American Journal of Botany 89(8): 1229–1236. 2002.

LANDSCAPE-LEVEL SPATIAL GENETIC STRUCTURE IN *QUERCUS ACUTISSIMA* (FAGACEAE)[1]

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Quercus acutissima (Fagaceae), a deciduous broad-leaved tree, is an important forest element in hillsides of South Korea. We used allozyme loci, Wright's *F* statistics, and multilocus spatial autocorrelation statistics to examine the distribution of genetic diversity within and among three local populations and the spatial genetic structure at a landscape scale (15 ha, 250 × 600 m) on Oenaro Island, South Korea. Levels of genetic diversity in *Q. acutissima* populations were comparable to mean values for other oak species. A moderate but significant deficit of heterozygotes (mean $F_{IS} = 0.069$) was detected within local populations and low but significant differentiation was observed among populations ($F_{ST} = 0.010$). Spatial autocorrelation analyses revealed little evidence of significant genetic structure at spatial scales of 100–120 m. The failure to detect genetic structure within populations may be due to intraspecific competition or random mortality among saplings, resulting in extensive thinning within maternal half-sib groups. Alternatively, low genetic differentiation at the landscape scale indicates substantial gene flow among local populations. Although wind-borne pollen may be the primary source of gene flow in *Q. acutissima*, these results suggest that acorn movement by animals may be more extensive than previously anticipated. Comparison of these genetic data for Oenaro Island with a disturbed isolated inland population suggests that population-to-population differences in internal genetic structure may be influenced by local variation in regeneration environment (e.g., disturbance).

Key words: allozymes; coancestry; Fagaceae; landscape scale; *Quercus acutissima*; seed dispersal; spatial genetic structure.

The spatial distribution of the genetic variation within plant populations has been widely studied using spatial autocorrelation techniques to investigate population genetic processes and interpreted as a result of evolutionary forces including limited seed and pollen dispersal, adult density, colonization history, and, potentially, microenvironmental selection (Schoen and Latta, 1989; Epperson, 1993; Smouse and Peakall, 1999; Kalisz et al., 2001). With respect to forest tree species, several studies have revealed significant fine-scale genetic structuring within populations (Schnabel and Hamrick, 1990a; Perry and Knowles, 1991; Schnabel, Laushman, and Hamrick, 1991; Knowles, Perry, and Foster, 1992; Hamrick, Murawski, and Nason, 1993; Sork, Huang, and Wiener, 1993; Geburek and Tripp-Knowles, 1994; Shapcott, 1995; Montalvo et al., 1997; Ueno et al., 2000), some have shown weak or ''near random'' short-distance genetic structure (Streiff et al., 1988; Berg and Hamrick, 1995; Loiselle et al., 1995; Leonardi, Raddi, and Borghetti, 1996; Epperson and Chung, 2001), while others have failed to detect any structure (Dewey and Heywood, 1988; Epperson and Allard, 1989; Knowles, 1991; Doligez and Joly, 1997; Epperson and Alvarez-Buylla, 1997; Chung et al., 2000; Parker et al., 2001). This variation may be due to the different ecological and genetic factors operating in natural populations, as well as different sampling spatial scales and statistical procedures (Streiff et al., 1988; Smouse and Peakall, 1999; Gram and Sork, 2001). For example, although a single population or study site has been analyzed for most spatial-genetic structure studies of tree species, different populations of animal-dispersed species can have very different spatial structures (Schnabel and Hamrick, 1990a; Aldrich et al., 1998; Schnabel, Nason, and Hamrick, 1998). Furthermore, the scale and magnitude of genetic structure can differ significantly between life stages, with juveniles often exhibiting greater within-population structuring than adults (Hamrick and Nason, 1996; but see Kalisz et al., 2001). As a result, genetic structure and its causal ecological and evolutionary processes may not be evident from the analysis of a single life stage (Tonsor, Kalisz, and Fisher, 1993; Epperson and Alvarez-Buylla, 1997; Aldrich et al., 1998; Schnabel, Nason, and Hamrick, 1998; Kalisz et al., 2001). Also, failure to detect significant genetic structure does not necessarily demonstrate the absence of genetic structure as structuring may occur at spatial scales smaller or larger than those investigated. Basic knowledge of the dispersal biology of a species is thus an important prerequisite in designing studies in which appropriate spatial scales can be examined.

Studies of fine-scale spatial genetic structure have been constrained mostly to a single population and yet often are interpreted as characterizing pattern and process indicative of the species. Implicit in this interpretation is the hypothesis that the spatial scale and magnitude of internal genetic structure is homogeneous across populations. Nevertheless, the extent to which populations differ in internal genetic structure is poorly

[1] Manuscript received 28 August 2001; revision accepted 28 March 2002.

