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Population genetic structure during aestivation in the sycamore aphid *Drepanosiphum platanoidis* (Hemiptera: Drepanosiphidae)

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***Drepanosiphum platanoidis*, sycamore aphid, allozyme variation, gene flow, population biology**

Abstract. Cellulose acetate electrophoresis was used to investigate genetic variation at 15 enzyme loci in aestivating populations of the sycamore aphid, *Drepanosiphum platanoidis* (Schrank) (Hemiptera: Drepanosiphidae). The level of polymorphism *P* (over all loci) was 20%. Of the polymorphic loci, only phosphoglucomutase (PGM), with four alleles, provided consistent, interpretable banding patterns and was subsequently used to investigate population structure and gene flow at various spatial levels in southern Britain. Of 13 aphid aggregations (from single leaves) collected from the lower canopy of a selected tree, only one deviated significantly from Hardy-Weinberg expectations. Genotypic diversity for the PGM locus was generally high and genetic identity measures showed homogeneity between leaf aggregations. Aphid samples collected from eight trees in close proximity, five sites in Hertfordshire and four other sites in southern Britain, also showed homogeneity for allele and genotype frequencies and, in almost all cases, conformed to Hardy-Weinberg expectations. It was concluded that gene flow, facilitated by trivial and migratory flight, was responsible for the genetic homogeneity observed, both within and between host trees.

INTRODUCTION

The sycamore aphid, *Drepanosiphum platanoidis* (Schrank), spends its entire life cycle on sycamore, *Acer pseudoplatanus* L. The aphid is holocyclic, producing sexuals in the autumn and overwinters in the egg stage. During the summer, when infestation is heavy and the nutritional value of the host is poor, embryogenesis and larviposition almost cease and the population consists almost entirely of second generation adults. This generation aestivates until autumn when conditions again become favourable (Dixon, 1985). The aphid is gregarious and members of heavy infestations are distributed patchily among whole leaves, and are often within a confined area on single leaves (Kennedy & Crawley, 1967).

All adult aphids, except the oviparous female, are winged and retain the ability to fly throughout their life. Indeed, much attention has been given to the frequent 'trivial flights' made by the aphids during which they remain within, or close to, the canopy of the host tree (Dixon, 1969; 1985). In contrast, the incidence of migratory flight (i.e. flights that 'occur when the thresholds for stimuli, such as a mate, food or shelter are high, resulting in an animal leaving its population territory or habitat': Dixon, 1969) has been somewhat neglected. Some authors (Haine, 1955; Kennedy & Stroyan, 1959; Southwood, 1962) consider the sycamore aphid as an infrequent migrant even though the species has been

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taken by both suction and sticky traps (Broadbent & Doncaster, 1949; Johnson & Eastop, 1951). Dixon (1969) investigated the extent to which *D. platanoidis* undertakes migratory and trivial flights. He demonstrated that migratory flight occurs regularly, with seasonal periodicity, and can result in the successful colonisation of other suitable sycamore trees.

Allozyme electrophoresis has been widely used to determine population structure and the extent of gene flow in many aphid studies (e.g. Loxdale et al., 1985; Steiner et al., 1985; Wöhrmann & Tomiuk, 1988; Loxdale & Brookes, 1990; Hebert et al., 1991). In the present study, allozymes were employed as genetic markers to investigate the importance of trivial and migratory flight on the population genetic structure of the sycamore aphid in southern Britain.

MATERIAL AND METHODS

Sampling

Aestivating adults of *D. platanoidis* were collected from infested leaves of the lower canopy of sycamore trees between 16 June and 27 July 1991. A single tree (T1), at Coach Lane, Rothamsted Experimental Station (RES), Herts., was selected to investigate clonal composition within, and distribution between, aphid aggregations at the "within tree" spatial scale. All aphids, from six individual leaves (L1–L6) on one branch (B1) were collected as well as those from seven other leaves (B2–B8) selected from around the lower canopy of the tree. To elucidate population structure at a local level, a further seven trees were sampled at RES: six trees (T2–T7) were from a single lane (Coach Lane) and one at Manor pond (MP), situated approximately 0.3 km south west of Coach Lane. To investigate geographic variation, samples were collected at several sites in Hertfordshire as well as around southern Britain. Hertfordshire sites were: Bayfordbury (BD) (near Hertford); Hemel Hempstead (HH); St Albans (SA); Harpenden (HN) and Rothamsted Experimental Station (RES). Sites sampled outside Herts. were: Wimbledon (WN); Southampton (SN); Swansea (SW) and Winterbourne Kingston, Dorset (WK).

