Original article

Macrogeographic and fine-scale genetic structure in a North American oak species, *Quercus rubra* L

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Summary — Northern red oak, *Quercus rubra* L, is a widely distributed forest-dominant tree in North America. In this paper, we present the results of 2 studies examining macrogeographic and fine-scale genetic structure in the North American oak species *Quercus rubra* L. The first study used allozymes as genetic markers to examine the distribution of genetic variation within and among 10 widely distributed populations in midwestern USA. Our results revealed a high level of genetic variability within the species and a moderate level of genetic differentiation among 10 populations sampled (F_{st} = 0.092). In the second study, we evaluated fine-scale genetic structure of northern red oak in a single forest site in Missouri, USA. First, we used F-statistics to determine whether subpopulations in adjacent microhabitats on the scale of 1 ha show genetic differentiation within a 4-ha plot. Our findings showed very low values of differentiation (F_{st} = 0.011). However, we also used a statistical technique called spatial autocorrelation analysis to evaluate the spatial dispersion of alleles within a 4-ha mapped plot. These analyses revealed that genetic structure exists on a much smaller scale. Using 3 different algorithms, we found that near-neighbors have significant spatial autocorrelation which suggests that family structure occurs within the study population.

population genetic structure / genetic variation / genetic differentiation / isozymes / spatial autocorrelation / *Quercus rubra*

Résumé — **Structure génétique du chêne rouge d'Amérique à l'échelle géographique et à celle du peuplement.** *Le chêne rouge d'Amérique (Q rubra L) est une espèce très répandue en Amérique du Nord. Cette contribution présente les résultats d'une analyse de la structure génétique de cette espèce faite à l'échelle géographique et du peuplement. La première partie concerne l'étude de l'organisation de la diversité génétique faite à partir de 10 populations éloignées les unes des autres et issues du Midwest des États-Unis et basée sur les isozymes. Les résultats ont montré une diversité génétique élevée à l'intérieur de l'espèce et une différenciation génétique moyenne entre les 10 populations étudiées (*F_{st}* = 0,092). Dans la seconde partie, l'étude a porté sur la structure génétique à l'intérieur d'un peuplement donné situé dans une forêt de l'État de Missouri (États-Unis). Tout d'abord les* F *statistiques ont été utilisées pour estimer le niveau de différenciation entre sous-populations d'une surface d'un ha, l'ensemble couvrant une surface de 4 ha. Les résultats ont montré que ce niveau restait faible (*F_{st}* = 0,011). Dans un second temps, les techniques d'autocorrélation spatiale ont révélé que la population était génétiquement structurée à une échelle plus fine. L'utilisation de 3 algorithmes différents a montré que les proches voisins au sein du peuplement sont génétiquement liés, indiquant qu'une structure familiale existe au sein de la population.*

structure génétique / variabilité génétique / différenciation génétique / isozymes / autocorrélation spatiale / Quercus rubra

INTRODUCTION

The distribution of genetic variability in a species is the outcome of gene flow, natural and artificial selection and genetic drift. Among wind-pollinated tree species, we expect widespread gene flow within and among populations (Loveless and Hamrick, 1984) and opportunities for genetic drift to be minimal. However, population differentiation and subdivision will occur if either pollen or seed dispersal is restricted or natural selection on a local scale is strong (Slatkin, 1973; Endler, 1977). Populations which occur in heterogeneous environments may be susceptible to locally varying selection pressures which could cause genetic subdivision of local populations (Wright, 1943). The extent to which population subdivision occurs in tree populations is valuable to know because the spatial scale of genetic differentiation may influence the evolutionary dynamics of the populations.