The authors thank M. J. Chung, Y. H. Chung, S. T. Ha, M. H. Kang, T. J. Song, G. M. Kim, J. H. Kim, Y. H. Kim, S. M. Im, S. G. Chung, and G. S. Oh for proving support and assistance in collecting samples and B. K. Epperson for helpful suggestions on spatial autocorrelation analysis. This work was supported by grant 1999-1-20100-001-5 from the Basic Research Program of the Korea Science & Engineering Foundation through K.-J. Kim to MGC.

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understood, even for patches in the same landscape. Although the proximity of such patches may lessen the opportunity for differentiation, various processes may operate at the landscape level to promote the spatial and temporal development of different internal genetic structures. For example, local variation in the type and abundance of seed dispersers can affect dispersal distances and thus the probability of establishment and spatial distribution of maternal families within a population (Aldrich et al., 1998; Schnabel, Nason, and Hamrick, 1998). The extent to which seed shadows overlap also influences genetic structure and will be strongly influenced by the local density of reproducing adults (Hamrick, Murawski, and Nason, 1993; Parker et al., 2001). For light-demanding species, variation across the landscape in the frequency and size of canopy gaps is a further source of variation in maternal reproductive success and the clustering of siblings. Some studies have found within-population genetic structure that is weaker in adults than juveniles, suggesting random mortality and the erosion of structure during stand thinning (Hamrick, Murawski, and Nason, 1993). Alternatively, biotic (e.g., pathogens: Parker, 1985; hervibory: Sork, Stowe, and Hochwender, 1993; density: Gram and Sork, 1999) and abiotic (e.g., recruitment microsites: Stanton, Galen, and Shore, 1997) environments may vary within a landscape, generating spatial variation in selection differentially affecting the survival of sibling groups. In light of these observations, the standard null hypothesis that internal genetic structure is homogeneous across populations seems perhaps naive, and the comparison of parameters of intrapopulation structure across multiple populations is warranted.

In oaks, geographic studies of population genetic structure (Schnabel and Hamrick, 1990b; Berg and Hamrick, 1993; Koop, 1996, cited in Smouse et al., 2001) and paternity analysis of mating patterns within populations (Dow and Ashley, 1996, 1998; Streiff et al., 1999; but see Smouse et al., 2001) indicate substantial pollen gene flow. Although such gene flow is expected to homogenize allele frequency variation among neighboring populations, it does not preclude the development of within-population genetic structure. Indeed, localized seed dispersal can generate substantial fine-scale genetic structuring within populations even in the face of panmictic pollen flow (Kalisz et al., 2001). The extent to which individual species develop within-population genetic structure largely depends on the mechanism of seed dispersal. In a stand of 11 *Quercus palustris* trees, for example, foraging blue jays (*Cyanocitta cristata*) were observed to transport and cache 54% of the acorn mast, moving seeds over distances of 0.1–1.9 km (mean 1.1 km; Darley-Hill and Johnson, 1981). Dispersion of this form is not expected to promote the development of significant fine-scale within-population genetic structure. In other species, however, less vagile dispersers (e.g., rodents), low adult densities, or recruitment of nondispersed seeds beneath maternal trees are factors likely to generate detectable genetic structuring within oak populations. Variation in these and other factors across natural landscapes will determine the extent to which neighboring populations differ in their internal genetic structure.

Although conducted to examine different population genetic processes and parameters, most studies for forest tree species have been restricted to spatial scales of <6 ha (250×250 m). As a result, little is known about the spatial genetic structure of forest tree species at larger landscape-level spatial scales. A larger scale approach may be important for inferring the extent of gene flow between local populations and the extent to which the magnitude and spatial dimension of fine-scale spatial genetic structuring varies among neighboring populations. In this study, multilocus allozyme genotypes were sampled and mapped from three local populations of the oak *Quercus acutissima* Carruth. (Fagaceae) occurring in an undisturbed forest landscape on Oenaro Island in southern Korea. Wright's *F* statistics and multilocus spatial autocorrelation statistics were calculated and analyzed to test the homogeneity of spatial genetic structure within and among local populations at a landscape level scale (15 ha, 250×600 m).

MATERIALS AND METHODS

Population samples—*Quercus acutissima* is a large deciduous tree of hillsides from South Korea to Japan. It occurs in many plant communities, often in monospecific stands. *Quercus acutissima* is a pioneer species that colonizes gaps after gap formation (Yamamoto, 2000). This wind-pollinated plant flowers in mid-to-late spring, is monoecious, and is commonly considered to be self-incompatible (Ducousso, Michaud, and Lumaret, 1993). Acorns of *Quercus acutissima* usually mature in the second season and germinate in the spring (Kitamura and Murata, 1987). For the 3-yr observation period of the study site, *Q. acutissima* appeared to be quite irregular in its masting (M. Y. Chung and M. G. Chung, personal observations).

