Heredity **76** (1996) 305–313 *Received 30 June 1995*

Genetic diversity and mode of reproduction in French populations of the aphid *Rhopalosiphum padi* L.

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Holocyclic individuals of the aphid *Rhopalosiphum padi* reproduce by cyclical parthenogenesis, while anholocyclic individuals are obligate parthenogens. Although admixed on the secondary hosts in summer, holocyclic and anholocyclic populations occur separately on the primary and secondary hosts during winter and spring. In this study, we compared the genetic diversity and population structure of holocyclic and anholocyclic populations collected in spring in the northern half of France. We also analysed the genetic composition of summer populations of *R. padi* on its secondary hosts. In spring, holocyclic populations were in Hardy–Weinberg equilibrium at individual loci and had a relatively high genotypic diversity. Conversely, anholocyclic populations deviated from Hardy–Weinberg equilibrium and often consisted of a single clone. Moreover, these populations showed very low mean heterozygosities compared with holocyclic populations. Analysis of summer populations suggested that in regions with cold winters, summer populations were largely recruited from holocyclic clones, whereas in areas with mild winters, summer populations were mainly derived from anholocyclic clones. These results permit an assessment of the geographical distribution of the two modes of reproduction on a large scale. The reasons for the diminished heterozygosity of anholocyclic populations are also discussed in relation to the mechanisms which may induce transitions to asexuality in aphids.

Keywords: allozymes, asexuality, breeding systems, cereal aphid, parthenogenesis, sexuality.

Introduction

Over the last two decades, variation in the mode of reproduction among animal species has received increasing attention, with the primary objective of determining the relative advantages of sexual reproduction and parthenogenesis. Both theoretical and experimental studies have aimed to resolve the paradoxical prevalence of sex given the two-fold advantage of asexual reproduction in population growth (Maynard Smith, 1971). It is now widely accepted that sexual forms have an advantage (see reviews by Michod & Levin, 1988 and Stearns, 1990) when environments show physical or biological variation (Van Valen, 1973; Williams, 1975; Young, 1981).

In examining the forces maintaining sexual reproduction, special attention has been directed toward species with sexual and asexual lineages. Work on these groups has aimed both to compare genetic diversity under different breeding systems and to understand how breeding system transitions have evolved. Past studies have examined fish (Vrijenhoek, 1979, 1993), frogs (Hotz *et al.*, 1985), snails (Lively, 1992), moths (Harshman & Futuyama, 1985) and cladocerans (Innes *et al.*, 1986; Hebert *et al.*, 1988). However, surprisingly little attention has been directed towards aphids which are excellent candidates for such studies. Although most aphid species reproduce by cyclical parthenogenesis, some species have abandoned sexuality entirely, whereas others include a mixture of cyclic and obligately asexual lineages (Lees, 1966; Dixon, 1985).

Rhopalosiphum padi L. is an aphid whose complete life cycle (or holocycle) is achieved on two different hosts. Sexual reproduction and cold-resistant egg production occur in the autumn on a primary host, which is *Prunus padus* L. in western Europe. Females hatch from the resting eggs early

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in spring and typically produce two generations parthenogenetically on the primary host. Winged females appear in the third generation and then fly to the secondary hosts. The latter consist of a large number of Gramineae, Juncaceae and Cyperaceae (Rautapää, 1970) on which parthenogenetic populations develop during the summer (Dixon & Glen, 1971). Where winters are mild and the primary host is scarce, *R. padi* sustains parthenogenesis all the year round on its secondary hosts, displaying an incomplete life cycle or anholocycle (Dedryver & Gellé, 1982; Tatchell *et al.*, 1988; Simon *et al.*, 1991a). Laboratory experiments have shown that this variation in mode of reproduction is under genetic control (Simon *et al.*, 1991a, 1994). Here, holocyclic clones or populations are aphids which both reproduce by cyclical parthenogenesis and show host alternation, whereas anholocyclic forms are obligate parthenogens which remain entirely on the secondary hosts. Although admixed on the secondary hosts in summer, holocyclic and anholocyclic populations occur separately on the primary and secondary hosts during winter and spring. Because of this host plant separation, it is possible to compare the genetic attributes of populations with differing breeding systems.