Northern red oak, *Quercus rubra* L, is a major forest-dominant tree species in North American deciduous forests (Braun, 1950). It is widely-distributed, ranging from southern Quebec and Ontario south to northern Florida, and from the eastern edges of Texas, Oklahoma and Kansas up through Iowa east to southeastern Minnesota (Schopmeyer, 1974). In this paper, we present the results of 2 studies examining macrogeographic and fine-scale genetic structure in the North American oak species *Q rubra* L. The first study used allozymes as genetic markers to examine the distribution of genetic variation within and among 10 widely distributed populations. A frequently-used method of describing genetic structure is hierarchical F-statistics analysis (Wright, 1951, 1965). These statistics describe the extent to which genetic variation is distributed within the total population (F_{it}), among subpopulations (F_{st}) and among individuals within subpopulations (F_{is}). F_{st} or G_{st}, a similar index derived by Nei (1973), provide a measure of genetic differentiation among subpopulations.

In the second study, we evaluated fine-scale genetic structure of northern and oak in a single forest site in Missouri, USA. First, we examined genetic structure within a location among adjacent subpopulations of *Q rubra* using F-statistics. If such structure exists, it suggests that differential selection may be responsible because gene flow is not likely to be restricted in this wind-pollinated species (Sork, unpublished data). Because F-statistics are not always sensitive enough to detect patterns of genetic patchiness, especially within the subpopulation (Heywood, 1991), we also used spatial autocorrelation statistics. These have been proposed as a means of identifying the scale of genetic structure without prior knowledge about that scale (Sokal and Oden, 1978; Epperson and Clegg, 1986; but see Slatkin and Arter, 1991).

MATERIALS AND METHODS

The sampling sites for the macrogeographical study were 10 locations situated in the midwestern United States (fig 1, table I). These sites include northern, southern and western limits of the distribution of *Q rubra*. During June and July of 1990 and 1991, we collected leaf tissue from 25 adults at each location. Individual trees sampled were > 10 m apart.

The intensive study site for the study of fine-scale genetic structure was located at Tyson Research Center, St Louis County, Missouri, USA, an 800-ha ecological reserve administered by Washington University. Tyson (38° 31'N, 90°33'W) is located on the northeastern end of the Ozark Plateau. The oak–hickory forest at Tyson comprises approximately 600 ha and is contiguous with approximately 2000 ha of forest on adjacent public and privately-owned property. Within the study site was located a 4-ha plot of

