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Life cycle strategies and genotypic variability in populations of aphids

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Abstract. Populations of the rose aphid (*Macrosiphum rosae*) from various latitudes show differences in their life cycles. In warm climates they are exclusively parthenogenetic, whereas in cold climates sexual reproduction allows the aphid to overwinter in the egg stage. In temperate zones both holocyclic and anholocyclic clones occur within the same population. It is assumed that the reproductive mode has consequences for the genotypic structure of the populations. Continuous parthenogenesis results in low genogypic variability caused by selection and/or random genetic drift. The greater genotypic variability of holocyclic populations is due to recombination during the sexual phase. This view is supported by the study of populations which revealed high genotypic variability and homogeneity between populations in areas with harsh winters (e.g. Norway). In temperate countries (e.g. England) the genotypic variability was lower but the uniformity between populations still high, and in warm climates (e.g. the Canary Isles) the variability was lowest and heterogeneity between populations largest.

Keywords. Aphids; life cycle; parthenogenesis.

1. Introduction

Most aphid species exhibit a life cycle in which parthenogenetic viviparous generations are followed by a single sexual generation in the autumn and hibernation in the egg stage. Such a life cycle is called holocyclic. In contrast, anholocyclic species reproduce parthenogenetically all the year round. In both cases variation with respect to the number of hosts may exist. Some aphids live only on one host species (monoecious), whereas others migrate from a primary host to one or several species of secondary hosts (heteroecious). Species which are geographically widely distributed show, depending on the climate, either holocyclic or anholocyclic life cycles, or even both within one population. In tropical and warm climate zones, as well as in greenhouses, it is possible that aphids only reproduce parthenogenetically. This life cycle variation is under genetic control and modified by environmental factors. That there is a genetical basis for the variation is supported by the observation that both life cycles coexist where the climate is temperate (Blackman 1971; Weber 1984). Moreover, in crossing experiments the F_2-generation segregates into holocyclic, anholocyclic and intermediate types which indicates a simple mode of inheritance (Blackman 1972). The type of life cycle should have consequences for the genetic variability in aphid populations.

Anholocyclic populations consist of a varying number of genetically distinct clones. Recombination as a source of genotypic change in the structure of such populations can be excluded (Blackman 1979; Suomalainen *et al* 1980; Tomiuk and Wöhrmann 1982). Intrapopulational and ecological factors act on these genotypes (phenotypes) and determine their reproductive rates, which can be equated with the fitness of genotypes (phenotypes) in asexually reproducing populations (Dixon 1985a, b, 1987). Even very small differences in reproductive rates between clones lead to large differences in the frequencies of the clones. Under such conditions the genetic variability will be reduced. A reduction in the genetic variability is also caused by founder effects during the search for new hosts and seasonal variation in the population size. However, asexual populations can maintain genetic variability by mutation, by anticyclic selection on different hosts or in different seasons. In addition, in holocyclic populations the sexual phase offers every year the possibility of regenerating genotypic variability by recombination. Therefore, in general, a higher genotypic variability can be expected in cyclic-parthenogenetic populations than in asexual ones.

We report the results from a study of enzyme polymorphism in geographic populations of the rose aphid, *Macrosiphum rosae*, sampled from different climatic zones, and show that the degree of the genotypic variability is correlated with the variability in different life cycle strategies.

2. Materials and methods

2.1 *Population sites*

Samples of the rose aphid were collected from rose bushes at different localities in Europe. The locality, the latitude and the sample size are given in table 1.

2.2 *Sampling*

Estimates of genotypic frequencies are influenced by sampling errors. This is of special importance in continuously parthenogenetic species. On each rose plant aphids form several colonies of various sizes depending on the reproductive rate of each member. A colony can be founded by more than one genotype. To minimize the sampling error the number of aphids collected was proportional to colony size and samples from many rose plants were taken.

2.3 *Electrophoresis*

Starch gel electrophoresis was used to determine the enzyme phenotypes of MDH and PGM (Shaw and Prasad 1970; Ayala *et al* 1972). So far the genetic basis of these systems has not been checked by crossing experiments. However, there is no doubt that the genetic system consists of two and three alleles, respectively, if all genotypes are found as in the present study (Tomiuk and Wöhrmann 1980, 1983).

3. Results

The frequencies of the MDH- and the PGM-genotypes from populations from Norway, the British Isles, Italy, Denmark, West Germany, Austria, Switzerland,

Table 1. Country, locations, latitudes, sample sizes (N) and genotypic frequencies at the MDH- and PGM-locus in populations of *Macrosiphum rosae*.

