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Species Associations with Spatial Autocorrelation Analysis of *Pinus rigida* and *Pyrola japonica*

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ABSTRACT: The spatial distributions of allelic frequencies and ecological traits by randomization were studied in the natural population of two species (*Pinus rigida* and *Pyrola japonica*). Both species showed significant positive spatial autocorrelation as measured by Moran's *I*. In *P. rigida*, the genetic similarity was shown in individuals within up to a scale of 18 m distance and this is partly due to combination of pollen and seed dispersal by wind or men. In *P. japonica*, significant spatial autocorrelation was consisted of a scale of 8 m intervals. These population structure in the distribution of allelic frequencies is related to mating systems such as outcrossing and vegetative spread. The results also indicate that positive species associations between *P. rigida* and *P. japonica* can occur when both species select the same habitat or require the same environmental conditions.

Key Words: *Pinus rigida*, *Pyrola japonica*, Spatial autocorrelation, Species associations.

INTRODUCTION

Ecologists and plant evolutionary biologists have long recognized that plants are not distributed at random within communities, but are rather clustered in distinct patches (Hamrick 1989). Environmental heterogeneity is usually cited as playing a critical role but colonization patterns and stochastic events affecting establishment and mortality are also important (Dewey and Heywood 1988). More recently, plant evolutionary biologists have demonstrated that genetic variation in plant populations is also nonrandomly distributed (Ludig and Reynolds 1988, Epperson 1995). Rather, like the plants themselves, gene and genotypes tend to be clumped, with marked genetic differences occurring over short distances (Schaal 1980). This nonrandom distribution of genetic variation is often referred to as the genetic structure of a population. Genetic structure is an integral part of the process of population genetics (Epperson and Allard 1989). Population structure interacts with a number of factors: microenvironmental heterozygosity (Bradshaw 1984), mortality due to stochastic events (Wright 1978), and mating systems that feature limited dispersal of seed or pollen (Epperson and Allard 1989). The most important factors are gene flow and natural selection which influence spatial patterns of the genetic population structure (Bradshaw 1984, Slatkin 1987, Epperson 1990).

Interspecific associations arise when two or more species co-occur more or less frequently than expected by chance alone (Roxburgh and Chesson 1998). For example, positive associations between two species can occur when both species select the same habitat or have the same environmental requirements. Conversely, negative associations can occur if species have differing ecological requirements (Dale 1977).

Indirect evidence for genetic correlations between neighboring plants has been obtained from data on mating systems (Epperson and Allard 1989). Localized seed and pollen dispersal produced family clusters within populations (Epperson 1990). Several studies revealed decreased seed set and seed survivorship from matings between genetically similar near neighbors, which has been interpreted as inbreeding depression (Price and Waser 1979, Waser and Price 1983, Levin 1984). In addition, a number of statistical tests have been utilized for detecting species associations. These include correlation analyses (Greig-Smith 1983), analysis by contingency table (Dale *et al.* 1991), variance tests (Schluter 1984), and the use of cross-variograms (Rossi *et al.* 1992). One major limitation of these tests is that they assume, for each species, within-species randomness of the spatial distribution patterns.

The purpose of this paper is to describe a statistical analysis for detecting species associations which is valid even when the assumption of within-species spatial randomness is violated.

MATERIALS AND METHODS

Sampling procedure and species association analysis

Pinus rigida (Pinaceae) is a widespread mon-

tane conifer in the Northern Hemisphere. The species was introduced into Korea in 1906 and has been planted widely for forestation (Kim 1996, Huh *et al.* 1997). This conifer is a long-lived, wind-pollinated, and predominantly outcrossed species. *Pyrola japonica* (Pyrolaceae), a widespread herb occurring throughout cooler, more temperate regions of the Northern Hemisphere, is most abundant in the boreal and arctic area (Woodland 1991). This species multiplies by both sexual and asexual reproduction (Huh *et al.* 1998).

The study was conducted at Sinhung-ri, Konmeong-meon, Sachen-ci, Kyungsangnam-do. Twigs with needle of *P. rigida* were mapped and sampled from 364 individual plants greater than 100cm in height between August 1997 and June 1998. One leaf per plant of *P. japonica* was gathered from the natural population. The distance between selected individuals of *P. japonica* was about 2.0m to avoid inclusion of those in common lineage. To demonstrate how invalidates traditional statistical techniques, the null hypothesis that two species occur within this plot independently of one another was tested through the use of standard 2 × 2 contingency table analysis (Ludwig and Reynolds 1988). The dimensions of the lattices were 2.0m × 2.0m.