The study site was at Oenaro Island, which is located on the southern Korea coast. The island is part of Dadohasang National Park and has been well preserved with no apparent human interference for centuries at the site. In March 2000, 468 individuals of all visually identified larger than 15 cm diameter at breast height (dbh) were collected and mapped and leaf samples were collected within three local populations: the first stand (LPA, a 120×150 m area, altitude 295–320 m above sea level [asl], $N = 283$, density [d] $= 157.2$ trees [$>$15cm dbh] per ha) is a dry habitat on northeast-facing hillsides; the second stand (LPB, a 150×150 m area, altitude 260–275 m asl, $N = 85$, $d = 37.7$ trees/ha) is a wet habitat on southeast-facing slopes; and the third (LPC, a 150×120 m area, altitude 170–195 m asl, $N = 100$, $d = 55.6$ trees/ha) is a dry habitat on northeast-facing hillsides (Fig. 1). In LPA and LPC, *Q. acutissima* is the dominant species under which seedlings and juveniles of several broad-leaved evergreen trees grow, whereas several mature deciduous and evergreen trees, including a low density of *Pinus thunbergii*, coexist in LPB. Seedlings and juveniles of *Q. acutissima* were extremely rare in the study sites. The study sites have no recorded history of fire disturbance, and there is no evidence of trees having been planted. As few adults occurring between the local study populations ($<$20 individuals) were scattered, these were not included in this study. Two young leaves per individual were shipped to the laboratory of M. G. Chung and stored at 4°C until protein extraction.

Enzyme extraction and electrophoresis—Leaves were cut finely and crushed with a mortar and pestle in a potassium phosphate extraction buffer (Mitton et al., 1979) without using liquid nitrogen. The crushed extract was absorbed onto 4×6 mm Whatman 3MM chromatography paper wicks, which were stored at -70°C until needed for electrophoretic analysis. Electrophoresis was performed using 12% starch gels. Nine putative loci for *Q. acutissima* from five enzyme systems were resolved using two electrophoretic buffer systems. A morpholine citrate buffer system (pH 6.1; Clayton and Tretiak, 1972) was used to resolve 6-phosphogluconate dehydrogenase (*Pgd-1, Pgd-2*) and shikimate dehydrogenase (*Skdh-1, Skdh-2*). A discontinuous histidine-citrate buffer system, a modification (Chung and Kang, 1994) of Soltis et al.'s (1983) "system 11," was used to resolve fructose-1,6-diphosphatase (*F1,6–1, F1,6–2*), isocitrate dehydrogenase (*Idh*), and phosphoglucoisomerase (*Pgi-1, Pgi-2*). Stain recipes were taken from Soltis et al. (1983). The genetic basis of allozyme banding patterns was inferred from segregation patterns with reference to typical subunit structure (Weeden and Wendel, 1989; Wendel and Weeden, 1989). Putative loci were designated sequentially, with the most anodally migrating isozyme designated *1*, the next *2*, and so on. Similarly, alleles