oak-hickory forest which had been permanently gridded into 20 m x 20 m quadrants with all individual trees with breast height diameter *(DBH)* > 2.5 cm labeled and mapped (Hampe, 1984). This plot included 4 microhabitats: north-facing slope which had the greatest inclination (mean = 20°, range = 15°–30°); southwest-facing (mean = 15°, range = 12–18°); and west-facing slope with intermediate inclination (mean = 13°, range = 10–15°) which we divided into lower west-facing slope and upper west-facing slope. During the summer of 1990, we collected leaf samples from all red oak adult trees (n = 226) on this plot with *DBH* > 20 cm.
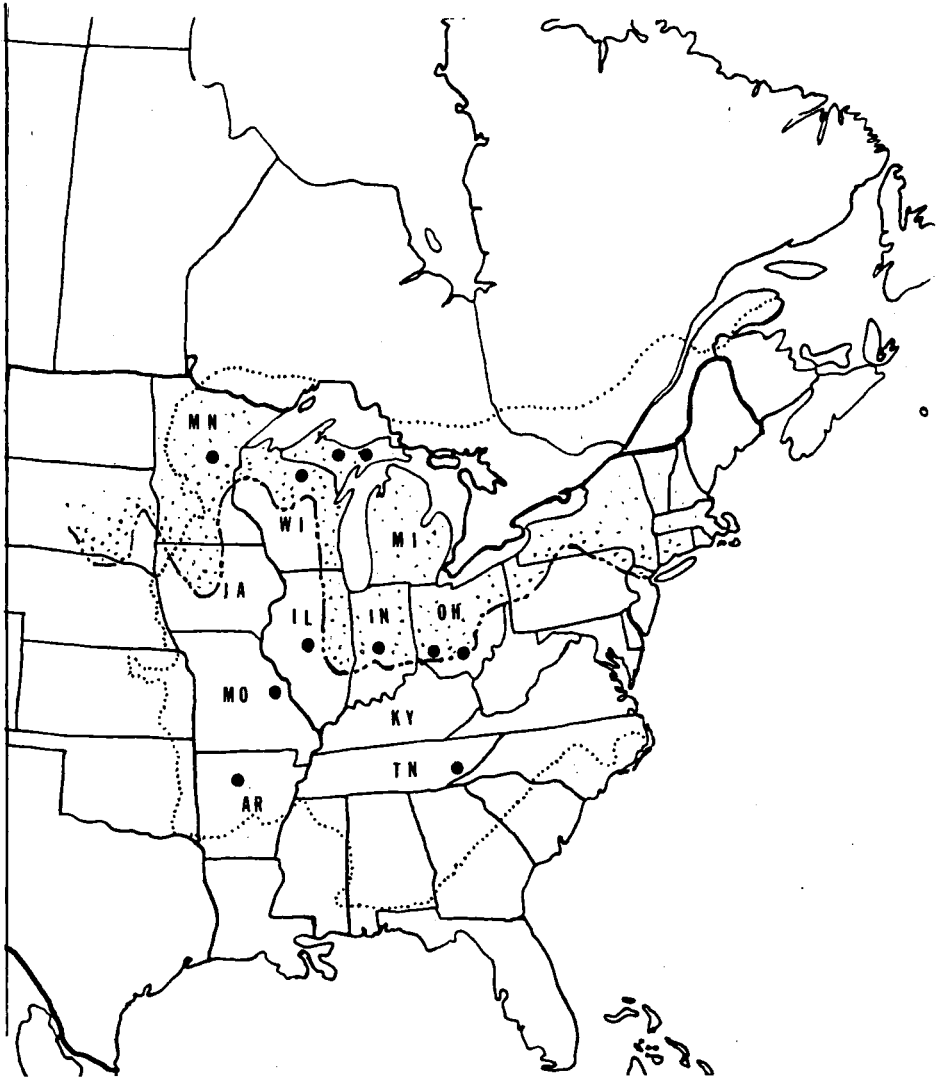
Fig 1. Map of eastern United States and Canada labeled with study populations of *Quercus rubra*. The dotted line indicates the limits of its range of distribution. The dashed line with dotted area above shows the area of the most recent glaciation, the Wisconsin.

Table I. Genetic variability measures for 10 populations of *Quercus rubra* based on 15 isozyme loci.

Nearest city, state	Latitude, longitude	Mean sample size per locus	Alleles/locus mean (SE)		Polymorphic index % [a]	Heterozygosity [b] Mean (SE)	
Russelville, AR	35°11'N, 93°30'W	24.9	2.3	(0.4)	41.7	0.196	(0.196)
Knoxville, TN	35°35'N, 84°00'W	24.7	2.3	(0.4)	50.0	0.167	(0.062)
Indianapolis, IN	39°15'N, 86°15'W	20.8	2.3	(0.3)	58.3	0.191	(0.058)
Colombus, OH	39°30'N, 83°30'W	19.9	2.1	(0.3)	58.3	0.145	(0.059)
Springfield, IL	39°40'N, 89°39'W	25.0	2.0	(0.3)	50.0	0.179	(0.059)
Lima, OH	40°15'N, 86°15'W	24.0	1.8	(0.2)	50.0	0.165	(0.057)
Wausau, WI	46°00'N, 89°00'W	24.6	2.1	(0.3)	50.0	0.199	(0.074)
Duluth, MN	46°00'N, 92°45'W	20.8	2.0	(0.3)	58.3	0.245	(0.073)
Manistique, MI	46°15'N, 86°30'W	24.9	2.0	(0.3)	46.7	0.197	(0.062)
Marquette, MI	46°30'N, 87°00'W	24.9	1.9	(0.3)	33.3	0.178	(0.070)

[a] A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95.
[b] Unbiased estimate (see Nei, 1978).