In this study, we compare allozyme variation at four polymorphic loci (Loxdale & Brookes, 1988; Simon & Hebert, 1995) among spring populations of *R. padi* from their primary and secondary hosts in order to analyse the influence of the mode of reproduction on genetic diversity and population structure. We also analyse the genetic composition of summer populations of *R. padi* on its secondary hosts, which should be a mixture of holocyclic and anholocyclic clones. This information is used both to infer the main mode of reproduction of local populations and to assess the geographical distribution of holocyclic and anholocyclic populations on a larger scale. Finally, we use the genetic data to gain insights into the processes important in the evolution of anholocyclic clones of aphids.

Materials and methods

Collections

Individuals of *R. padi* were collected in the spring and summer of 1994 at a broad range of sites in the northern half of France (Fig. 1). Spring collections were made between March 23 and April 27. Twenty-four populations were sampled from the primary host, *P. padus*, in five regions (Brittany, Normandy, Nord-Picardie, Champagne-Ardennes and Lorraine) and eight populations were collected on secondary hosts (wheat, barley and oats) in two regions where parthenogenetic overwintering is successful (Brittany and Normandy). Summer collections were made between June 30 and July 12 for 13 populations from four regions (Brittany, Normandy, Nord-Picardie and Champagne-Ardennes). These collections, which were made primarily on maize, included at least 50 individuals per site, each from a different plant. Collections on the primary host included only fundatrices (the first parthenogenetic generation after sexual reproduction), whereas those from the secondary hosts included both alate and apterous virginiparae. All samples were stored at −80°C prior to electrophoresis.

Allozyme analysis

Allozyme analysis was carried out on single individuals and performed on cellulose acetate gels using standard methods (Hebert & Beaton, 1989). Each individual was assayed for variation at four enzymes; *Sdh* (sorbitol dehydrogenase, EC 1.1.1.44), *Pgm* (phosphoglucomutase, EC 5.4.2.2), *Pep* (peptidase, EC 3.4.11–13) and *Aat* (aspartate aminotransferase, EC 2.6.1.1). These enzymes were chosen for analysis because they were found to be reliably resolved and polymorphic in previous surveys of allozyme variation in *R. padi* (Loxdale & Brookes, 1988; Simon & Hebert, 1995).

Data analysis

Data were analysed using the PC version of BIOSYS-1 (Swofford & Selander, 1989) and GENEPOP version 1.2 (Raymond & Rousset, 1995a). The significance of allelic differences between populations was tested by the exact test for population differentiation of Raymond & Rousset (1995b). Genotypic frequencies were compared with Hardy–Weinberg expectations using the method described by Louis & Dempster (1987). Metric multidimensional scaling of Rogers's distance (Rogers, 1972) was used to assess genetic divergence among populations. *F*-statistics (Weir & Cockerham, 1984) were calculated to quantify gene frequency divergence among holocyclic and summer populations.

Results

Allelic diversity

In agreement with earlier studies (Loxdale & Brookes, 1988; Simon & Hebert, 1995) on *R. padi*,