Generally (apart from T1) several infested leaves were sampled from a single tree, but at two sites (HH and SW) three trees, in close proximity, were sampled.

Aphids were brought back to the laboratory alive and kept frozen, at –25°C, until analysed by electrophoresis.

Electrophoretic methods

Frozen aphids were thawed and then homogenized in 10 µl of sample buffer (Loxdale et al., 1983) using the multiple homogenizer described by Brookes & Loxdale (1985). Electrophoresis was performed at constant voltage (200 V) for 20–30 minutes, using the cellulose acetate (CA) system supplied by Helena Laboratories Ltd (P.O. Box 752, Beaumont, Texas 77704) (see Wynne et al., 1992 for details) and CA plates were stained using the agar overlay technique described by Easteal & Boussy (1987).

A total of 12 enzymes (representing 15 putative loci) were screened (at least 20 individuals per locus) for polymorphism suitable for population analysis. These were: alcohol dehydrogenase (ADH; EC 1.1.1.1), adenylate kinase (AK; EC 2.7.4.3), glutamate-oxaloacetate transaminase (GOT; EC 2.6.1.1), glucose-6-phosphate dehydrogenase (G6PDH; EC 1.1.1.49), glycerol-3-phosphate dehydrogenase (αGPD; EC 1.1.1.8), isocitrate dehydrogenase (IDH; EC 1.1.1.42), malic enzyme (ME; EC 1.1.1.40), manno-sephosphate isomerase (MPI; EC 5.3.1.8), peptidase (PEP; EC 3.4.11), phosphoglucose isomerase (PGI; EC 5.3.1.9), 6-phosphogluconate dehydrogenase (6PGD; EC 1.1.1.44) and phosphoglucomutase (PGM; EC 2.7.5.1). Enzyme staining recipes were taken directly, or modified, from Richardson et al. (1986) whilst running buffer systems were as follows: 25 mM tris-glycine, pH 8.5 (for GOT, PEP, PGI, PGM), 100 mM tris-citrate, pH 8.2 (for ADH, AK, αGPD, G6PDH, ME, MPI,) and 50 mM tris-citrate pH 7.8 (for IDH, 6PGD).

Of the 12 enzymes screened, only two, PGM and IDH, showed polymorphism of a clear genetic (Mendelian) basis (a polymorphic locus here is defined as having the frequency of its commonest allele ≤ 0.95). The remainder were either monomorphic (AK, GOT, G6PDH, αGPD, ME, MPI, PGI, 6PGD),

displayed polymorphism that was difficult to interpret (PEP) or were poorly resolved (ADH). Although one IDH locus (*Idh*-2) displayed at least two alleles (with heterozygotes), it stained weakly and was often impossible to score (*Idh*-1 was monomorphic). Therefore, after the initial screening, *D. platanoidis* samples were tested only for PGM. When the number of aphids collected was large, sub-samples were used (generally not less than 100). However for leaves collected individually, or when sample sizes were less than 100, all aphids were tested for PGM.

Genotypic diversity within populations was measured according to the formula for average heterozygosity $Hg = 1 - \sum p_i^2$, where p_i is the frequency of the ith genotype. The degree of genetic differentiation between any two populations was calculated using Hedrick's probability of genotypic identity (Hedrick, 1971) and tested for significance using pairwise chi-squared analysis (pooling data where necessary). Population differentiation was measured by the standardized gene frequency variance, F_{st} (Wright, 1978), amongst populations in Hertfordshire and southern Britain.

RESULTS

PGM was found to be polymorphic in all samples studied. Four isozymes (hereafter referred to as alleles) were found and labelled a to d in order of increasing mobility from the cathode (with relative mobilities: 0.40, 1.00, 1.40, and 1.80 respectively). Alleles b and d were predominant and common to all samples, whereas a and c were either rare or absent. Although allele frequency data are not given they may be calculated from the genotype frequency data presented in Table 1.