For both studies, leaves were collected from each individual with clipper poles, shot gun or sling shot and then kept on ice until transported back to the laboratory. Leaves were stored at –75 °C until ready for electrophoretic analysis. Starch–gels were run following the techniques of Gottlieb (1981) and Soltis *et al* (1983) using a phosphate extraction buffer (Mitton *et al*, 1977), modified to 10% polyvinylpyrrolidone (Manos and Fairbrothers, 1987). The recipes for all enzymes were modified from Soltis *et al* (1983). We used buffer system 1 from Soltis *et al* (1983) to detect 6-phosphogluconic dehydrogenase (6PGD, EC 1.1.1.44), shikimate dehydrogenase (SDH, EC 1.1.1.25), phosphoglucomutase (PGM, EC 5.4.2.2), isocitrate dehydrogenase (IDH, EC 1.1.1.42) and malate dehydrogenase (MDH, EC 1.1.1.37). Buffer system 2 (Soltis *et al*, 1983) was used for peroxidase (PER, EC 1.11.1.7). Buffer system 6 (Soltis *et al*, 1983) was used for phosphoglucoisomerase (PGI, EC 5.3.1.9), triose-phosphate isomerase (TPI, EC 5.3.1.1), and acid phosphatase (ACPH, EC 3.1.3.2). Buffer system 8 (Haufler, 1985) was used for fluorescent esterase (FES, EC 3.1.1-) and leucine- amino-peptidase (LAP, EC 3.4.11.1). All these enzymes have shown inheritance patterns consistent with an interpretation of Mendelian inheritance.

The *F*-statistics and genetic descriptive statistics for the 10 widely distributed populations and the 4 subpopulations within the intensive study plot were calculated using the program, BIOSYS-1 (Swofford and Selander, 1981). We used 15 loci for the macrogeographic analysis of genetic diversity and 11 polymorphic loci (0.99 level) for the estimation of *F*-statistics for both studies. For the spatial autocorrelation (SA) analysis of *Q rubra*, we selected the 3 most variable isozyme loci. The SA analysis was done using the program of Heywood (Dewey and Heywood, 1988). This program uses allozyme variation to calculate Moran's *I*, a coefficient of spatial autocorrelation (Sokal and Oden, 1978), which varies between + 1 (complete positive autocorrelation) and –1 (complete negative autocorrelation) for any comparison of 2 individuals. We used 3 methods to calculate Moran's *I*: nearest-neighbor maps which compare only 2 individuals, Gabriel-connected maps which compare several neighboring individuals, and correlograms which examine all pairs of individuals within a specified distance class as a function of distance class. This latter method provides insight about the scale of genetic structure if it exists within the distance classes examined (for a more detailed description of these methods, see Sokal and Oden, 1978).

RESULTS AND DISCUSSION

Macrogeographic genetic structure

Individual populations of *Q rubra* maintain relatively high levels of genetic variation (table I). We found that the average percent polymorphism across populations was 43%, the average number of alleles/locus was close to 2 (mean = 1.97), and the mean heterozygosity ranged between 0.136 and 0.231 with a mean of 0.167. We caution that these data may be biased upward because we selected loci that are likely to be polymorphic. At the species level, we observed 3.19 alleles/locus with 94.1% showing some level of polymorphism in at least 1 population.

Our estimate of 0.167 average heterozygosity is less than a mean value of 0.270 reported for a sample of 11 studies of conifer species (Mitton, 1983). However, our values are similar to those found in *Q gam-*

belii and *Q macrocarpa* (Schnabel and Hamrick, 1990a) and 18 other North American oak species (Guttman and Weigt, 1989). In contrast, a mean heterozygosity of 0.081 was observed for 7 species of oaks in New Jersey, USA (Manos and Fairbrothers, 1987) but this area sampled is much smaller than that tested in other studies.