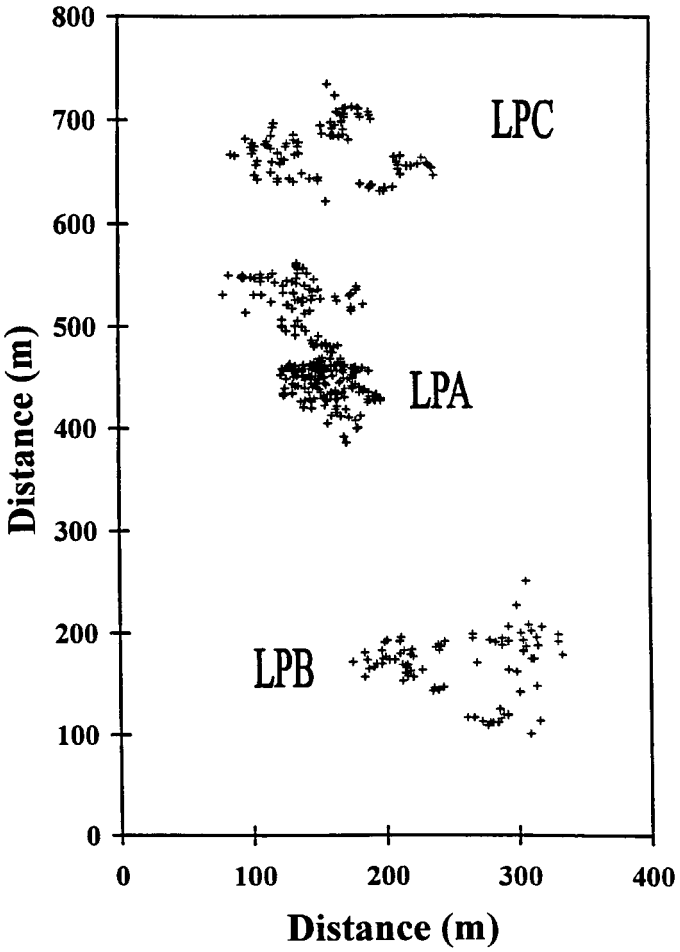

Fig. 1. Spatial distribution of three local populations (LPA, LPB, and LPC) within the study plot (15 ha) on Oenaro Island, South Korea.

were designated sequentially with the most anodally migrating alleles designated with superscript a.

Data analysis—A locus was considered polymorphic if the frequency of the most common allele did not exceed 0.96. Genetic diversity parameters were estimated using the program POPGENE (Yeh, Yang, and Boyle, 1999): percentage polymorphic loci (%*P*); mean number of alleles per locus (*A*); observed heterozygosity (H_o); and Nei's unbiased gene diversity (H_e).

Observed heterozygosity was compared to Hardy-Weinberg (H-W) expected values per individual locus and population using Wright's (1922) fixation indices (*F*). Statistical significance of these values was determined based on 2700 randomizations of alleles among individuals within local populations. A Bonferroni adjustment was used to achieve an experiment-wide Type I error (α) of 0.05 for tests of loci and populations (Rice, 1989). Wright's (1965) *F* statistics (F_{IS}, F_{IT}, and F_{ST}) were calculated using Weir and Cockerham's (1984) multilocus estimators (*f*, *F*, and θ, respectively) to measure deviations from H-W equilibrium at each polymorphic locus. These fixation indices measure levels of inbreeding within individuals in local populations (F_{IS}), inbreeding due to each local population subdivision (F_{ST}, an indicator of the degree of differentiation among local populations), and overall levels of inbreeding (F_{IT}). The significance of individual locus F_{IS}, F_{ST}, and F_{IT} estimates was based on 1000 permutations of alleles among individuals within samples, genotypes among samples, and alleles among samples, respectively. Means and standard errors over loci were obtained by jackknifing over polymorphic loci. Bootstrap confidence intervals (95% CI) were constructed around jackknifed means of the *F* statistics; observed mean *F* statistics were considered significant when confidence intervals did not overlap zero. These calculations were made using the program FSTAT (version 2.9.1 by Goudet, 2000; see Goudet, 1995).

TABLE 1. Summary of genetic diversity measures and mean *F* values observed in three local populations of *Quercus acutissima* on Oenaro Island. *N*, sample size; *%P*, percentage of polymorphic loci; *A*, mean number of allele per locus; H_o, mean observed heterozygosity; H_e, mean expected heterozygosity; and SE, standard error.

Population	*N*	*%P*	*A*	H_o (SE)	H_e (SE)	*F*
LPA	283	66.7	2.00	0.146 (0.063)	0.156 (0.064)	0.064
LPB	85	66.7	2.00	0.132 (0.053)	0.140 (0.056)	0.055
LPC	100	66.7	2.00	0.138 (0.061)	0.156 (0.072)	0.117
Mean	156	66.7	2.00	0.139 (0.004)	0.151 (0.005)	0.079

The continuous spatial distributions of allozyme polymorphisms within local populations were analyzed using spatial autocorrelation methods employing the coancestry coefficient, f_{ij}, as an estimator of the correlation in frequencies of alleles at each locus for each pair of individuals *i* and *j* (Cockerham, 1969). This measure has been used previously (e.g., Loiselle et al., 1995; Peakall and Beattie, 1996; Foster and Sork, 1997; Burke et al., 2000; Kalisz et al., 2001; Parker et al., 2001), and as a multilocus method it provides a more powerful test for the presence of fine-scale genetic structure than single-allele, single-locus methods (Heywood, 1991; Smouse and Peakall, 1999; Kalisz et al., 2001).

