Spatial genetic structure within three sugar maple (*Acer saccharum* Marsh.) stands

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Approximately 100 trees were sampled and mapped in each of three natural Sugar Maple (*Acer saccharum* Marsh.) stands in northwestern Ontario. Starch-gel electrophoresis was used to resolve five polymorphic enzyme loci from bud tissue and spatial genetic structure was examined in each of the three stands using spatial autocorrelation techniques. A significant small scale genetic structure was detected in all stands and patch widths were inferred to be approximately 20–30 m. A non-random distribution of genotypes may be a reflection of restricted gene flow, selection and/or patchy establishment of genetically distinct cohorts.

Keywords: gene flow, genetic structure, Moran's *I*, spatial auto correlation.

Introduction

Most tree species are genetically diverse with the vast majority of their genetic variation residing within populations (Hamrick *et al.*, 1981; Boyle & Yeh, 1988). It is generally agreed that the distribution of this variation within populations is not likely to be random owing to the effects of factors such as limited seed and pollen dispersal and microhabitat selection (Levin & Kerster, 1974; Loveless & Hamrick, 1984; Turner *et al.*, 1982). Knowledge of genetic structure within populations is important to forest geneticists. For example, the existence of groups of related individuals could cause inbreeding that in turn may confound the analysis of wind-pollinated provenance or progeny tests, leading to overestimation of additive genetic variance and genetic gain (Namkoong, 1966; Squillace, 1974). In addition, if an assumption of a lack of substructure is in error, biased estimates of mating system parameters may result (Ennos & Clegg, 1982; Ritland, 1985).

Intuitively one might suspect the existence of substructuring within populations. However, the detection of a pronounced structure in natural populations of forest trees has largely eluded forest geneticists. A number of methods, most involving the use of allozymes as genetic markers, have been employed in an effort to detect and describe the genetic structure within stands. Methods have ranged from a simple visual inspection of maps depicting tree genotypes (Tigerstedt, 1973), to an examination of the correlation between complex genetic similarity measures and geo-

graphic proximity (Brunel & Rodolphe, 1985). While some investigations have revealed genetic structure (Sakai & Miyazaki, 1972; Coles & Fowler, 1976; Linhart *et al.*, 1981; Cheliak *et al.*, 1984; Knowles, 1984; Brunel & Rodolphe, 1985), it is often weak and others have indicated nothing but a random distribution of genotypes (Tigerstedt, 1973; Guries & Ledig, 1977; Roberds & Conkle, 1984). Recently, spatial autocorrelation statistics (Cliff & Ord, 1973; Sokal & Oden, 1978a) have gained popularity among those who study genetic structure within populations of forest trees and other plant communities (Waser, 1987; Dewey & Heywood, 1988; Epperson & Allard, 1989; Schoen & Latta, 1989; Knowles, 1990). Investigations of spatial autocorrelation in lodgepole pine (*Pinus contorta* ssp. *latifolia*; Epperson & Allard, 1989) and black spruce (*Picea mariana* (Mill.) B.S.P.; Knowles, 1990) have indicated that in the populations studied, the distribution of single-locus genotypes is nearly random.

Genetic variation within Sugar Maple (*Acer saccharum*, Marsh.) is well documented. A variation has been demonstrated in growth rates among provenances (Wendel & Gabriel, 1980), in sugar concentration among clones (Kriebel, 1989), in seed and fruit characters among and within provenances (Gabriel, 1978), and in allozyme frequencies among populations (Perry & Knowles, 1989). Ledig & Korbobo (1983) observed differentiation in physiological characteristics of progeny from stands separated by less than 0.8 km. However, allozyme analysis has indicated that only about 3 per cent of the total variation at individual loci

is among populations (Perry & Knowles, 1989). In the present study, we focus on the approximately 97 per cent of the variation thought to reside within stands. We applied spatial autocorrelation analysis to allozyme data of three naturally occurring Sugar Maple populations with the objective of determining whether the distribution of genotypes over space is random or structured within stands.