Variation on a single tree

In all individual leaves sampled, alleles b and d predominated and were found in roughly equal frequency (with mean values, ± SD, of 0.490 ± 0.044 and 0.487 ± 0.051 respectively). Alleles a and c were rare in all samples (freq. ≤ 0.047 and ≤ 0.050 respectively). Only one aphid sample (B4) out of 13 leaves examined was found to deviate significantly from Hardy-Weinberg (H-W) expectations ($P < 0.05$), although overall there was a deficiency in heterozygotes which is reflected in the combined data for the tree (Table 1). Genotypic diversity ranged from 0.571 (B1L2) to 0.713 (B7) with a mean value of 0.655 ± 0.041. The number of genotypes detected per leaf was never less than three or more than six, with a mean of 4.77 ± 0.89. Genotypic identities were high in all pairwise comparisons between all leaves sampled (≥ 0.862). The mean genotypic identity value between leaves on Branch 1 (0.940 ± 0.039) was similar to (but slightly less than) the mean value for between-branch comparisons (0.960 ± 0.027). In 78 pairwise chi-squared analyses of genotype counts, only four were significantly heterogeneous at $P < 0.05$ (and none at $P < 0.01$). This is not much greater than the number of significant differences that would be expected by chance (3.9 at $P < 0.05$), for such a large number of comparisons.

Local variation

Allele and genotype frequencies were similar for all samples collected from eight trees at Rothamsted. Alleles b and d predominated (with mean frequencies of 0.527 ± 0.049 and 0.464 ± 0.048 respectively) whereas a and c, when detected, were rare (≤ 0.017 and ≤ 0.009 respectively). All samples, except Tree 1, conformed to H-W expectations. Genotypic diversity ranged from 0.580–0.674 and the mean number of genotypes detected per tree was 4.38 ± 1.22. Genotypic identities were high in all pairwise comparisons (≥ 0.931). In 28 pairwise chi-squared comparisons of genotype counts between the eight trees, only two were significant at $P < 0.05$ (chance would predict 1.4).

TABLE 1. Genotypic composition and frequencies of *D. platanoidis* samples (see Materials and Methods for key to sample codes). Also provided are the number of specimens investigated (N), the number of genotypes found (Ng), genotypic diversity (Hg) and observed (Obs.) and expected (Exp.) heterozygosity (Het.) frequencies (*indicates that a sample deviates significantly from H-W expectations, $P < 0.05$).

Site	Tree	Branch	Leaf	N	Ng	Genotype										Het.		Hg
						aa	ab	ac	ad	bb	bc	bd	cc	cd	dd	Obs.	Exp.	
RES	T1	B1	L1	69	5					0.304	0.229	0.420		0.014	0.232	0.464	0.518	0.676
			L2	33	3					0.273		0.576			0.152	0.576	0.493	0.571
			L3	17	3					0.176		0.471			0.353	0.471	0.484	0.623
			L4	58	5		0.017			0.276	0.017	0.431			0.259	0.466	0.516	0.670
			L5	40	6				0.025	0.225	0.025	0.525		0.075	0.125	0.650	0.556	0.651
			L6	39	5		0.051			0.359		0.308		0.026	0.256	0.385	0.530	0.707
		B2	–	70	5		0.014		0.014	0.157		0.529			0.286	0.557	0.506	0.613
		B3	–	50	4				0.020	0.200		0.460			0.320	0.480	0.501	0.646
		B4	–	70	5		0.014			0.329		0.343		0.014	0.300	0.371*	0.514	0.684
		B5	–	86	6		0.035		0.023	0.244		0.384		0.012	0.302	0.453	0.532	0.700
		B6	–	76	5		0.013		0.013	0.211		0.553			0.211	0.579	0.513	0.605
		B7	–	64	5		0.031		0.063	0.313		0.359			0.234	0.453	0.542	0.713
		B8	–	57	5				0.035	0.263		0.474		0.018	0.211	0.526	0.525	0.660
RES	T1	(comb.)	–	729	7		0.015		0.016	0.258	0.005	0.443		0.011	0.251	0.491	0.523	0.674
	T2	–	–	88	5		0.011		0.023	0.364		0.386			0.216	0.420	0.507	0.671
	T3	–	–	92	5		0.011		0.011	0.293		0.565			0.120	0.587	0.496	0.580
	T4	–	–	100	4				0.020	0.260		0.520			0.200	0.540	0.509	0.622
	T5	–	–	54	3					0.370		0.481			0.148	0.481	0.475	0.610
	T6	–	–	56	4		0.018			0.196		0.518			0.268	0.536	0.507	0.621
	T7	–	–	68	3					0.235		0.500			0.265	0.500	0.500	0.625
	MP	–	–	100	4					0.270		0.460		0.010	0.260	0.470	0.505	0.648
RES		(comb.)	–	1287	7		0.011		0.013	0.270	0.003	0.463		0.007	0.233	0.497	0.516	0.658
SA	–	–	–	100	4				0.010	0.270		0.460			0.260	0.470	0.505	0.648
BD	–	–	–	100	6	0.010			0.050	0.230	0.010	0.480			0.220	0.540	0.538	0.666
HH	–	–	–	100	5		0.040		0.010	0.260		0.500			0.190	0.550	0.520	0.645
HN	–	–	–	100	6		0.010		0.010	0.220	0.020	0.530			0.210	0.570	0.519	0.626
WN	–	–	–	100	6		0.030		0.010	0.280	0.010	0.490			0.180	0.540	0.518	0.648
SW	–	–	–	99	5		0.010		0.010	0.273		0.475			0.232	0.495	0.509	0.646
WK	–	–	–	100	5		0.010		0.020	0.260		0.540			0.170	0.570	0.511	0.611
SN	–	–	–	150	4				0.007	0.307		0.473			0.213	0.480	0.499	0.637