Enzyme assay and statistical measures of genetic structure

Homogenization, starch gel electrophoresis and enzyme assay procedures were conducted following the methods of Soltis *et al.* (1983). Leaves were homogenized to release enzymes from cell and organellar membranes by mechanical grinding with Tris-HCl grinding buffer-PVP solution. Electrophoresis was performed using 10% starch gels. Four enzyme systems were assayed: alcohol dehydrogenase (ADH, EC 1.1.1.1), isocitrate dehydrogenase (IDH, EC 1.1.1.42), malate dehydrogenase (MDH, EC 1.1.1.37), and phosphoglucomutase (PGM, EC 2.7.5.1).

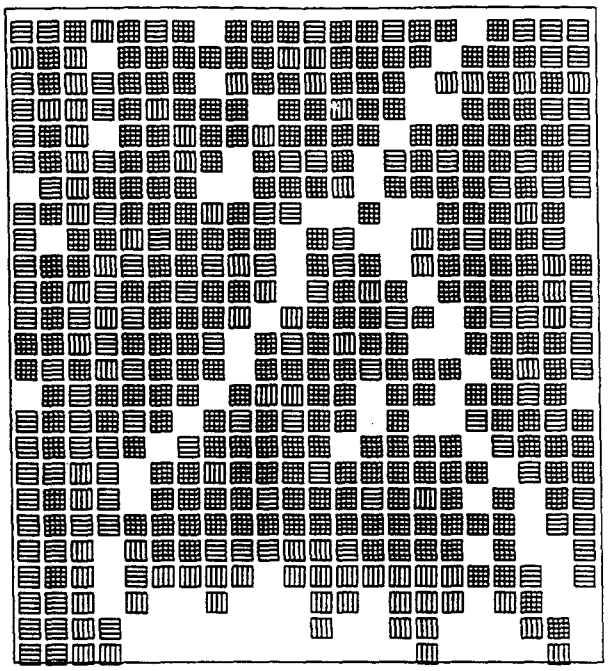
For enzymes that resolved in more than one zone of activity, the most anodal isozyme was arbitrarily designated as '1' and subsequent isozymes were sequentially assigned higher numbers. Likewise, alleles were designated sequentially with the most anodally migrating allozyme designated as 'a' and progressively slower forms 'b', 'c', and so on.

The spatial structuring of allozyme variation was quantified by Moran's *I*, a coefficient of spatial autocorrelation (Sokal and Oden 1978). As applied in this study, Moran's *I* quantifies the genetic similarity of pairs of spatially adjacent individuals relative to the population sample as a whole. The value of *I* ranges between +1 (complete positive autocorrelation, i.e., paired individuals have identical values) and −1 (complete negative autocorrelation). Each plant was assigned a value depending on the presence or absence of a specific allele. If the *i*th plant was a homozygote for the allele of interest, the assigned p*i* value was 1. If the individual was a heterozygote, the value 0.5 was assigned, and if the allele was absent, the value 0 is assigned. Pairs of individuals were classified according to the Euclidian distance d*ij* so that the class k included d*ij* satisfying $k-1 < dij < k+1$, where k takes 1 to 11. The interval of each distance class was 2.0 meter. Moran's *I* statistic for the class k was calculated as follows: $I(k) = n\Sigma i\Sigma j(i \neq j)\, ijZiZj / S\Sigma Zi^2$, where Z*i* is p*i* - p (p is the average of p*i*), W*ij* is 1 if the distance between *i*th and *j*th plants is classified into class k; otherwise W*ij* is 0, n is the number of all samples and S is the sum of W*ij* $\{\Sigma i\ \Sigma j(i \neq j)Wij\}$ in class k. Under the randomization hypothesis, *I*(k) has the expected value $u1 = -1/(n-1)$ for all k. Its variance *u2* has been given in Sokal and Oden (1978). Thus, if an allele is distributed randomly for class k, the normalized *I*(k) for the standard normal deviation (SND) for plant genotype $g(k) = \{I(k) - u1\}/u2^{1/2}$ is distributed asymptotically as a standard normal distribution (Cliff and Ord 1981). Hence, SND g(k) exceeding 1.96, 2.58, and 3.27 are significant at probability levels 0.05, 0.01, and 0.001, respectively.

For diallelic loci, only those with allele frequencies less than 0.95 and greater than 0.05 were employed, and then only one allele was considered because the second allele would contribute identical information. For multiallelic loci, all alleles at that locus, regardless of their frequencies, were used for the spatial analysis.