Methods

Three mature, naturally regenerated Sugar Maple stands were selected in northwestern Ontario. Stands 1 and 2 were located near Thunder Bay while stand 3 was located near Wawa. Sugar Maple grows at moderate densities as the principal species of locally disjunct stands at both locales. Bud tissue was collected from approximately 100 contiguous trees in each stand (stand 1, $n = 99$; stand 2, $n = 98$; stand 3, $n = 103$) and the positions of the sampled trees were mapped. The tissue was subjected to starch-gel electrophoresis and five polymorphic enzyme loci (*Ald-2*, aldolase, E.C.4.1.2.13; *Dia-3*, diaphorase, E.C.1.6.4.3; *Mdh-3*, malate dehydrogenase, E.C.1.1.3.7; *Pgi-2*, phosphoglucose isomerase, E.C.5.3.1.9; and *Pgm-1*, phosphoglucomutase, E.C.1.15.1.1) were resolved. Electrophoretic conditions were as previously described (Perry & Knowles, 1989). The genetic data was coded such that single trees received allele frequency values of 0.0, 0.5 or 1.0 for each allele of every locus.

For each stand, spatial autocorrelation analysis was conducted on the coded data of individual alleles of each locus using the FORTRAN program SAAP developed by Daniel Wartenberg. Alleles with a population frequency less than 0.02 were excluded and only one allele was considered at diallelic loci as the second allele would contribute identical information. Moran's I (Cliff & Ord, 1973; Sokal & Oden, 1978a) was estimated for each of 10 distance classes, the ranges of which were selected by equalizing sample sizes. Tests of significance ($\alpha = 0.05$), which followed equations given in Cliff & Ord (1973), were also performed by SAAP. Values of I significantly larger than the expected value of $E(I) = -(n-1)^{-1}$ indicate a greater similarity of individuals within that distance class than would be expected by chance, while values of I significantly lower than $E(I)$ signify less similarity among individuals within that class than would be expected were chance the only factor determining the spatial distribution of the allele in question.

Visual examination of spatial genetic structure was facilitated through the construction of correlograms. Overall significance of individual correlograms, each constructed from a series of non-independent I values,

was assessed using Bonferroni's criterion (Sakai & Oden, 1983).

Results

Spatial autocorrelation analysis yielded 8 out of 110, 13 out of 60, and 13 out of 130 significant Moran's I statistics for stands 1, 2 and 3, respectively (Table 1). Several observations were noteworthy. Seven of 30 test statistics for the shortest distance (class 1) were significant with the proportions per stand being 0.18, 0.50 and 0.15 for the three stands respectively. All of these significant I values were greater than $E(I)$, indicating that individuals possessing similar alleles were proximal more often than expected by chance alone. Throughout the midrange, mean I values tended to decrease in successive distance classes, which suggests that in this range pairs of individuals were generally less akin with increasing inter-tree distances. In the highest distance classes many of the significant I values were positive. The patterns associated with either positive or negative I values in these distance classes are difficult to ascertain. While negative autocorrelation is expected in higher distance classes where individuals occur on a gradient or cline (Sokal & Oden, 1978b), positive autocorrelation may result if the gradient is circular or symmetrical (Sokal & Oden, 1978b) or if patch distribution is 'regular' (Epperson & Clegg, 1986). The signs at high distance classes could also be influenced by certain patches occurring near the borders of the sampled area (Epperson & Clegg, 1986).

According to Sokal (1979), the distance at which a correlogram first intercepts the abscissa [in this case $E(I)$] represents the shortest side of an irregularly

Fig. 1 Mean correlograms for each of three sugar maple stands: stand 1 (●), Stand 2 (■) and Stand 3 (▲). The dotted line at -0.01 is $E(I)$, the expected value of Moran's I .

Table 1 Spatial autocorrelation coefficients (Moran's I) over 10 distance classes for allozymes in three Sugar Maple populations