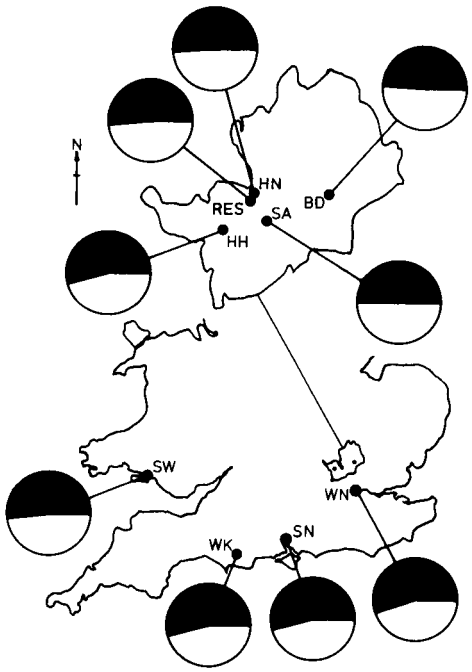

Fig. 1. Relative frequencies of the two commonest PGM alleles, b (black) and d (white), of *D. platanoidis* at sample sites in southern Britain: Bayfordbury (BD); Hemel Hempstead (HH); St Albans (SA); Harpenden (HN); Rothamsted Experimental Station (RES); Wimbledon (WN); Southampton (SN); Swansea (SW) and Winterbourne Kingston (WK).

Geographic variation

Fig. 1 shows the location of trees sampled in Hertfordshire and southern Britain and the relative frequency of the commonest alleles. As with trees at Rothamsted, the most frequent alleles at all sites were b and d at roughly equal frequency. All samples conformed to H-W expectations. Genotypic diversity ranged from 0.611–0.658 and the mean number of genotypes detected per site (omitting combined Rothamsted data) was 5.13 ± 0.781. Genotypic identities were high in all pairwise comparisons (with a mean of 0.992 ± 0.004) and chi-squared analysis revealed no significant differences between any two sites. Estimates of the standardized gene frequency variance were the same among populations in Hertfordshire and those in southern Britain (F_{st} = 0.002) (the subpopulation collected from Manor Pond being used to represent Rothamsted and Hertfordshire respectively).

DISCUSSION

The relatively low average (over all loci) biochemical polymorphism presently found in *D. platanoidis* [P = 0.2 or 20% (3/15 loci)] is characteristic of aphids, which are generally less variable genetically than many other insect species studied to date (cf. Nevo et al., 1984; Loxdale et al., 1985; Loxdale & Brookes, 1989; Wöhrmann & Tomiuk, 1989 for details). This value is intermediate between the mean of 15.5% calculated for 11 aphid species by Loxdale et al. (1985), and the mean of 24.6% which we calculate from the data for six species provided by Wöhrmann & Hales (1989).

In the case of PGM in *D. platanoidis*, four alleles were detected. Two alleles (b and d) were roughly equally common in all samples, whereas the other two (a and c) were rare or sometimes absent. Of the possible ten clones (genotypes) detectable, only eight were found and only genotypes bb, dd and bd were present in all samples. This was because the frequencies of the rare alleles were so low that the probability of detecting three of the genotypes (aa, ac and cc) was remote (the expected frequency of each of these genotypes was ≤ 0.000164).