RESULTS

Fig. 1 shows the spatial patterns of two species, *Pinus rigida* and *Pyrola japonica*, within a 44.0m × 50.0m natural population. The two species were observed to co-occur in 256 out of 550 lattices. The expected number of lattices to contain both species, calculated under the assumption of independence between species, is 225.02 (Table 1). Based on the standard contingency table chi-squared test, which assumes randomness within species as well as independence between species, this overlap was significant ($\chi^2 = 33.032$, df = 1). The same trend was observed at 22 × 21 cells (the remainder of being eliminated part by artificial action) and simulated pattern of the presence of the same species in neighboring cells. Namely, *Pinus rigida* and *Pyrola japonica*



■: *Pinus rigida;* ■: *Pyrola japonica;* ■: Both species present (=overlap).

Fig. 1. An example of the overlap between two species exhibiting positive spatial autocorrelation. Lattice size is 2 × 2m.

are positively associated.

Both *Adh* and *Idh-1* loci were monomorphic at all sites. Therefore, the data on two loci will be omitted from discussion in this paper. The spatial autocorrelation coefficient, Moran's *I*, for a polymorphic locus is presented in Tables 2 and 3. Moran's *I* of *P. rigida* was significantly different from the expected value in only 27 of 121 cases (22.3%). Twelve of these values (44.4%) were negative, indicating a partially genetic dissimilarity among pairs of individuals in the eleven distance classes. Fifteen of the significant values (55.6%) were positive, indicating a genetic similarity among individuals in the distance class nine, i.e., pairs of individuals separated by more than 18m. Separate counts of each type of join (combination of genotypes at a single locus) for each allele, and for each distance class of separation, were tested for significant deviation from random expectations by calculating SND. Figs. 2 and 3 show the distribution of spatial autocorrelation for *P. rigida* across the distance class 11. For all distance classes, only six SND statistics were significant. *Pgm-2b* showed significantly positive SND values for all distance classes. *Pgm-2b* and *Pgm-2c* had significantly negative SND values for distance classes within 7. The aggregation of an identical allele, called a "patch", resulted in those loci. The two significantly negative SND values indicate an excess of different allele pairs at the two loci for classes 8 and 9, respectively. This suggests that neighbor patches in which different alleles are predominant are 18 to 22m apart, on average.

Moran's *I* of *P. japonica* was significantly different from the expected value in only 29 of 121 cases (24.0%) (Table 3). Eighteen of these values (62.1%) were positive, indicating a partial genetic similarity among individuals in the distance classes. Most forms of population structure are expected to result in positive spatial autocorrelation at the shorter distance classes. Significantly positive Moran's *I* coefficients at *Pgm-1a* were mostly found in the first four distance classes (0m to 8m) and also the distance interval of second positive correlation was from 10m to 16m (*Idh-2b, Mdh-1b, Pgm-1b,* and *Pgm-2c*). Negative values attained statistical significance below the ninth distance class (18m). In *P. japonica*, population structure in the distribution of allelic frequencies consists of a scale of 8m intervals.

DISCUSSION

Although significant aggregation of an identical allele was partially observed at seven loci (*Idh-*

Table 1. Chi-square test of association and from data in Fig. 1

		Pinus rigida				χ^2
		Present		Absent		
Pyrola japonica	Present	256	(225.02)	84	(114.98)	33.032
	Absent	108	(138.98)	102	(71.02)	
22 × 21 cells	Present	244	(224.46)	54	(73.53)	19.398
	Absent	104	(123.53)	60	(40.47)	
SP.	Present	240	(208.47)	75	(106.53)	33.002
	Absent	124	(155.53)	111	(79.47)	

( ): Expected value.
22 × 21 cells: The remainder of being eliminated part by artificial action.
SP.: Simulated pattern of the presence of the same species in neighboring cells.

Table 2. Spatial autocorrelation coefficients (Moran's *I*) of 11 alleles among populations of *Pinus rigida* for eleven distance classes