The enzyme systems of each location are marked by asterisks when significant deviations from the Hardy-Weinberg equilibrium were observed. * $p < 5\%$; ** $p < 1\%$; *** $p < 0{\cdot}1\%$.

Country[1], location	Year	Latitude	N	MDH			PGM					
				FS	SS	FF	FM	FS	MS	FF	MM	SS
E* La Laguna	84	28·19	136	0·0	0·0	1·0 a	0·0	0·0	0·0	0·0	1·0	0·0 a
Santa Cruz	84	28·19	113	0·0	0·0	1·0 a	0·0	0·0	0·0	0·0	1·0	0·0 a
San José	84	28·19	37	0·0	0·0	1·0 a	0·0	0·0	0·0	0·0	1·0	0·0 a
P Madeira	86	32·44	98	0·43	0·16	0·41	0·01	0·0	0·0	0·0	0·99	0·0 a
T Izmir	84	38·25	100	0·41	0·02	0·57	0·07	0·0	0·0	0·0	0·93	0·0 a
E Barcelona	86	41·23	95	0·80	0·0	0·20***	0·0	0·0	0·0	0·0	1·0	0·0 a
CH Lago di Como	85	45·47	25	0·80	0·0	0·20***	0·08	0·0	0·0	0·0	0·92	0·0 a
Lago di Lugano	85	46·0	25	0·96	0·0	0·04***	0·0	0·0	0·0	0·0	1·0	0·0 a
Lago Maggiore	81	46·10	180	0·97	0·0	0·03***	0·0	0·0	0·0	0·0	1·0	0·0 a
I Bolzano	86	46·31	98	0·31	0·31	0·38**	0·47	0·0	0·01	0·02	0·50	0·0*
A Wien	85	48·13	25	0·36	0·36	0·28	0·36	0·0	0·0	0·04	0·60	0·0
H Budapest	87	47·30	91	0·55	0·11	0·34***	0·23	0·0	0·01	0·0	0·75	0·01 a
D Tettnang	81	47·40	77	0·30	0·47	0·23**	0·33	0·01	0·0	0·10	0·56	0·0
Tübingen		48·31					see table 2					
Hamburg	80	53·33	81	0·47	0·14	0·39	0·49	0·0	0·0	0·09	0·42	0·0
DK Aalestrup	81	56·42	76	0·43	0·20	0·37	0·40	0·02	0·02	0·04	0·53	0·0
N Kristiansand	81	58·10	184	0·43	0·29	0·28	0·24	0·17	0·01	0·42	0·11	0·05***
Hardanger Fj.	81	60·23	96	0·32	0·26	0·42***	0·17	0·09	0·04	0·0	0·57	0·13***
GB England	79	52·30	505	0·45	0·42	0·13	0·0	0·0	0·10	0·0	0·90	0·0 a
Wales	79	52·30	191	0·49	0·36	0·15	0·01	0·0	0·24	0·0	0·74	0·0 a
Scotland	79	57·0	212	0·46	0·37	0·17	0·12	0·02	0·0	0·0	0·86	0·0 a
N* Gjörvik	81	60·48	94	0·10	0·0	0·90 a	0·34	0·15	0·01	0·34	0·11	0·05
Hamar	81	60·48	188	0·09	0·0	0·91 a	0·24	0·21	0·06	0·34	0·10	0·06*
Lillehammer	81	61·08	158	0·17	0·0	0·83 a	0·40	0·15	0·02	0·29	0·05	0·09***

a: Only few and/or small classes

[1]Abbreviations: A – Austria; CH – Switzerland; D – Germany; DK – Denmark; E – Spain; E* – Spanish Isles; GB – Great Britain; H – Hungary; I – Italy; N – South Norway; N* – North Norway; P – Portugal; T – Turkey.

Turkey, Spain (Barcelona, Canary Isles) and Portugal (Madeira) are given in table 1. Significant deviations from the *Hardy-Weinberg* expectation are marked by an asterisk. There is no obvious correlation between the χ^2 values and the degree of latitude or the mean temperature in January which is assumed as an indication of the harshness of winter.

At Tübingen genotype frequencies were recorded over a period of seven years (table 2). The data from 1977, 1978, 1979, 1984 and 1985 are the mean values of samples taken from the population every week during the asexual phase. The genotypic structure of the population varied over different years. The homogeneity

Table 2. Frequencies of MDH- and PGM-genotypes in the *Macrosiphum rosae* population at Tübingen from 1977 to 1984.

N = sample size. The enzyme systems within years are marked by asterisks if significant deviations from the *Hardy-Weinberg* equilibrium were observed: * $p < 5\%$; ** $p < 1\%$; *** $p < 0{\cdot}1\%$.