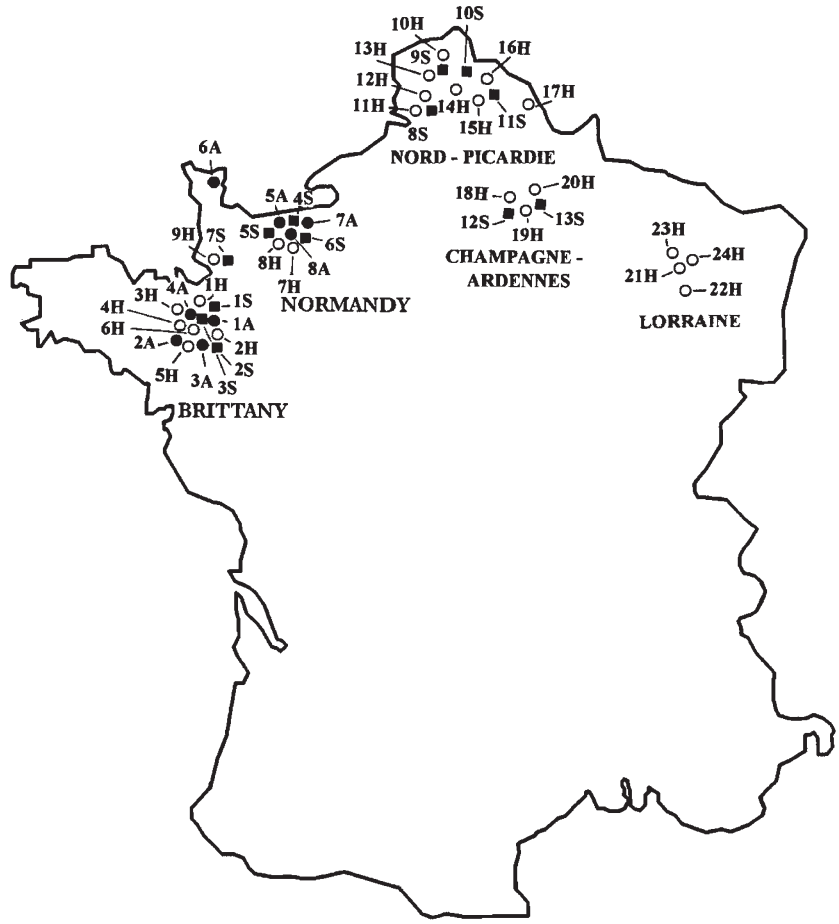

Fig. 1 Origins of the 45 populations of *Rhopalosiphum padi* collected throughout France in spring and summer 1994 and analysed for allozyme variation at four loci. 1H to 24H = holocyclic populations (○); 1A to 8A = anholocyclic populations (●) and 1S to 13S = summer populations (■).

four alleles were detected at S*dh*, three at *Pep* and *Pgm* and two at *Aat*. Mobility differences (Table 1) among the gene products were so large, that there was no uncertainty in allelic assignments at any of the four loci.

Genetic structure of holocyclic and anholocyclic populations

Genotypic frequencies among holocyclic populations showed no significant deviations ($P > 0.01$) from Hardy–Weinberg expectations and this absence of heterozygote deficits was confirmed by low F_{IS} values (Table 2). However, heterozygote deficits were noted in two of the eight anholocyclic populations (7A, 8A) at *Pgm*; the other anholocyclic populations were too weakly polymorphic to be tested.

Holocyclic populations showed near-fixation at the *Aat* locus, and a single allele was most common at each of the other three loci (Table 1). However, the cumulative frequency of rare alleles averaged 8 per cent at *Sdh*, 8 per cent at *Pgm* and 10 per cent at *Pep*. There was no evidence of gene frequency variation among holocyclic populations at any of the latter loci, as evidenced by pairwise comparisons of allelic composition ($P > 0.05$) and very low F_{ST} values (Table 2). Anholocyclic populations showed less diversity, as they were effectively fixed for a single allele at three of the four loci, and were only weakly polymorphic at the remaining locus, *Pgm* (Table 1). The exact test for population differentiation showed significant allelic differences in all pairwise comparisons between holocyclic and anholocyclic populations at *Sdh* and *Pep* ($P < 0.05$), but 140/192 (74 per cent) pairwise comparisons were not significantly different at *Pgm* ($P > 0.05$).

Correlated with the gene frequency differences, the mean heterozygosity ($\overline{H}$) over the four loci also was significantly higher ($P < 0.01$; Bonferroni test for comparison of means) in holocyclic than anholocyclic populations ($\overline{H} = 0.126$ vs. 0.016). Genotypic diversity was also higher in holocyclic than anholocyclic populations. Thirty-eight different multilocus genotypes were found in holocyclic populations with

Table 1 Allele frequencies at four allozyme loci in French populations of *Rhopalosiphum padi* on primary hosts in spring and on secondary hosts in spring and summer. Alleles are coded by their relative mobilities.