The 10 populations surveyed showed a moderate degree of genetic differentiation based on the analysis of 11 polymorphic loci (overall F_{st} = 0.092, table II). This estimate of genetic differentiation among populations is at the high end of the range of values expected for wind-pollinated, long-lived woody species (G_{st} = 0.07–0.09; Hamrick and Godt, 1989) and in the middle of the range of G_{st} values summarized for conifer species by El-Kassaby (1990), who reported a ranged of G_{st} values from 0 to 16.2% from 54 studies. However, our estimate of F_{st} is similar to that Schnabel and Hamrick (1990a) measured (G_{st} = 0.076

Table II. Summary of *F*-statistics across 10 subpopulations of *Quercus rubra* occurring throughout midwestern USA (see fig 1 for locations) and across 4 microhabitats within 1 location in Missouri, USA. Analyses are based on 11 polymorphic loci for sets of analyses. Arithmetic means of the *F*-values are given.

Locus	Across midwestern USA			Across adjacent subpopulations		
	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{IT}
PGI-1	0.650	0.665	0.042	−0.006	0.002	0.005
PGI-2	0.070	0.232	0.174	−0.015	0.010	0.025
TPI-1	−0.023	−0.004	0.018	−0.012	−0.003	0.009
PGM-2	−0.056	0.090	0.138	−0.036	−0.031	0.005
IDH	0.040	0.085	0.046	−0.060	−0.055	0.005
6-PGD	0.196	0.234	0.047	−0.052	−0.028	0.023
SDH	−0.054	0.036	0.085	0.023	0.024	0.001
FEST-1	−0.050	−0.043	0.007	−0.029	−0.027	0.002
FEST-2	−0.091	−0.064	0.025	−0.077	−0.062	0.013
LAP	0.568	0.592	0.055	0.061	0.080	0.020
PER-1	0.180	0.243	0.077	0.270	0.282	0.017
Mean	0.100	0.183	0.092	0.067	0.077	0.011

for 19 populations of *Q macrocarpa* and G_{st} = 0.11 for 18 populations of *Q gambelii*), but higher than that observed for 8 populations of *Q rubra* in Pennsylvania, USA (Schwarzmann and Gerrold, 1991). The pattern of genetic differentiation that we observed in *Q rubra* is likely to be due to a combination of factors. Because northern red oak occupies a great latitudinal range, natural selection due to environmental factors associated with that gradient may influence population differentiation. In addition, because of the glacial history of midwestern United States, bottleneck effects, genetic drift and uneven migration patterns may all contribute to a high degree of genetic differentiation (Schlarbaum *et al,* 1982).

Fine-scale genetic structure

The pattern of genetic variation based on 11 polymorphic loci measured on individual adults within the intensive study plot in Missouri is relatively high (table III) and quite comparable to the values reported for the macrogeographic survey (table I). Moreover, even within the microhabitats which are in the order of 1 ha in area, northern red oak maintains a large amount of variation. Although the microhabitats have unequal sample sizes (see table III), the general conclusions from these data should not be biased. That is, on every spatial scale–microhabitat, location and species, northern red oak has moderately high allelic diversity and heterozygosity.

We analyzed the genetic structure of our intensive study site and found that the amount of genetic differentiation across 4 microhabitats is extremely low (F_{st} = 0.011, table II). This low estimate is consistent across all 11 loci, suggesting that selection or some other factor has not acted on any of the individual loci. Thus, for

this population, the hypothesis that isozyme loci are neutral may be valid. The average fixation index is also low (F_{is} = 0.067) which suggests that the adult subpopulations are not inbred. This value is slightly lower than the average level observed across populations (F_{is} = 0.10, table II).

Our finding that genetic differentiation across adjacent microhabitats is extremely low indicates that little population subdivision has occurred on this scale. However, this result contrasts with findings from a reciprocal transplant experiment at the same study site where we found evidence for local adaptation in seedling populations (Sork *et al,* in press). In that study, a reciprocal transplant experiment utilizing acorns from maternal parents living in each microhabitat revealed that percent leaf damage by insect herbivores was lower on seed-

Table III. Genetic variability measures based on 11 polymorphic loci and mean sample size for 4 subpopulations of *Quercus rubra* located in adjacent microhabitats within a 4-ha plot in an oak–hickory forest in Missouri, USA. Microhabitat types are upper-west facing slope (UW), lower-west facing slope (LW), north-facing slope (NO) and southwestern facing slope (SW).