		MDH			PGM					
Year	N	FS	SS	FF	FM	FS	MS	FF	MM	SS
1977	771	0·50	0·28	0·22	0·26	0·01	0·07	0·03	0·63	0·0
1978	4156	0·53	0·15	0·32***	0·33	0·01	0·03	0·04	0·60	0·0
1979	1122	0·47	0·30	0·23	0·43	0·01	0·02	0·06	0·48	0·0*
1980	102	0·52	0·36	0·12	0·45	0·01	0·0	0·0	0·54	0·0**
1981	94	0·52	0·18	0·30	0·38	0·01	0·03	0·06	0·50	0·01
1983	1371	0·53	0·36	0·11***	0·28	0·0	0·02	0·09	0·61	0·0***
1984	1023	0·54	0·35	0·11***	0·29	0·0	0·05	0·08	0·58	0·0***

tests for both enzyme loci resulted in significant deviations (MDH: $\chi^2 = 599{\cdot}20$, d.f. = 12, $p \approx 0$; PGM: $\chi^2 = 256{\cdot}49$, d.f. = 24, $p \approx 0$). Considering first the MDH data, there is a remarkable constancy in the frequency of the MDH-heterozygotes from year to year. If the sampling data from 1979 are excluded, the test parameter for the homogeneity between years and between both homozygotes and heterozygotes (FS: SS + FF) decreases from $\chi^2 = 16{\cdot}47$ (d.f. = 6, $p = 0{\cdot}01$) to $\chi^2 = 3{\cdot}22$ (d.f. = 5, $p = 0{\cdot}67$). Considering the population structure within one year, again the heterozygotes did not show large fluctuations whereas large frequency changes of the MDH-homozygotes occurred (Tomiuk and Wöhrmann 1981, unpublished data).

In contrast, no such consistent patterns were found at the PGM-locus. The relative number of heterozygote individuals differed significantly between years ($\chi^2 = 79{\cdot}16$, d.f. = 6, $p \approx 0$). Moreover, taking both loci into consideration, the annual average populations within a region have a high interpopulational identity (Tomiuk and Wöhrmann 1984). This happens, e.g., in the British Isles, East Norway (Gjörvik, Hamar, Lillehammer), West Germany (Tettnang, Tübingen, Hamburg) and Denmark (Aalestrup).

To analyse allelic dependence on the geographic origin and the temperature (mean temperature in January), correlation coefficients were calculated from the data in table 1. The allele frequencies were transformed by the arcsin Γ-function. To avoid an overestimation from the data from Tübingen, mean frequencies were calculated from the data given in table 2. Mean values were also used for the extreme localities, Canary Isles and North Norway, in order to avoid an overestimation from these values. In table 3 the correlation coefficients between the most common allele at each locus and the degree of latitude and the temperature respectively are given. There are significant correlations at the 5% level between all parameters, but if the dependence of temperature on the degree of latitude ($r = -0{\cdot}82$, $p < 5\%$) is excluded, the resulting partial coefficients are not significant.

The patterns of allelic distributions were investigated more in detail by *Wright's* F-statistics. The estimation procedure was done according to Nei and Chesser

Table 3. a) Correlation coefficients between the degree of latitude (L), the temperature (T) and the frequency of the common allele at the enzyme loci MDH and PGM. b) Partial correlation coefficients are given which exclude the dependence of the temperature on the latitude.

Variables	MDH	PGM
a) *Correlation coefficients*		
L	−0·50*	−0·74*
T	0·54*	0·72*
b) *Partial correlation coefficients*		
L	−0·12	−0·38
T	0·26	0·29

*$p < 5\%$

(1983). F_{ST} measures the allelic heterogeneity between local populations (or between years in the populations from Tübingen). F_{IS} is a measure of deviations from within random mating populations. In table 4 the results of the comparison between the population in Tübingen from 7 different years as well as between the populations from different geographic locations are given. In Tübingen, both loci are influenced within the years by some factors which cause a slight excess of heterozygotes ($F_{IS} \leq -0{\cdot}03$). The genetic differences between the years are highly significant, but only 2% of the mean allelic heterogeneity ($F_{ST} \leq 0{\cdot}02$) observed can be attributed to differences between years.

The allelic distribution with respect to the geographic origin of the populations is different from the preceeding local structure regarded between different years. To avoid again an overestimate of the data from Tübingen the mean sample size was calculated by the harmonic mean of the data from table 2. Mean values were also used from the extreme localities (Canary Isles, North Norway). The amount of heterogeneity caused by differences between populations significantly increases to about 20%. Now there is no evidence that within local populations genetic polymorphism is stabilized with respect to the total population ($F_{IS} = 0{\cdot}01$).