To obtain a multiallelic-multilocus measure of spatial genetic structure per a given distance, f_{ij} was estimated between all pairs of individuals within each local populations and the total sample ($N = 468$) following the methods of Loiselle et al. (1995) and Kalisz et al. (2001). Mean values of f_{ij} were obtained for distance intervals (lags) of 5 and 10 m by averaging over all pairs of individuals located within that interval. The results were combined over loci by weighting each locus by its polymorphic index [$\Sigma p_i (1 - p_i)$]. When $f_{ij} = 0$, there is no significant correlation among individuals at the spatial scale of interest; when $f_{ij} > 0$, individuals in a given distance class are more closely related than expected by chance; and when $f_{ij} < 0$, individuals within a given distance class are less related than expected by chance. Assessment of statistical significance for each f_{ij} estimate per given distance was conducted by the randomization procedures described in Kalisz et al. (2001). All calculations and simulations were performed using a program developed by J. Nason.

Finally, to test whether the slope (β) of a correlogram is statistically significant, f_{ij} estimates were permuted with respect to distance (999 times) using the program Permute! (version 3.4 alpha; Casgrain, 2001) to construct the distribution of the slope under the null hypothesis $\beta = 0$. When testing for negative spatial autocorrelation (one-tailed test), we reject the null hypothesis if there are fewer than 50 random values at least as large as the actual observed β value.

RESULTS

Genetic diversity and structure—Of the nine loci examined, six were polymorphic while *F1,6-1*, *F1,6-2*, and *Pgi-1* were monomorphic. The mean percentage of polymorphic loci within local populations was 66.7% (Table 1). Genetic diversity was moderate at the local population level and for the samples as a whole ($H_e = 0.152$ and 0.154, respectively).

Analysis of fixation indices (*F*), calculated for the polymorphic loci in each population, showed that none of the 17 single-locus estimates was statistically significant when type I error was adjusted for multiple tests ($\alpha = 0.0029$). However, significant positive values at *Pgd-1*, *Idh*, and *Skdh-2* were detected in LPA by chi-square tests unadjusted for multiple tests (Li and Horvitz, 1953). These loci and *Pgd-2* also showed a significant deficit of heterozygosity at local and total population levels while remaining loci did not deviate from H-W expectations at either level. Levels of inbreeding within local

TABLE 2. *F* statistics (Wright, 1965) following the method of Weir and Cockerham (1984) for six polymorphic loci from three local populations of *Quercus acutissima.*

Locus	F_{IS}	*P*	F_{IT}	*P*	F_{ST}	*P*
Idh	0.235	0.012	0.240	0.001	0.006	0.043
Pgd-1	0.123	0.004	0.125	0.001	0.003	0.116
Pgd-2	0.100	0.002	0.120	0.001	0.022	0.001
Pgi-2	0.001	0.520	0.003	0.451	0.002	0.056
Skdh-1	−0.014	0.799	−0.007	0.103	0.007	0.179
Skdh-2	0.112	0.024	0.118	0.007	0.007	0.073
Mean	0.069		0.078		0.010	
±1 SE	0.038		0.042		0.007	
95% CI	(0.020, 0.128)		(0.022, 0.134)		(0.002, 0.019)	

populations and in the sample as a whole were significant as indicated by jackknifed F_{IS} and F_{IT} estimates calculated over loci (0.069 and 0.078, respectively; Table 2).

Overall, we found that 99% of the total variation in the study area resides within local populations ($F_{ST} = 0.010$). Despite the limited differentiation, allele frequencies were significantly different among local populations for two of six loci (Table 2) and bootstrap confidence limits (95% CI) about the mean F_{ST} showed that differentiation among local populations was significantly different from zero (Table 2).

Spatial genetic structure—Relative to 99% confidence limits, autocorrelation analyses showed that mean coancestry values calculated for shorter distance intervals were not significantly different from zero within local populations or when the populations were taken as a whole (total samples), while significant values were detected in the total samples at distances of 80 and 200 m (Fig. 2). At the 95% level, in contrast, a significant but weak positive value ($f_{ij} = 0.03$) at 30 m was found in LPC, while significant but weak negative coancestry values were observed in three local populations at longer distance classes: 70 m in LPA; 100–200 m in LPB; and 90 and 110 m in LPC. The overall slope of the correlogram was not significantly negative in analyses of the LPA or LPB populations conducted at 5-m intervals. The LPC population and total sample, in contrast, did show a significant negative relationship for this interval (LPC: $\beta = -0.683$, $P = 0.001$, $R^2 = 0.467$; total samples: $\beta = -0.223$, $P = 0.007$, $R^2 = 0.050$). Similar results were obtained at the local and total sample levels for a lag of 10 m (data not shown). The significant