Parameter	UW	LW	NO	SW
Mean sample sizes	36.5	45.7	81.3	53.9
Mean alleles/locus	2.27	2.45	2.82	2.36
Polymorphic index (%)[a]	54.6	63.6	72.7	54.5
Mean heterozygosity[b]	0.182	0.213	0.214	0.198

[a] A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95. [b] Unbiased estimate (see Nei, 1978).

lings grown in the maternal microhabitat. Consequently, the set of isozyme genetic markers as measured on the adult population in this study area seems neutral with respect to the selection of characters related to resistance to herbivores. This result indicates that quantitative characters which are related to seedling performance may show significantly different patterns of genetic differentiaton than isozyme genetic markers.

Our additional analysis of fine-scale genetic structure using spatial autocorrelation analysis on 3 loci (table IV) suggests that structure may exist on a scale smaller than the microhabitat. We found that PER-1 and FEST-2 had positive SA for both the Gabriel-connected map and the nearest-neighbor map at all 6 alleles (table IV). Moreover, Moran's *I* was significantly greater than 0 for 2 alleles of PER-1 using the Gabriel-connected map and 1 allele of PER-1 and 2 alleles of FEST-2 using the nearest-neighbor map. Although the Gabriel-connected map provides a more powerful test of SA due to the greater number of

connections (Dewey and Heywood, 1988), both algorithms demonstrate a pattern of spatial autocorrelation. The 2 different methods yield slightly different mean distances of nearest-neighbors with the Gabriel-connected map having a larger radius than the nearest-neighbor map (table V). However, the scale of these differences is similar.

The correlogram suggests positive autocorrelation for the 5 m distance class which was significant ($P < 0.05$) for the FEST-2 and PER-1 loci (fig 2). Because this first distance class is the most likely one to reveal autocorrelation if there is isolation by distance, we only used this class to test for significance from zero. After that distance class, the values vary around zero with an occasional value occurring much higher or lower but no clear pattern resulting. Consequently, we conclude that the correlogram demonstrates a pattern of high relatedness among near-neighbors which is consistent with previous analyses based on Gabriel-connected and nearest-neighbor maps but random fluctuations after that distance.

Table IV. The coefficient of spatial autocorrelation (Moran's *I*) based on ranks, its standard deviation (SD) and the standard normal deviate (SND) testing the null hypothesis $I = 0$ (* = $P < 0.05$). The results are presented for 2 methods of pairing individuals along with the mean distance between pairs for each allozyme. Lower case letters indicate alleles.