				Sdh				*Pgm*			*Pep*			*Aat*	
Region	Population	n	$\overline{H}$	1.21	1.00	0.73	0.53	1.21	1.00	0.79	1.45	1.00	0.70	1.00	0.88
Brittany	1H	117	0.118	0.0	0.919	0.0	0.081	0.0	0.949	0.051	0.0	0.893	0.051	0.996	0.004
	2H	96	0.109	0.005	0.917	0.016	0.063	0.005	0.948	0.047	0.057	0.917	0.026	1.0	0.0
	3H	95	0.109	0.0	0.926	0.0	0.074	0.0	0.901	0.099	0.073	0.911	0.016	1.0	0.0
	4H	96	0.124	0.0	0.926	0.0	0.074	0.0	0.889	0.111	0.063	0.895	0.042	0.995	0.005
	5H	92	0.096	0.0	0.932	0.010	0.057	0.0	0.948	0.052	0.047	0.938	0.016	0.990	0.010
	6H	96	0.068	0.0	0.962	0.0	0.038	0.0	0.962	0.038	0.038	0.940	0.022	1.0	0.0
Normandy	7H	96	0.141	0.005	0.927	0.0	0.068	0.0	0.901	0.099	0.078	0.885	0.036	0.984	0.016
	8H	96	0.146	0.0	0.938	0.0	0.063	0.005	0.891	0.104	0.068	0.880	0.052	1.0	0.0
	9H	94	0.138	0.011	0.888	0.0	0.101	0.005	0.915	0.080	0.064	0.910	0.027	1.0	0.0
Nord-Picardie	10H	96	0.130	0.0	0.917	0.016	0.068	0.0	0.911	0.089	0.073	0.901	0.026	1.0	0.0
	11H	96	0.107	0.0	0.943	0.005	0.052	0.0	0.917	0.083	0.042	0.917	0.042	1.0	0.0
	12H	96	0.138	0.0	0.917	0.005	0.078	0.010	0.901	0.089	0.083	0.885	0.031	1.0	0.0
	13H	96	0.117	0.0	0.906	0.005	0.089	0.0	0.927	0.073	0.073	0.901	0.026	1.0	0.0
	14H	96	0.102	0.0	0.958	0.0	0.042	0.0	0.927	0.073	0.068	0.917	0.016	0.995	0.005
	15H	96	0.115	0.0	0.896	0.0	0.104	0.005	0.943	0.052	0.047	0.943	0.010	0.990	0.010
	16H	96	0.151	0.0	0.891	0.0	0.109	0.005	0.885	0.109	0.083	0.896	0.021	0.990	0.010
	17H	96	0.138	0.005	0.927	0.010	0.057	0.005	0.911	0.083	0.026	0.865	0.109	0.990	0.010
Champagne-Ardennes	18H	96	0.133	0.005	0.917	0.0	0.078	0.0	0.927	0.073	0.073	0.896	0.031	0.995	0.005
	19H	96	0.135	0.0	0.865	0.005	0.130	0.0	0.911	0.089	0.068	0.911	0.021	1.0	0.0
	20H	96	0.146	0.005	0.891	0.016	0.089	0.005	0.917	0.078	0.083	0.885	0.031	0.995	0.005
Lorraine	21H	96	0.156	0.0	0.885	0.005	0.109	0.010	0.891	0.099	0.052	0.911	0.036	1.0	0.0
	22H	96	0.148	0.0	0.901	0.0	0.099	0.0	0.917	0.083	0.078	0.891	0.031	0.984	0.016
	23H	96	0.138	0.0	0.938	0.0	0.063	0.0	0.875	0.125	0.083	0.885	0.031	0.984	0.016
	24H	48	0.104	0.0	0.938	0.0	0.063	0.010	0.938	0.052	0.052	0.906	0.042	1.0	0.0
		$n = 2270$													
Brittany	1A	96	0.013	0.0	1.0	0.0	0.0	0.0	0.974	0.016	0.0	1.0	0.0	1.0	0.0
	2A	96	0.008	0.0	1.0	0.0	0.0	0.0	0.984	0.026	0.0	1.0	0.0	1.0	0.0
	3A	96	0.016	0.0	1.0	0.0	0.0	0.0	0.974	0.026	0.0	1.0	0.0	0.995	0.005
	4A	85	0.015	0.0	1.0	0.0	0.0	0.0	0.971	0.029	0.0	1.0	0.0	1.0	0.0
Normandy	5A	96	0.031	0.0	1.0	0.0	0.0	0.0	0.917	0.083	0.0	1.0	0.0	1.0	0.0
	6A	99	0.015	0.0	1.0	0.0	0.0	0.0	0.960	0.040	0.0	1.0	0.0	1.0	0.0
	7A	96	0.029	0.0	1.0	0.0	0.0	0.0	0.958	0.042	0.0	1.0	0.0	0.984	0.016
	8A	96	0.003	0.0	1.0	0.0	0.0	0.0	0.984	0.016	0.0	1.0	0.0	1.0	0.0
		$n = 760$													
Brittany	1S	86	0.012	0.0	1.0	0.0	0.0	0.0	0.977	0.023	0.0	1.0	0.0	1.0	0.0
	2S	87	0.003	0.0	1.0	0.0	0.0	0.0	0.994	0.006	0.0	1.0	0.0	1.0	0.0
	3S	93	0.005	0.0	1.0	0.0	0.0	0.0	0.989	0.011	0.0	1.0	0.0	1.0	0.0
Normandy	4S	75	0.033	0.0	1.0	0.0	0.0	0.0	0.947	0.053	0.0	0.987	0.013	1.0	0.0
	5S	90	0.019	0.0	1.0	0.0	0.0	0.0	0.983	0.017	0.022	0.978	0.0	1.0	0.0
	6S	86	0.038	0.0	1.0	0.0	0.0	0.0	0.942	0.058	0.023	0.971	0.006	1.0	0.0
Nord-Picardie	7S	95	0.024	0.0	1.0	0.0	0.0	0.0	0.953	0.047	0.0	1.0	0.0	1.0	0.0
	8S	92	0.087	0.0	0.957	0.0	0.043	0.0	0.913	0.087	0.033	0.935	0.033	1.0	0.0
	9S	92	0.068	0.0	0.995	0.0	0.005	0.0	0.935	0.065	0.054	0.940	0.005	0.995	0.005
	10S	50	0.060	0.0	1.0	0.0	0.0	0.0	0.929	0.071	0.024	0.952	0.024	1.0	0.0
Champagne-Ardennes	11S	48	0.030	0.0	1.0	0.0	0.0	0.0	0.920	0.080	0.020	0.980	0.0	1.0	0.0
	12S	94	0.112	0.0	0.952	0.0	0.048	0.0	0.915	0.085	0.059	0.910	0.032	1.0	0.0
	13S	93	0.126	0.0	0.946	0.0	0.054	0.0	0.892	0.108	0.081	0.887	0.032	1.0	0.0
		$n = 1081$													