Alleles	Class										
	1	2	3	4	5	6	7	8	9	10	11
Idh-2a	0.002	-0.000	0.005	-0.001	0.004	-0.001	0.003	-0.000	0.003	-0.000	0.002
Idh-2b	0.027	0.001	-0.039	-0.000	0.006	-0.063*	0.009	-0.075*	0.019	-0.084*	0.009
Idh-2c	0.013	-0.064*	0.014	-0.045	0.047*	0.107**	0.023	-0.100**	0.132***	0.034	0.027
Mdh-1a	0.130***	-0.070	0.136***	-0.012	0.247***	0.358***	0.001	0.006	0.070*	0.038	0.010
Mdh-1b	-0.001	-0.002	-0.002	-0.002	-0.008	-0.006	-0.006	-0.017	-0.020	0.062*	-0.055*
Pgm-1a	0.009	0.062*	0.035	0.010	0.005	0.001	0.013	0.061*	-0.140***	-0.000	-0.014
Pgm-1b	-0.001	-0.001	-0.007	-0.008	-0.015	-0.014	-0.002	-0.000	-0.055	0.282***	-0.083*
Pgm-1c	-0.001	-0.003	-0.001	0.049*	-0.002	-0.001	0.042	-0.013	-0.000	-0.000	0.000
Pgm-2a	0.002	0.021	0.008	0.004	-0.003	0.005	0.002	-0.008	-0.041	0.004	-0.020
Pgm-2b	0.088*	0.028	0.007	-0.088*	0.029	0.019	0.016	0.016	0.131***	0.015	0.006
Pgm-2c	-0.012	-0.076*	-0.065*	-0.048	-0.047	-0.030	-0.014	0.052*	0.006	0.028	0.002

* P<0.05; ** p<0.01; ***P<0.001.

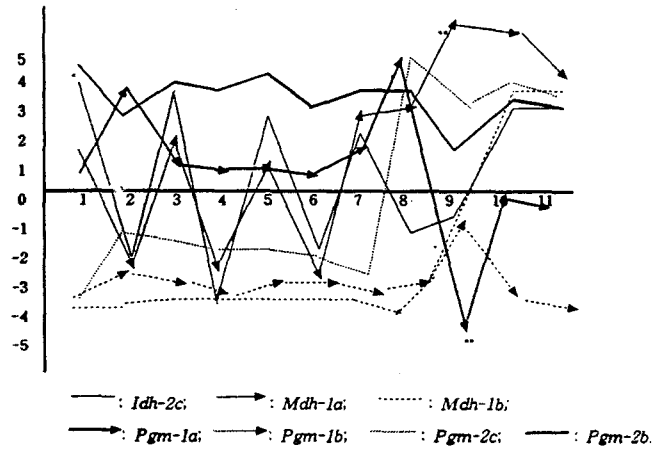


Fig. 2. Correlograms of autorrelation statistics for *P. rigida* as a function of distance. * and ** show significance at the 5% and 1% level, respectively.

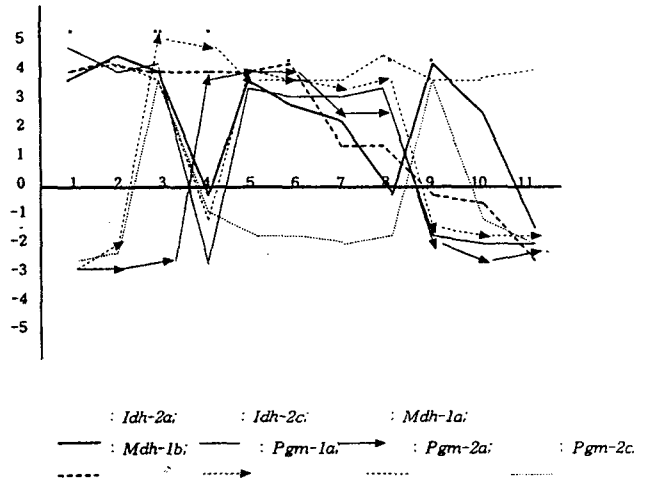


Fig. 3. Correlograms of autorrelation statistics for *P. japonica* as a function of distance. * and ** show significance at the 5% and 1% level, respectively.

Table 3. Spatial autocorrelation coefficients (Moran's *I*) of 11 alleles among populations of *Pyrola japonica* for eleven distance classes