| Allele	Gabriel-connected map				Nearest-neighbor map			
	I	SD	SND	Mean distance (m)	*I*	SD	SND	Mean distance (m)
PER-1a	0.039	0.0512	0.845	10.5	0.180	0.0813	2.271*	6.0
PER-1b	0.143	0.0512	2.878*		0.146	0.0813	1.859	
PER-1c	0.050	0.0512	1.180		0.095	0.0813	1.229	
PER-1d	0.098	0.0512	2.006*		0.124	0.0813	1.583	
FES-2a	0.054	0.0515	1.143	10.5	0.179	0.0827	2.218*	5.79
FES-2b	0.040	0.0515	0.858		0.163	0.0827	2.033*	
SDH-1a	−0.116	0.0505	−2.222*	10.1	−0.099	0.0790	−1.206	5.70
SDH-1b	0.010	0.0505	0.289		0.047	0.0790	0.651	
SDH-1c	−0.030	0.0505	−0.509		0.003	0.0790	0.097	
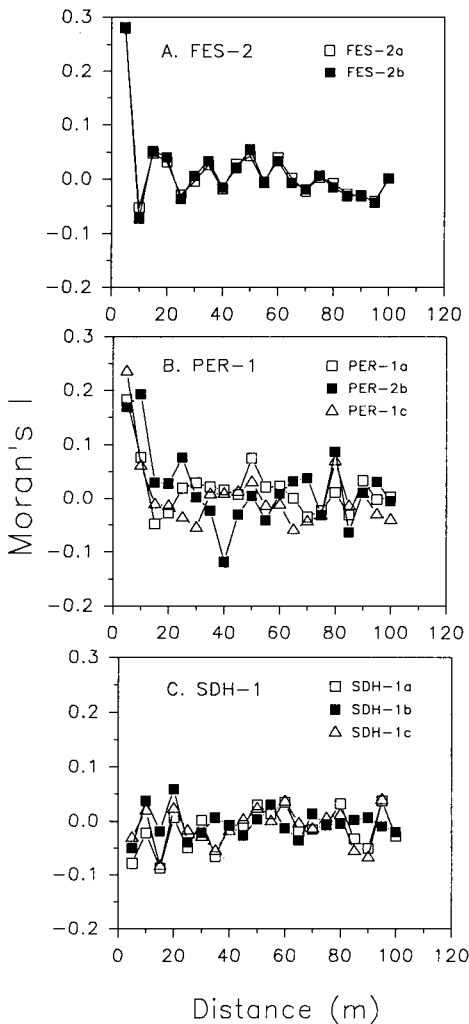
Fig 2. Moran's *I* as a function of distance class for alleles at 3 isozyme loci, FEST-2 (A), PER-1 (B) and SDH-1 (C). The *X*-axis value indicates the maximum value in that distance class; lower case letters indicate alleles.

In contrast to this pattern of near-neighbor autocorrelation, SDH showed a significant negative SA at 1 of the 3 allozymes using a Gabriel-connected map

and none of the allozymes using the nearest-neighbor map (table IV). This pattern was not significant in the correlogram (fig 2) where all 3 alleles at the 5 m distance class have slightly negative values of Moran's *I*. This result is too weak to determine whether selection or disassortative mating is acting on the SDH1^a allele or whether the correlation is spurious.

While it is not easy to infer mechanisms from spatial autocorrelation analyses (Slatkin and Arter, 1991), we suggest that this pattern is more likely due to restricted gene dispersal than spatially variable selection. Because we know that *Q rubra* in this population and elsewhere (Schwartzmann and Gerhold, 1991; Sork *et al,* 1992) has high outcrossing rates, it is unlikely that pollen dispersal is restricted to the scale of 5 m. However, seed dispersal by mammals is restricted and often results in dispersal distances of less than 10 m (Sork, 1984).

While it is also possible that acorns may be dispersed by birds at greater distances, if a large proportion of the acorn crop falls beneath the canopy or is removed only short distances by mammals, local family clusters may result. The spatial autocorrelation observed in this study is consistent with that scenario. Family clusters resulting from restricted seed dispersal have also been proposed for ponderosa pine (Linhart *et al,* 1981).

Our finding of significant spatial autocorrelation is similar to that found in *Gleditsia triacanthos* where the occurrence of significant autocorrelation at several loci for sampled juveniles indicates genetic substructuring that also might be due to family clusters (Schnabel and Hamrick, 1990b). In contrast, a study of *Pinus contorta* where individuals were sampled at 15-m intervals in 2 Washington, USA populations (Epperson and Allard, 1989) reported little autocorrealtion except for a few loci. Those authors concluded that long dis-

tance pollen and seed dispersal reduces the opportunity for genetic structure but selection may be affecting the genotypes at those significant loci. The *Pinus* results may differ from our oak results because dispersal of pine seeds differs dramatically from acorns. Until we see a broader range of studies which evaluates the genetic structure within tree populations, we cannot determine the extent to which this component of genetic variation is important.

ACKNOWLEDGMENTS

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