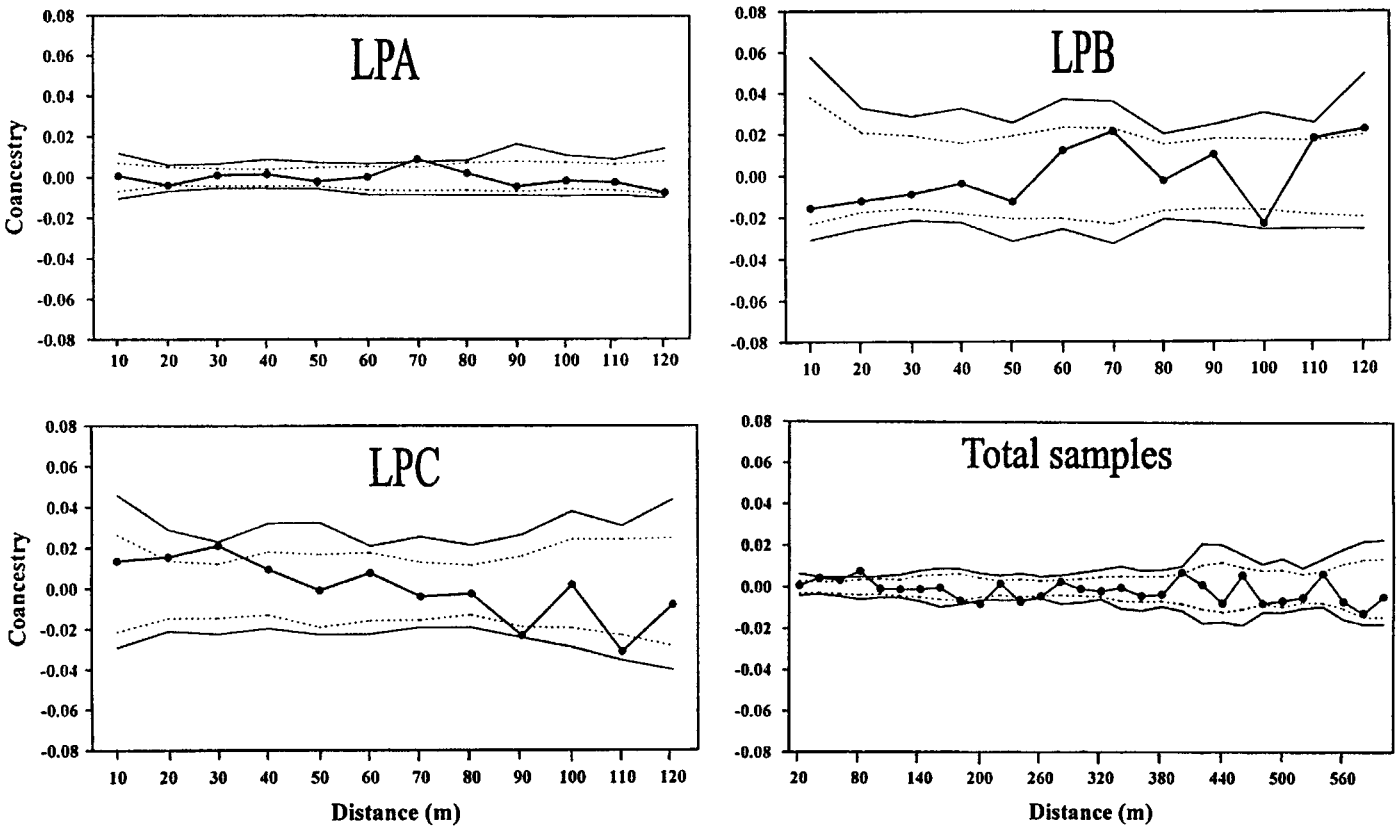

Fig. 2. Correlograms of estimated coancestry (f_{ij}) for three local populations (LPA, LPB, and LPC) and total samples within study plot on Oenaro Island. Closed circles indicate mean coancestry values for successive distance classes. The solid and dashed lines represent upper and lower 99% and 95% confidence envelopes, respectively, around the null hypothesis of $f_{ij} = 0$.

negative slope in correlogram observed in LPC was in agreement with the results for the individual distance classes.

DISCUSSION

Genetic diversity and structure—The levels of genetic diversity of *Quercus acutissima* examined in this study were found to be comparable to the mean for other oak species ($N = 28$, $H_e = 0.186$; Hamrick, Godt, and Sherman-Broyles, 1992). In general, observed heterozygosity in oak populations has been found to be lower than the expected H-W equilibrium values (e.g., Guttman and Weigt, 1989; Schnabel and Hamrick, 1990b; Berg and Hamrick, 1993, 1994; Samuel, Pinsker, and Ehrendorfer, 1995). A moderate deficiency of heterozygotes was also observed within local populations of *Q. acutissima* (mean $F_{IS} = 0.069$, population range 0.055–0.117), indicating low levels of inbreeding or fine-scale genetic subdivision within populations. *Quercus* is generally self-incompatible and wind-pollinated so that inbreeding and associative mating are unlikely to be major factors contributing to a deficit of heterozygotes in the study populations. Further, spatial autocorrelation analysis revealed ''near random'' genetic structuring on the scale of 10 m (see discussion below), indicating little family clustering resulting from localized fruit dispersal. An alternative, untested hypothesis is that the observed deficit of heterozygotes for individuals larger than 15 cm at dbh in our study is attributable to episodic reproductive events leading to a ''temporal'' Wahlund effect over generations (Epperson and Chung, 2001).