Table 4. F-statistics on the data from rose aphid populations in Tübingen sampled from 1977 to 1984. and on the data sampled from different European locations.

Enzyme	F_{IS}	F_{ST}	χ^2	d.f.
Tübingen				
MDH	−0·07	0·03	448·71***	6
PGM	−0·03	0·004	152·92***	12
mean	−0·05	0·02	601·63***	18
Europe				
MDH	−0·03	0·08	416·02***	18
PGM	0·06	0·27	2725·43***	36
mean	0·01	0·17	3141·45***	54

*** $p < 0{\cdot}1\%$.

It is evident, that populations from cold areas (mean temperature in January below 0°C e.g. Norway, Denmark, West Germany, Austria) have more genotypes than those from temperate climates e.g. British Isles, Madeira and Spain (table 1). To compare the genotypic variability the measure $V = \Sigma P_i^2$ proposed by Hedrick (1971) was calculated. In this expression P_i is the frequency of the ith genotype in the population. V equals 1 if the population consists of only one genotype as in the Canary Isles. In the case of the MDH-locus two alleles and in the case of the PGM-locus three alleles are known and thus 18 genotypes are possible. In this case the smallest possible value of V is 0·06. The calculated values of V are plotted against the mean temperature (°C) in January (figure 1) (Müller 1980). From figure 1 it is evident that all populations from areas with temperatures below zero exhibit low V-values, i.e. high genetic variabilities. Populations from warmer areas exhibit mostly reduced genotypic variabilities, though the V-values cover a wide range.

4. Discussion

In general, is the testing of deviations from *Hardy-Weinberg* equilibrium of biological significance in aphid species? The population size and structure of rose aphids can change rapidly within years due to environmental factors (Maelzer 1977; Tomiuk and Wöhrmann 1981; Wöhrmann 1984). Thus the data can be randomly close or distant to *Hardy-Weinberg* (HW) equilibrium, and this is indeed observed in the populations from different locations and different years (tables 1, 2). Furthermore, the HW expectation cannot be estimated in many of the investigated populations because of the small numbers of genotype classes. In aphids more attention must be paid to the allelic composition and the genotypic variability. Our investigations indicated that in cyclic parthenogenetic populations (Tübingen) there exist influences which might stabilize the genetic population structure between years ($F_{ST} = 0{\cdot}02$). Considering geographically distinct populations, these factors do not act in general ($F_{ST} = 0{\cdot}17$). Furthermore, Tomiuk (1987) could show that the distribution of allelic frequencies is random and that in most cases selection at enzyme loci can be excluded in aphid species. Thus, the results are most simply explained by the induction and suppression respectively of the sexual phase. The rose aphid, *M. rosae* , is usually a heteroecious holocyclic species in North and Middle Europe. It is not exactly known what factors induce the sexuals in *M. rosae*. However, these factors are likely to be similar to those acting on the peach aphid, *Myzus persicae*, which is extensively investigated with regard to its reproduction mode (Blackman 1972). If *M. rosae* overwinters as an egg in regions with cold winters then a sexual phase is requisite for completing the life cycle. The genotypic variability might be increased by recombination, which would compensate for the effects of drift and selection during the parthenogenetic phase. This is supported (1) by results from investigations on the MDH-locus in populations from Germany (Tomiuk and Wöhrmann 1981) where the shifting of genotypic frequencies within the asexual phase was adjusted during the sexual phase and (2) by the results for all populations from regions with a mean temperature lower than zero. Populations from Norway, Denmark, West Germany and Austria exhibit V-values between 0·1 and 0·2. In regions where both types of reproduction may be practised a lower