a mean of 12 per population, but only four genotypes were detected among anholocyclic populations with an average of 2.7 per population. Moreover, 95 per cent of the latter individuals belonged to a single allozyme genotype (homozygous for the common allele at all four loci). Multidimensional scaling of genetic distances among all spring populations revealed a clear genetic divergence between the group of 24 holocyclic populations and the eight anholocyclic populations (Fig. 2).

Genetic composition of summer populations

Summer populations of *R. padi* showed significant regional variation in gene frequencies. Populations from western France (Brittany and Normandy) showed similar allele frequencies ($P > 0.05$) but these were significantly different from those in the north-eastern regions (Nord-Picardie, Champagne-Ardennes) at both *Sdh* and *Pep*. The only exception was for population 7S (Nord-Picardie) which showed no significant difference from western populations ($P > 0.05$) in allelic composition. In addition, multilocus genotype diversity was much higher in the north-eastern than the western populations. Summer populations from western France showed allele frequency distributions that were not different from those of anholocyclic populations ($P = 0.70$), but significantly different from those of holocyclic populations ($P < 0.001$). Conversely, allele frequencies of the north-eastern populations were not different from those of spring holocyclic populations ($P = 0.75$), but significantly different from anholocyclic populations ($P < 0.001$). Multiple comparisons of means using the Bonferroni test showed that heterozygosities of summer populations from Champagne-Ardennes and holocyclic populations in spring were not different ($P = 0.109$) but were both significantly different from those of summer populations from western France and anholocyclic populations in spring ($P < 0.001$). Summer populations from Nord-Picardie showed heterozygosities intermediate between those of anholocyclic and holocyclic populations (Table 1).