Most studies of genetic differentiation have been conducted across geographical regions on the scale of tens of kilometers between populations. Berg and Hamrick (1993) conducted allozyme study in 11 populations of *Q. laevis* in the southeastern United States and found low genetic diversity among populations (mean Nei's [1973, 1977] $G_{ST} = 0.032$). They interpreted the interpopulation homogeneity as a relic of a previously more continuous distribution of longleaf pine-turkey oak forest in the region, as well as high rates of past gene flow by long-distance pollen flow coupled with bird-dispersal of acorns. Using Wright's (1965) F statistics, Koop (1996) conducted an allozyme study among 36 adult subpopulations within a region 20 km in diameter in the Missouri Ozarks and found no evidence of genetic structure ($F_{ST} = 0.00$) among subpopulations (but see results based on multivariate analysis; Gram and Sork, 2001). Our results also revealed low differentiation among three local populations of *Q. acutissima* on Oenaro Island (mean $F_{ST} = 0.01$). Such limited differentiation is likely to be attributable to long-distance pollen movement by wind, which should enhance homogeneity of allele frequencies between adjacent local oak populations (Dow and Ashley, 1996, 1998; Streiff et al., 1999). In addition, given little fine-scale genetic structure, seed dispersal may also contribute to the homogenization of genetic variation across study populations (see discussion below).

Spatial genetic structure—Darley-Hill and Johnson (1981) found that blue jays (*Cyanocitta cristata*) transported and cached 54% of the acorn mast from a stand of 11 trees of *Q. palustris* in Virginia. The jays carried 1–5 acorns per foraging trip and moved them over distances of 0.1–1.9 km (mean 1.1 km). If typical of oaks, then seed dispersal is likely to be an effective means of gene flow in addition to wind-borne pollen dispersal. Indeed, if dispersal rates and distances were similar, dispersal of acorns would contribute twice as much to gene flow as pollen because the diploid acorn carries twice the genetic component (Hamrick and Nason, 1996). When insects are scarce in late summer and winter, large birds are known to eat fruit of broad-leaved evergreen trees in southern Korea, including Oenaro Island (Chung et al., 2000). However, there is no direct evidence for acorn dispersal by birds in *Q. acutissima*.

Like other temperate nut-bearing trees, it is likely that *Q. acutissima* relies at least in part on seed predators for secondary seed dispersal. In the mid-western United States, these dispersal agents are primarily birds and rodents (e.g., grey squirrel *Sciurus*: Thompson and Thompson, 1980; Fox, 1982). In Japan, Miyaki and Kikuzawa (1988) found that most acorns of *Q. mongolica* were disseminated by mice (*Apodemus specious* and *A. argenteus)* up to distances of 30–40 m from their mother tree. Direct, observational information on seed dispersal mechanisms in *Q. acutissima* is not available; however, as acorn size and shape in *Q. acutissima* are similar to that of *Q. mongolica*, it is inferred that acorns are primarily transported by rodents (e.g., squirrels and mice) in our study population. If most acorns of *Q. acutissima* are dispersed by rodents, one might expect the development of strong spatial genetic structure within local populations, a pattern not observed in this study despite local differences in habitats and adult density.

Another hypothesis for the minimal intrapopulation genetic structure observed in *Q. acutissima* populations is a ''thinning effect'' during recruitment (Hamrick, Murawski, and Nason, 1993; Epperson and Alvarez-Buylla, 1997; Parker et al., 2001). If seed dispersal is highly localized, then forest gaps favorable for seedling establishment may be colonized primarily by the offspring of one or a few surrounding maternal trees. As clusters of saplings grow within gaps, competition and mortality among them will increase, resulting in extensive thinning in groups of half-sibs. Ultimately, for a population at carrying capacity, only one such offspring, on average, will survive per maternal family. Further, saplings growing from seeds dispersed away from the maternal tree by animals may have more opportunities to survive to adult stage (Howe, 1986). To determine whether this form of thinning occurred during recruitment in the study populations of *Q. acutissima*, further study on genetic structure in terms of demography is needed. This study is now in progress.