Allele	Class										
	1	2	3	4	5	6	7	8	9	10	11
Idh-2a	0.001	0.055*	0.006	-0.000	0.015	0.004	0.000	-0.000	0.035	0.000	-0.001
Idh-2b	-0.001	-0.001	-0.007	0.012	0.047*	0.019	0.059*	0.068**	-0.025	-0.043*	-0.004
Idh-2c	0.020	0.004	0.007	0.011	-0.014	0.014	0.006	0.014	-0.002	-0.003	-0.006
Mdh-1a	0.077**	0.006	0.044*	-0.010	0.033*	0.002	0.000	0.012	-0.062*	-0.001	-0.011
Mdh-1b	-0.015	-0.004	0.001	0.011	0.015	0.049*	0.074**	0.067**	0.002	-0.066**	-0.015
Pgm-1a	-0.015	-0.054*	0.064**	0.041*	0.002	0.003	0.002	0.002	-0.042*	-0.049*	-0.056*
Pgm-1b	0.034*	0.020	0.016	0.009	0.014	0.063**	0.080**	-0.004	0.003	0.008	0.028
Pgm-1c	-0.008	-0.009	-0.018	-0.011	0.043*	0.013	0.006	-0.021	-0.052*	0.014	0.021
Pgm-2a	0.003	0.015	0.011	-0.025	-0.050*	-0.050*	-0.028	-0.044*	0.006	0.003	-0.001
Pgm-2b	0.013	0.018	0.012	0.015	0.012	0.017	0.001	0.003	-0.000	-0.002	-0.034
Pgm-2c	-0.002	-0.024	0.008	-0.031	0.051*	0.014	0.012	0.045*	0.012	-0.008	-0.013

* P<0.05; ** p<0.01.

2c, *Mdh-1a*, *Mdh-1b*, *Pgm-1a*, *Pgm-1b*, *Pgm-2b*, and *Pgm-2c*) for some classes, no spatial structure of allele frequencies was found for either of four polymorphic loci (*Idh-2a*, *Idh-2b*, *Pgm-1c*, and *Pgm-2a*) within the natural population of pine (Fig. 2). The results from this study are consistent with the prediction that plant populations are subdivided into local demes or neighborhoods of related individuals (Ehrich and Raven 1969, Bradshaw 1972, Levin and Kerster 1974). Previous reports on the local distribution of genetic variability suggested that microenvironmental selection and limited gene flow are the main factors causing substructuring of alleles within a population (Epperson and Allard 1989, Epperson 1990, Huh and Huh 1999). Local genetic differentiation at isozyme or other marker loci caused by microenvironmental heterogeneity has been observed in a variety of plant species (Bradshaw 1984). Those loci showed significant aggregation of an identical allele, which persisted for generations, as long as the same microenvironmental conditions continued. This persistence was demonstrated, for example, in the *Got-1* locus in lodgepole pine (Epperson and Allard 1989) and for the genetic variation for quantitative traits in *Impatiens capensis* (Argyres and Schmit 1991). In the present study, *Mdh-1a* and *Pgm-2b* alleles showed significant aggregation in the Korean *P. rigida* population. This aggregation, however, did not persist at all loci. The average Moran's *I* values for each distance class in this study indicate that *P. rigida* population apparently is less structured than *P. japonica* population. Possible contributing factors include differences in density, topography, and human interference. For example, cutting of branches and stems of pine have often been done from hillside to nearby farmhouse during the past several years. This occasional cutting of seed bearing stems for the purpose of firewood may bring high level of gene flow. Even a small amount of gene flow is sufficient to counteract the diversifying effects of genetic drift or weak selection (Wright 1978, Devlin and Ellstrand 1990).

The results from *P. japonica* are also consistent with the prediction that plant populations are structured into local demes or neighborhoods of related individuals (Ehrich and Raven 1969, Bradshaw 1972, Levin and Kerster 1974). Population structure (a scale of 8m interval) of *P. japonica* in the distribution of allelic frequencies is shorter than that of *P. rigida* (a scale of 18m interval). One possible explanation for the differences of the sizes of population structure is gene flow by means of mating system. *P. rigida* is outcrossing and wind-pollinating species. Wind-pollinating species have the highest levels of gene flow whereas inbreeding species have somewhat less levels of gene flow (Hamrick 1982, Hamrick and Godt 1989, Maki and Masuda 1994). In addition, *P. rigida* has winged seeds. Since most parachute seeds of pine do not fall near maternal plants, gene flow via seed produced a markedly scattered distribution (Huh and Huh 1998). *P. japonica* is insect-pollinating species and can asexually propagate by rhizomes (Huh *et al.* 1998). In Korea, *P. japonica* inhabits understory of Pinus- and Larix-dominated forests.

A more likely explanation for the spatial structure of *P. rigida* is life history. Theoretical prediction shows that old populations have more spatial genetic structure than recently established population (Epperson 1990). In addition, spatial autocorrelation requires time (generations) to develop. Simulation studies have shown that under isolation by distance, significant spatial autocorrelation may result within five generations but development of coerce gene frequency surfaces may take many more generations (Rohlf and Schnell 1971, Sokal and Watenberg 1983). In Korea, *Pinus densiflora* had been one of the dominant trees in forest until several years ago.

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