Multidimensional scaling of genetic distances among summer populations (Fig. 3) revealed clear regional differentiation, with populations from Champagne-Ardennes in one group and those from Brittany and Normandy in another. Populations from Nord-Picardie showed an intermediate position between western and north-eastern populations on the scattergram which can be related to their specific mean heterozygosities.

Summer populations (Table 2) again showed very low F_{IS} values, but F_{ST} values were higher than for holocyclic populations, reflecting the gene differentiation among summer populations.

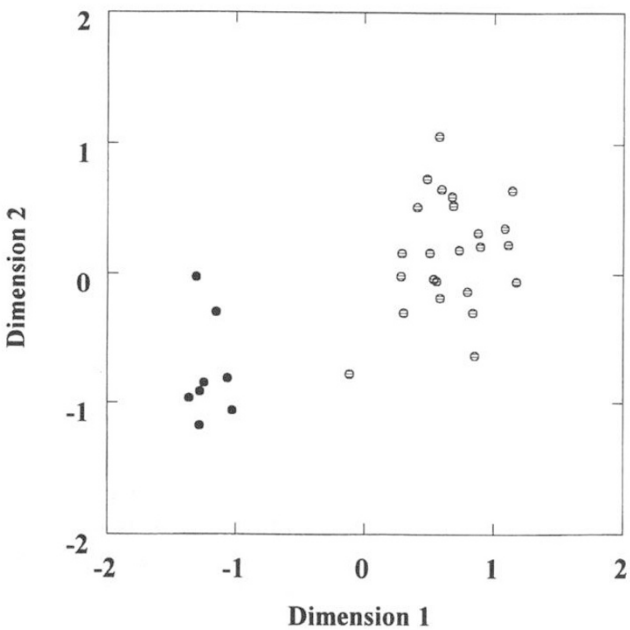

Fig. 2 Two-dimensional scaling of Rogers's genetic distances among spring populations of *Rhopalosiphum padi* collected on their primary host (holocyclic populations, ⊖) or their secondary hosts (anholocyclic populations, ●).

Discussion

Populations of *R. padi* in France possessed higher allelic diversity at the four polymorphic loci (12 alleles vs. seven) than their Canadian counterparts

Table 2 *F*-statistics for holocyclic and summer populations of *Rhopalosilphum padi*

Locus	F_{IS}	F_{IT}	F_{ST}
(a) Holocyclic populations			
Sdh	−0.0191	−0.0156	0.0035
Pgm	−0.0198	−0.0187	0.0011
Pep	−0.0377	−0.0386	0.0008
Aat	−0.0058	−0.0041	0.0017
All loci	−0.0259	−0.0247	0.0011
(b) Summer populations			
Sdh	0.0307	0.0318	0.0615
Pgm	−0.0119	0.0051	0.0168
Pep	−0.0021	0.0279	0.0299
Aat	0.0009	−0.0001	−0.0010
All loci	−0.0024	0.0209	0.0233