At the scale of an undisturbed natural landscape (15 ha), local populations of *Q. acutissima* exhibit little variation in their internal genetic structures. This suggests that the causal mechanisms generating genetic structure (e.g., seed dispersal, recruitment processes, etc.) are relatively homogeneous at this scale. Further insight into these processes may be gained by comparison to populations occurring in more disturbed settings. Although not formally examined as part of the present study, genetic structure data is available for a disturbed, isolated population of *Q. acutissima* located on the mainland approximately 150 km from Oenaro Island (M. Y. Chung and M. G. Chung, unpublished data). A preliminary spatial autocorrelation analysis of 413 individuals (dbh $>$ 15 cm) at this site (LPD, a 200 $\times$ 300 m area, altitude 110–120 m asl, $d =$ 68.8 trees/ha) revealed significant, positive fine-scale genetic structure extending from 10 m to almost 50 m (Fig. 3) as well as a significant decrease in coancestry estimates with increasing distance ($\beta = -0.918$, $P = 0.01$, $R^2 = 0.842$). The greater internal genetic structure observed in the LPD relative to Oen-

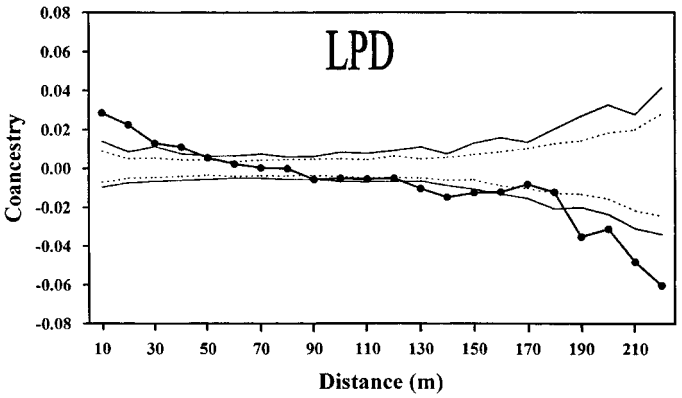

Fig. 3. Correlograms of estimated coancestry (f_{ij}) for in disturbed, inland population (LPD, $N = 413$, 6 ha). The solid and dashed lines represent upper and lower 99% and 95% confidence envelopes, respectively, around the null hypothesis of $f_{ij} = 0$.

aro Island populations may be due to several factors, including the effects of habitat disturbance on seed dispersal and recruitment. The LPD stand is located near Gyeongsang National University, South Korea, and is isolated about 500–2000 m from hillsides on which other *Q. acutissima* are scattered. Traditional Korean villages, roads, and paddy fields were created at least several hundred years ago between LPD and surrounding hillsides, suggesting that rodents are unlikely to move acorns into and out of surrounding *Q. acutissima* stands (Johnson and Adkisson, 1985). Seedlings and various-aged juveniles of the species are common within LPD, in contrast to Oenaro Island, indicating that regeneration may be enhanced by higher light levels resulting from local disturbance. In general, other studies have found within-population genetic structure to be greater in juveniles than adult trees. However, if favorable recruitment conditions translate into an increase in adult density, then the significant spatial genetic correlations in the LPD population may be the result of fine-scale genetic structure within maternal seed shadows persisting into the adult generation. This disturbance-based hypothesis has previously been proposed to explain the persistence of significant internal genetic structure in a population of the Neotropical tree *Swartzia simplex* var. *ochnacea* (Hamrick, Murawski, and Nason, 1993). Although significant, our estimate of near-distance f_{ij} in LPD (0.028) is still considerably lower than that expected for half-sibs (0.125) under random mating, suggesting secondary seed dispersal and substantial overlap of seed shadows. The comparison of LDP and Oenaro Island populations suggests that local variation in regeneration environments may underlie the development of different internal genetic structures, heterogeneity that is likely to be maximized in habitat mosaics (e.g., fragmented landscapes). These conclusions could be tested directly by future studies comparing the genetic structures of successive life stages in disturbed and undisturbed, natural habitats.

In summary, the moderate deficit of heterozygotes within populations on Oenaro Island may be attributable to episodic reproductive events leading to a ''temporal'' Wahlund effect over generations. In addition, low but significant differentiation was observed between local populations. Spatial autocorrelation analyses showed that fine-scale genetic structuring was weak within one local population and absent for the other two and for the populations taken as a whole. Comparison with an isolated, disturbed mainland population suggests that regenerative environments may further influence levels and spatial scales of within-population structuring. The present study describes relatively subtle differences in genetic structure among populations within an undisturbed natural landscape while presenting suggestive evidence of processes contributing to the interpopulation variance in internal genetic structures in fragmented landscapes.

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