Stand	Locus	Allele	Distance class†										Significance of correlogram	Allele frequency
			1	2	3	4	5	6	7	8	9	10		
1	<i>Ald-2</i>	1	0.09*	0.10**	-0.05	0.00	-0.04	-0.07	-0.11*	-0.01	0.00	-0.02	ns	0.79
	<i>Dia-3</i>	1	0.02	-0.01	0.07	-0.01	-0.02	0.01	-0.02	-0.02	-0.06	-0.06	ns	0.88
	<i>Mdh-3</i>	1	0.02	0.04	-0.05	-0.01	-0.03	0.00	-0.01	0.02	-0.11*	0.05	ns	0.92
		2	-0.03	0.03	-0.03	0.01	-0.02	0.01	0.01	-0.05	-0.05	0.01	ns	0.06
		3	0.03	0.04	-0.03	-0.02	-0.03	-0.04	-0.04	0.04	-0.08*	0.04	ns	0.02
	<i>Pgi-2</i>	1	-0.07	0.01	0.02	0.03	-0.05	-0.03	-0.03	0.03	-0.01	-0.01	ns	0.90
		2	-0.02	0.04	-0.07	-0.01	-0.01	0.01	-0.06	-0.04	0.09*	-0.03	ns	0.06
		5	-0.02	-0.03	0.07*	-0.02	-0.04	-0.03	-0.04	-0.04	0.06	-0.02	ns	0.03
	<i>Pgm-1</i>	1	0.14**	-0.01	-0.04	-0.09	-0.07	-0.03	-0.04	0.03	0.04	-0.04	**	0.85
		2	0.07	-0.06	-0.04	-0.02	0.00	0.00	0.03	-0.04	-0.01	-0.04	ns	0.07
2		3	-0.01	-0.03	0.00	-0.03	-0.01	-0.04	-0.03	0.04	0.02	-0.01	ns	0.08
	<i>Ald-2</i>	1	0.06	0.01	-0.04	0.05	0.02	-0.06	0.00	-0.15**	0.07	-0.06	*	0.82
	<i>Dia-3</i>	1	0.11**	-0.12*	-0.01	0.04	0.00	-0.09	-0.10*	0.01	0.07*	-0.01	ns	0.88
	<i>Mdh-3</i>	1	0.03	-0.03	-0.01	-0.02	0.03	-0.07	0.10**	-0.05	-0.05	-0.04	ns	0.96
		1	0.12**	-0.05	0.05	0.00	-0.01	-0.13**	-0.09	-0.09	-0.04	-0.06*	*	0.58
	<i>Pgm-1</i>	2	0.03	-0.03	0.00	-0.03	0.06	-0.05	-0.04	0.02	-0.03	-0.03	ns	0.19
		3	0.08*	-0.02	0.02	-0.02	-0.10*	-0.10*	-0.03	-0.05	0.09**	0.04	ns	0.23
	<i>Ald-2</i>	1	-0.02	0.02	-0.01	-0.04	0.07	0.02	0.01	-0.09	-0.01	-0.04	ns	0.68
	<i>Dia-3</i>	1	0.01	-0.06	0.04	-0.04	0.00	0.02	-0.05	-0.01	0.01	0.00	ns	0.86
		2	0.00	-0.06	0.03	-0.03	-0.03	-0.01	-0.02	-0.01	0.01	0.01	ns	0.09
3		3	-0.03	-0.03	-0.01	0.00	0.07*	0.00	-0.04	-0.00	-0.03	-0.02	ns	0.04
	<i>Mdh-3</i>	1	-0.01	0.11**	-0.05	-0.01	-0.03	-0.02	-0.05	0.02	0.03	-0.10	*	0.90
	<i>Pgi-2</i>	1	0.15**	0.02	0.03	0.01	-0.07	-0.05	-0.12**	-0.02	-0.04	-0.01	**	0.78
		2	0.06	0.00	0.02	-0.04	0.00	-0.01	-0.06	-0.10*	-0.04	0.07*	ns	0.08
		3	-0.02	0.02	0.07*	-0.05	-0.02	-0.05	0.00	-0.01	-0.03	0.00	ns	0.02
		4	0.09**	0.07*	0.03	0.01	-0.09	-0.05	-0.10*	-0.03	-0.01	-0.03	ns	0.09
		5	0.04	-0.04	-0.05	0.07*	0.01	-0.03	-0.02	-0.06	-0.05	0.04	ns	0.03
	<i>Pgm-1</i>	1	-0.04	-0.07	-0.01	0.04	-0.04	0.02	0.01	-0.03	0.00	0.02	ns	0.89
		2	-0.04	-0.07	0.00	0.00	-0.01	-0.03	0.05	-0.02	0.01	0.00	ns	0.08
		3	0.02	-0.03	-0.01	0.00	-0.04	-0.05	-0.01	0.03	-0.02	0.01	ns	0.03

* $P < 0.05$, ** $P < 0.01$.