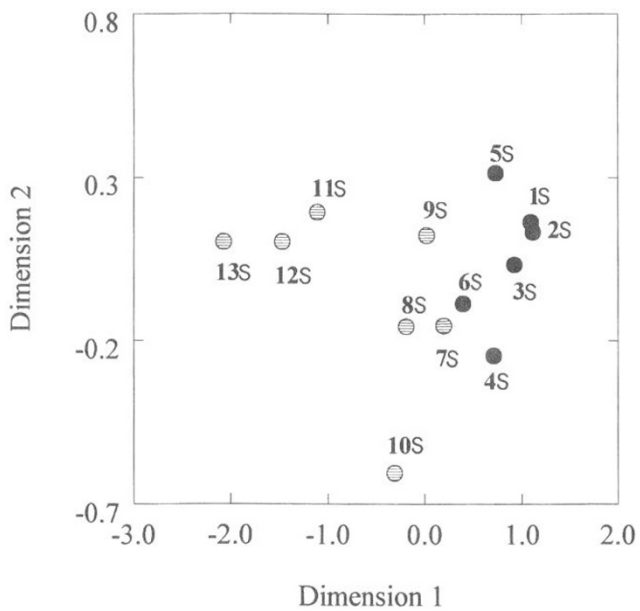

Fig. 3 Two-dimensional scaling of Rogers's genetic distances among summer populations of *Rhopalosiphum padi* collected on their secondary hosts in western (●) or eastern (○) France.

(Simon & Hebert, 1995), but similar diversity to English populations (Loxdale & Brookes, 1988). Canadian populations also showed differences in allele frequency distribution when compared with European ones. In particular, the frequency of the $Pep^{1.45}$ allele was higher in Canadian than European populations. Holocyclic populations in France also showed the genetic attributes of bisexual species, such as the congruence of genotypic frequencies to Hardy–Weinberg equilibrium and the absence of linkage disequilibrium (data not shown), as is typical for cyclic parthenogens (Hebert, 1987). These same populations showed little regional differentiation in genotypic frequencies as evidenced by very low F_{ST} values, providing further evidence for the high vagility of this species (Loxdale & Brookes, 1988; Simon & Hebert, 1995). The mean heterozygosity of individuals from holocyclic populations in France ($\overline{H} = 0.126$) was similar to that noted in Canadian populations ($\overline{H} = 0.149$) (Simon & Hebert, 1995). These figures are, however, inflated by the fact that the analysis focused solely on polymorphic loci. An earlier survey of 51 loci showed that individuals of *R. padi* were heterozygous at only 0.6 per cent of their loci (Simon & Hebert, 1995). Although this value is far lower than the 10 per cent average for invertebrates (Nevo, 1978), it is similar to values for other holocyclic aphids (Tomiuk & Wöhrmann, 1980; Hebert *et al.*, 1991).

This study has revealed several striking differences between the genetic characteristics of holocyclic and anholocyclic populations of *R. padi* in France (Table 3). As a group, anholocyclic populations showed lower heterozygosity, as evidenced by their near-fixation at two of the three loci which were commonly polymorphic in holocyclic populations. Evidence for asexual reproduction in anholocyclic populations was also supported by their frequent Hardy–Weinberg deviations because of heterozygote deficit. Similar Hardy–Weinberg deviations have been reported in the aphid *Sitobion avenae* and attributed to its complete loss of sexual reproduction (Loxdale *et al.*, 1985). Holocyclic and anholocyclic populations of *R. padi* also show striking differences in genotypic diversity, with holocyclic populations containing four times as many clones as anholocyclic populations (12 vs. three). In fact, asexual populations of *R. padi* consisted of only one dominant allozyme clone that was widely distributed in France and which has apparently achieved tremendous ecological success, at least in the short-term. A comparable reduction in genotypic diversity has been demonstrated in obligately asexual populations of cladocerans when compared with their cyclically parthenogenetic relatives (Innes *et al.*, 1986; Hebert *et al.*, 1988).

This study has shown that the genetic composition of summer populations of *R. padi* in France depends on the regional balance between anholocyclic and holocyclic reproduction. Summer populations from western France, where winters are usually mild enough to allow parthenogenetic overwintering (Dedryver & Gellé, 1982), showed more genetic similarity with anholocyclic than holocyclic populations. Conversely, populations from north-eastern France, where cold winters eliminate parthenogenetic individuals, were genetically closer to holocyclic than anholocyclic populations. These results suggest that in regions with cold winters, summer populations are largely recruited from holocyclic clones, whereas in areas with milder winters, summer populations are mainly derived from anholocyclic clones. Intermediate situations, where summer populations are an admixture of types, were found in the north of France, confirming the results of earlier morphological studies (Simon *et al.*, 1991b).