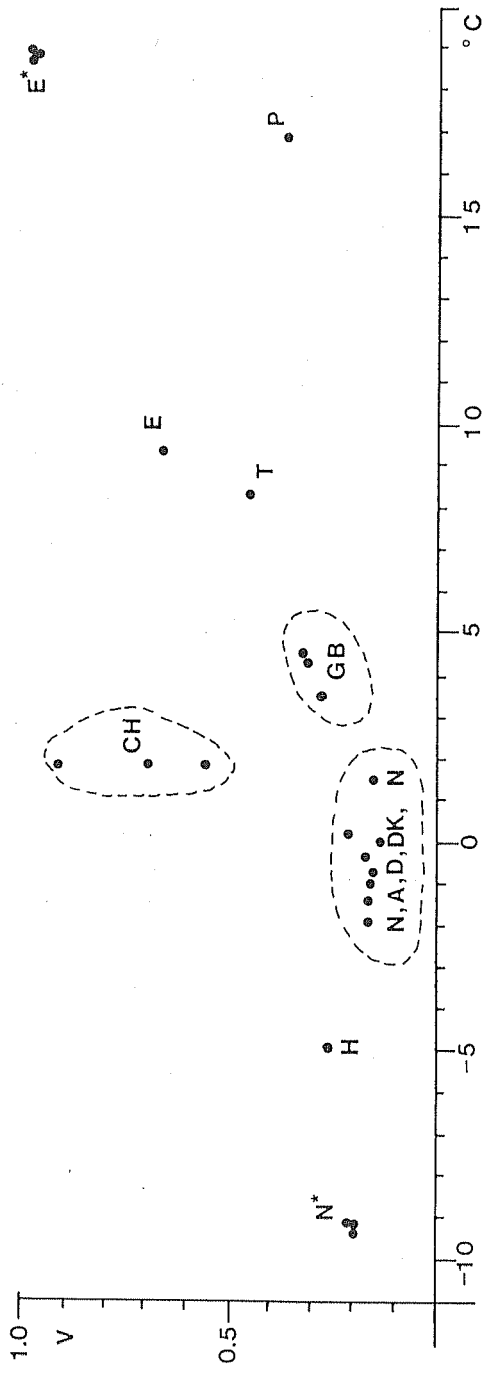

Figure 1. The genotypic variability $V = \Sigma p_i$ for populations at different locations in Europe depending on the lowest mean temperature in January. A = Austria; CH = Switzerland; D = Germany; DK = Denmark; E = Spain; E* = Canary Isles; GB = Great Britain; H = Hungary; N = Norway; N* = North Norway; P = Portugal (Madeira); T = Turkey.

variability is expected (e.g. British Isles). Where selection pressures are strong one expects asexual populations to consist of few genotypes or to be even genotypically fixed. When drift is important, however, all possible population structures are conceivable: the MDH and PGM homozygotes are fixed in the Canary Isles, there is an excess of MDH heterozygotes in Switzerland and all combinations at the MDH-locus and low variability at the PGM-locus occur in Turkey and Madeira.

Investigations on populations of the rose aphid in North America also fit this model (Rhomberg *et al* 1985). In this region *M. rosae* is described as a monoecious and holocyclic species. Rhomberg *et al* demonstrated large changes in genotypic frequencies of the colour locus and a loss of genotypic heterogeneity within the asexual period but a regeneration of the former population structure at the beginning of the next year.

In contrast, Steiner *et al* (1985) and Voegtlin *et al* (1986) investigated anholocyclic populations of *Rhopalosiphum maidis* in several states of the USA (Georgia, Alabama, Mississippi, Louisiana, Texas, Arkansas, Oklahoma and Illinois). In Illinois this species cannot overwinter because of low temperatures and the incapacity to reproduce sexually. Therefore, it is assumed that recurrent recolonization of this area occurs every year. A total of 21 enzyme loci were investigated of which 9 were variable. Out of these, 6 enzymes were investigated over three years. The number of genotypes present in the populations varied from year to year and from site to site.

These data were discussed by the authors in terms of endomeiotic recombination, mutations and backmutations. However, recombination is unlikely in aphids (Blackman 1979; Suomalainen *et al* 1980; Tomiuk and Wöhrmann 1982). Mutations and backmutations are likewise very rare and cannot explain the patterns at these marker loci. Again, the data are better explained as a result of random drift effects (founder effects and bottle-neck-effects) and the lack of sexual reproduction as in our results for populations of *M. rosae*.

This view is also supported by the investigations of Singh and Rhomberg (1984) on *Aphis pomi*. This species was found to be polymorphic at EST1, EST2 and GOT. All loci exhibit two alleles, yet, only 6 genotypes consisting of combinations of EST1 and GOT and only five for combinations of EST2 and GOT were found in natural populations. The authors subdivided this sample of 1200 individuals in two groups, one (type A) with the GOT slow homozygote variable for EST1 and EST2 and the other (type B) with the GOT fast homozygote fixed for EST1 and EST2. This population structure can be understood only if one assumes a mixture of different reproductive types. The populations consist of two groups, one holocyclic and the other anholocyclic. In these cold areas only holocyclic aphids survive the winter and immigration of anholocyclic clones from elsewhere takes part every year. Summarizing, there is neither intra- nor inter-specifically a uniform reproductive type. The degree of sexuality is modified by the environment, and the genotypic variability within a population and the population structure is strongly determined by the reproductive type. Populations with cyclic parthenogenesis show a high degree of heterogeneity. On the other hand asexual aphid populations often have a low genetic heterogeneity and strong local and temporal unstable population structure.

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