†Distance classes in metres: Site 1 (1, 0.0-11.9; 2, 11.9-18.2; 3, 18.2-23.2; 4, 23.2-28.8; 5, 28.8-34.5; 6, 34.5-40.5; 7, 40.5-47.8; 8, 47.8-57.5; 9, 57.5-69.8; 10, 69.8-107.2). Site 2 (1, 0.0-17.7; 2, 17.7-25.8; 3, 25.8-32.8; 4, 32.8-38.9; 5, 38.9-45.3; 6, 45.3-52.1; 7, 52.1-59.2; 8, 59.2-67.8; 9, 67.8-79.9; 10, 79.9-124.8). Site 3 (1, 0.0-11.8; 2, 11.8-18.2; 3, 18.2-23.3; 4, 23.3-27.6; 5, 27.6-32.1; 6, 32.1-36.3; 7, 36.3-41.2; 8, 41.2-47.0; 9, 47.0-54.5; 10, 54.5-83.2).

shaped patch. The mean correlograms of each of the three stands (Fig. 1) indicate that patch sizes were approximately 20–30 m across.

Discussion

Comparisons among spatial autocorrelation studies are not easily made as there is no test available for the difference between correlograms (Sokal & Wartenberg, 1983) and factors such as sample sizes, and allele frequencies may affect one's ability to detect an existing genetic structure. However, one observation suggests that the amount of structure within these maple stands may be greater than that of two Black Spruce populations studied via similar methods (Knowles, 1990). Although the sample sizes (numbers of trees per population) of the present study are notably smaller than those of the Knowles (1990) study, the proportions of significant I values observed in the smallest distance class of each population were greater in the present study. While Knowles described the genetic structure within Black Spruce stands as 'subtle', we suggest that the degree of structuring within the present Sugar Maple stands may be better described as moderate.

Factors that may contribute to genetic structure include restricted pollen and seed dispersal, and spatially varying selection. Little information is available concerning seed dispersal in natural Sugar Maple stands. In open conditions, an order of magnitude decrease in seedling density was reached over a distance of 31 m from a seed source (Johnson, 1988). The potential dispersal distance of Sugar Maple samaras is great, perhaps hundreds of metres, but in dense stands where samaras may strike other trees and shrubs in the course of flight, dispersal may be limited (Guries & Nordheim, 1984). Information pertaining to pollen flow is even less complete. One might predict pollen dispersal in Sugar Maple to be relatively low because it is at least partially entomophilous and insects may tend to visit proximal trees, but it has been shown that wind alone can provide sufficient pollen for pollination (Gabriel & Garrett, 1984). Selection has been suggested by some researchers as a possible causal mechanism contributing to observed spatial structure (Linhart *et al.*, 1981; Epperson & Allard, 1989) and evidence that may refute the selective neutrality of some allozyme loci has been presented (Johnson, 1972; Nevo *et al.*, 1986).

Perhaps a patchy genetic structure within stands is a product of the dynamics of Sugar Maple regeneration. In the extreme case, vegetative reproduction would result in clusters of genetically identical individuals. Sugar Maple is capable of producing clones (Fayle, 1964) but, based on field observations and examina-

tion of multilocus genotypes, we judged the sampled trees to be of seed origin. While studying 'gap phase replacement' in a maple-basswood forest, Bray (1956) found that areas where the canopy was opened by disturbance were quickly covered by Sugar Maple seedlings. Willis & Coffman (1975) noted even-aged groups of saplings where disturbances had occurred. They suggest that there may be a 'spatial contagious pattern' with respect to age in Sugar Maple, with stands being composed of even-aged groups and that within a stand such groups may mature, die, and be replaced by new regeneration in a relatively short period of time. Of course, such a process could only account for the observed spatial genetic patterns if genetic differences exist among the even-aged groups (or cohorts). Mulcahy (1975) presents evidence of such differentiation. We did not determine ages of sampled trees and this is clearly an area in need of further study.

Variation in size and distinctness of patches among sampled areas of the three stands could be due to a number of factors. With isolation-by-distance (limited dispersal) the size of homogenous areas increases with larger neighbourhood sizes but as the areas increase in size, contrast is lost (Sokal & Wartenberg, 1983). Under selection, patches of genetic similarity would be expected to correspond to environmental patch structure. If the presence of cohorts was a source of genetic architecture, patches of genetically similar individuals would be affected in size by the magnitude of founding disturbances and in distinctness by the degree of genetic differentiation among cohorts.

If demographic patterns contribute to the formation of a spatial genetic structure within Sugar Maple stands as we propose, then the potential for the development of a spatial genetic structure may be greater in species that exist in uneven-aged stands than in species such as Black Spruce or Lodgepole Pine, whose populations are more typically even-aged. The validity of this hypothesis can only be determined through continued research. To this end, joint examination of genetic structure and age distribution within populations is likely to prove most efficacious.

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