Our results suggest that allozyme analyses can be employed to infer the dominant mode of reproduction employed by populations of *R. padi*. Although the incidence of sexual reproduction might be esti-

Table 3 Comparison of genotypic characteristics between holocyclic and anholocyclic populations of *Rhopalosiphum padi* based on allozyme analysis at four loci

Populations	Allelic variation*	No. of multilocus genotypes	Heterozygosity	Hardy–Weinberg deviation
Holocyclic	*Sdh, Pep* and *Pgm*	<7 up to 38	$\overline{H} \geq 0.07$	none or rare
Anholocyclic	*Pgm* only	<4	$\overline{H} \leq 0.03$	frequent

*Loci were considered polymorphic if the mean frequency of the common allele was <0.95.

mated more accurately using DNA fingerprinting (Brookfield, 1992), allozyme analysis is both more rapid and less expensive. However, before employing genotypic markers to assess the relative proportion of holocyclic and anholocyclic clones, there is a need to establish that the genetic differences between these groups are persistent. It is, for example, possible that genotypic diversity in anholocyclic populations undergoes attrition throughout the winter. It also remains important to analyse how host alternation between grasses and *P. padus* affects the genetic structure of holocyclic populations, by assaying the autumn and spring generations on the primary host.

The present study has indicated that anholocyclic populations of *R. padi* in France have lower levels of heterozygosity than their holocyclic counterparts. This difference leads to a reduction of heterozygosity on secondary as opposed to primary hosts in regions dominated by anholocyclic clones. A congruent pattern has been detected in Canadian populations of *R. padi*, suggesting that anholocyclic clones in North America also have lower levels of heterozygosity than their holocyclic counterparts. As similar differences have been reported in other species, such as *Aphis pomi* (Singh & Rhomberg, 1984) and *Macrosiphum rosae* (Tomiuk & Wöhrmann, 1984), there appears to be general evidence that obligately parthenogenetic lineages of aphids are less heterozygous than their cyclically parthenogenetic counterparts.

The diminished level of heterozygosity in anholocyclic clones of aphids has three potential explanations, each of which has important biological implications. If transitions to asexuality have occurred infrequently, then lowered heterozygosity may have arisen through the chance fixation of the commonest homozygous genotypes. If, on the other hand, transitions to obligate parthenogenesis occur frequently, then the loss of diversity must arise either from selection following transitions to asexuality or from the mechanism leading to asexuality itself. The loss of variation through selection would result if rare alleles are maintained by their selective advantage on the primary host or if heterozygosity enhances fitness in the annual host cycle. The restriction of anholocyclic clones to the secondary host would then lead to the elimination of rare alleles. Alternatively, there may be a simple genetic explanation for the lack of variation. If, for example, the genes controlling obligate parthenogenesis are both rare and recessive (which seems to be the case in aphids; Blackman, 1972), then asexual lineages will frequently arise as a result of inbreeding, which would be reflected by their diminished heterozygosity at other loci. Although discrimination between these three hypotheses will require further work, their resolution seems possible. Comparative studies of mtDNA diversity in holocyclic and anholocyclic lineages would, for instance, make it possible to ascertain the number of occasions on which anholocycly has evolved.

Genetic studies have now made it clear that the routes to obligate asexuality are varied. All parthenogenetic vertebrates, as well as many asexual invertebrates, are far more heterozygous than their closest sexual relatives, reflecting their origin through interspecific hybridization. Different mechanisms, such as sex-limited meiosis suppression or infectious agents, have lead to the generation of other obligately asexual lineages, but in these cases the heterozygosity of parthenogens mirrors that of their parent taxa. Aphids appear to be one of the few groups in which transitions to asexuality lead to diminished heterozygosity. Hence further work on these organisms may well reveal a novel pathway to parthenogenesis.

Acknowledgements

The authors thank J. P. Gauthier for help with data analysis. T. J. Crease and two anonymous reviewers provided useful comments on an earlier version of the manuscript.

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