also evaluated as a linear combination of all the measured variables chosen to discriminate between samples, but requiring additionally that the values of CV1 and CV2 are uncorrelated within samples. In *M. persicae*, scores on CV2 were uncorrelated with temperature and body length but showed some correlations with the size index Σx, which is mainly a measure of appendage length. These two CV's seem to be describing two different, possibly uncorrelated, aspects of the phenotypic response of *M. persicae* to temperature.

In *M. antirrhinii*, the effects observed were much the same, except that the roles of CV1 and CV2 were reversed in comparison with *M. persicae*. Although this consistent difference between two closely-related species was interesting, there was no evidence that the permanently apomictic species, *M. antirrhinii*, was exhibiting significantly greater overall phenotypic plasticity in its response to temperature than *M. persicae*.

The "two-way" phenotypic response to temperature still held good when the CVA included data from more than one genotype of a species, and even when data from two closely related species were included. In such cases, most of the variance of the data was very effectively partitioned by CVA, into a major part due to temperature (CV1 and CV2), and a lesser part due to genotype (CV3, CV4, etc.). The clear partitioning of the variance between environment and genotype suggests that genotype-environment interactions might play a minimal part in the temperature response. If so, it might be possible to construct a general model of the phenotypic response to temperature that could apply to genetically diverse samples, and perhaps to more than one species. Such a model might help in the interpretation of temperature-related variation in field-collected specimens, by enabling morphological discriminants to be "corrected" for hot or cold conditions.

However, examination of the responses of single variables to temperature, as well as the inconsistencies in correlations between the first two CV's and both body length and Σx (Table 3) show that there is indeed variation in the temperature response between genotypes. Adults produced by clone FrR of *M. persicae*, for example, were much smaller than those of clone R3 at 26.5°C, and relatively larger than those of R3 at 10°C. CV1 and CV2 exclude or minimise such variation. The combined CVA of all clones of both species (Fig. 6) demonstrates how effective the method is at making genetically diverse material conform to a common pattern of response to temperature.

Many of the 19 characters used in this analysis are highly correlated among individuals within samples. Such correlations are not apparent in the CV coefficients, because this method discounts within-group correlations. We persisted with the full set of characters throughout this work, because we wanted to detect all possible patterns of variation. However, most analyses were also carried out with a reduced set of 8 characters (those marked * in Table 2), selected as those having consistently high coefficients for the "temperature-specific" CV (i.e., CV1 in *persicae* and CV2 in *antirrhinii*). The results obtained for CVA's with this 8-character set were almost as consistent as those with the full set of 19 characters, and in some cases equally as good, not only in terms of the temperature response but also, somewhat surprisingly, in the separation of genotypes by CV3, etc.

The multivariate approach using CVA is thus an effective way to provide an overall picture of the response of an aphid clone to temperature. CVA identifies characters contributing most to the temperature-specific part of the response pattern, provides information about the speed, extent and direction of change of phenotype with temperature, and distinguishes between variation due to environment and that due to genotype. It thus points the way for further studies of changes in the allometric growth relationships of particular characters with respect to temperature change.

These results are in general agreement with two well-known "rules", that have been shown to apply to field data for a wide range of organisms. According to Bergmann's Rule, individual body size tends to be less in the warmer parts of a species' range, while Allen's Rule states that "protruding body parts" are relatively shorter in cooler climates.

Such changes do not necessarily involve genetic differences between populations. Ray (1960) demonstrated experimentally that both Bergmann's and Allen's rules applied to laboratory populations of *Drosophila* reared at different temperatures. It seems possible that the the "two-way" multivariate response shown here for aphids is a reflection of these two different aspects of the phenotypic response to temperature, perhaps reflecting different metabolic pathways by which temperature affects the pattern of growth.

While it seems logical to extend Bergmann's and Allen's rules to the successive generations of a multivoltine insect such as an aphid, which in a temperate climate may develop at markedly different temperatures, caution is needed in interpreting seasonal variation in field populations. The midsummer "dwarfs" of many aphid species may be more due to inadequate nutrition than to a direct effect of high temperature, and the relatively short appendages typical of the fundatrix morph are probably an adaptation to a sedentary life in a relatively exposed habitat, rather than the result of early-season development at low temperature. Dixon (1974) found that temperature did not affect the morphology of fundatrices of *Drepanosiphum platanoidis* (Schrank). If the phenotypic response to temperature can be suppressed in certain morphs such as the fundatrix, this is a further indication that it is an adaptive phenomenon rather than an obligatory outcome of the interaction of temperature and metabolic processes.

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