Some aphid species such as the blackberry-grain aphid, *Sitobion fragariae* (Walker), are known to have clonal structures in their summer (parthenogenetic) populations infesting the secondary host, cocksfoot grass, *Dactylis glomerata* (Loxdale & Brookes, 1990). Thus an individual colony may be composed of only a few clones (nine genotypes are known at the GOT locus) and consequently, their genotype frequencies may deviate significantly from H-W expectations (Loxdale, 1990; Loxdale & Brookes, 1990). If the leaf aggregations exhibited by *D. platanoidis* were clonal in nature, genotypic diversity and the number of clones detected would be expected to be small and average genotypic identity between any two leaves also low for a given variable locus. Samples would also be expected, more often than not, to deviate from H-W expectations because of the low number of clones present. However, samples taken from individual leaves on Tree 1 were found to conform broadly to H-W expectations (only B4 deviated significantly) and possess high genotypic diversity. The mean number of clones (genotypes) detected per leaf on Tree 1 was no less (and in fact slightly greater) than the mean value for whole trees at Rothamsted. Allele and genotype frequencies were similar on all 13 leaves sampled from Tree 1. Genotypic identities were found to be no higher, in pairwise comparisons, between leaves on a single branch than between branches.

Dixon (1969) showed that trivial flight in *D. platanoidis* is correlated with the change in the vertical distribution of the aphid within the canopy of the tree. He concluded that trivial flight is density induced and is important in regulating the distribution of aphids on a tree. It seems likely that the mobility of the aphid, in the form of trivial flight, is responsible for the genetic homogeneity observed, and that gregariousness, in the aestivating phase, is not related to a clonal aggregation structure.

Genetic homogeneity was also found both between trees in close proximity, and those geographically separated in southern Britain. All samples shared similar allele and genotype frequencies, and in most cases, conformed to H-W expectations. The low F_{st} value found among populations in Hertfordshire and Southern Britain is consistant with values calculated for species known to be highly mobile (Korman et al., 1993). *D. platanoidis* is taken regularly in suction traps operated throughout Britain by the Rothamsted Insect Survey (Dixon, 1979; Woiwod et al., 1988) and such migrations have been shown to result in the colonisation of other suitable trees (Dixon, 1969). If it is assumed that the PGM locus is neutral (i.e. not under the influence of natural selection) (Nei & Graur, 1984; Tomiuk, 1987), gene flow, facilitated by migration may explain the geographic homogeneity observed (Slatkin, 1985). Alternatively the historical pattern of gene flow, associated with the range expansion of the host tree, may have had a substantial influence on the distribution of genetic variation in modern populations, to which seasonal migration contributes to some extent. However, if natural selection were acting on the PGM locus (or loci to which it is linked) it may be that genetic homogeneity is maintained

by some form of balancing selection (e.g. Ayala et al., 1972; Jones et al., 1981; Loxdale & Brookes, 1988). With information from only one locus (which may be unrepresentative), it is difficult to assess the relative importance of these processes at the geographic scale. However, even if balancing selection is maintaining homogeneous allele frequencies at the geographic scale, any model, whether selectionist or neutralist, would have to involve some degree of movement to explain the high clonal diversity found within, and homogeneity between, aphid aggregations at the within tree level.

Due to the low number of detectable clones (a consequence of only one useable locus) any comparison of clonal diversity among spatial levels (from leaf to geographic) must be tentative. However, these results indicate that, within the spatial range sampled, most of the total population diversity may be found among aphids on a single sycamore leaf. The spatial distribution of genetic diversity in *D. platanoidis* may therefore be similar to that of the greenbug *Schizaphis graminum* (Rondani), in which 82.3% of the total population diversity (characterised by DNA fingerprinting) was found among aphids on one sorghum leaf (Shufran et al., 1991).

Dixon (1969) concluded that migratory and trivial flight are of considerable importance in regulating numbers and distribution of sycamore aphids on their host tree. The present study indicates that these two modes of dispersal have an important bearing on gene flow, both within and between host trees, and result in genetically homogeneous populations during the summer aestivation period. This population structure closely parallels that of *S. fragariae* on its primary overwintering host, blackberry (*Rubus fruticosus* agg.) (Loxdale & Brookes, 1990), and the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), on its primary host, bird cherry (*Prunus padus*) (Loxdale & Brookes, 1988). Both species display geographically homogeneous allozyme patterns, indicating that enough gene flow occurs to stabilize populations against the effects of drift and founder effects.

However, it is possible that when *D. platanoidis* is reproductively active in the spring and autumn, when a high proportion of the population are nymphs, gene flow between leaves and/or adjacent trees is more restricted, leading to seasonal genetic heterogeneity – as with *S. fragariae* on its secondary host (Loxdale & Brookes, 1990). This aspect of the sycamore aphid's population biology is currently under investigation.

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