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Spatial Genetic Structure in Disturbed Populations of *Quercus acutissima* (Fagaceae)

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Abstract

Quercus acutissima is a large deciduous tree of hillsides ranging from South Korea to Japan. It occurs in many plant communities, often as a pioneer species in monospecific stands which colonized gaps after gap formation. This study used multilocus allozyme genotypes mapped from two disturbed populations near farm houses in southern Korea to compare our results with previous studies conducted on undisturbed populations of trees in southern Korea. Coancestry measures (f_{ij}), RIPLEY's L -statistics, and WRIGHT's F -statistics were then calculated

to examine the distribution of individuals and spatial genetic structure both within and between populations. RIPLEY's L -statistics indicated significant aggregation of individuals at interplant distances. A weak but significant positive fine-scale genetic structure at 10 m distance was detected in the two disturbed populations, which is consistent with the structure found in an inland, disturbed population in southern Korea. Estimates of near-distance f_{ij} in the two populations (0.020 and 0.036) were considerably lower than that expected for half-sibs (0.125) under random mating, suggesting secondary seed dispersal and substantial overlap of seed shadows. The levels of genetic diversity within the two disturbed populations of *Q. acutissima* were found to be comparable to the within-mean for populations of other oak species. Significant deficits of heterozygosity were detected in both populations, probably due to several parent-offspring and sib matings. Finally, a significant but low differentiation between the two disturbed populations of *Q. acutissima* was found, which is likely to be attributable to long-distance pollen movement by wind, which should enhance homogeneity of allele frequencies between adjacent local oak populations.

Key words: allozymes, disturbance, Fagaceae, *Quercus acutissima*, spatial genetic structure.

Introduction

Fine-scale genetic structure is evident within plant populations when the distribution of genetic variation among individ-

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uals is nonrandom (EPPERSON, 1989). Fine-scale genetic structure has been widely studied using spatial autocorrelation analysis to investigate population genetic processes (SOKAL and ODEN, 1978; EPPERSON, 2003; HEYWOOD, 1991). Many evolutionary factors including limited seed and pollen dispersal, adult density, colonization history, and, potentially, microenvironmental selection, affect the development of genetic structure within plant populations (WRIGHT, 1943; SCHOEN and LATTA, 1989; SOKAL and JACQUEZ, 1991; EPPERSON, 1993; SMOUSE and PEAKALL, 1999). In addition to the biological factors, environmental factors including natural and anthropological disturbances can also influence the spatial genetic structure of individuals within plant populations. Local variation in type and abundance of seed dispersers could affect dispersal distance from year to year and thus spatial distribution of maternal families within a population (e.g., ALDRICH et al., 1998; SCHNABEL et al., 1998). Furthermore, habitat fragmentation, presence of ground cover (e.g., *Sasa* cover), forest fire, wind damage, and forest logging can also influence spatial genetic structuring in plant populations (e.g., BOYLE et al., 1990; ELLSTRAND, 1992; KNOWLES et al., 1992; YOUNG and MERRIAM, 1994; EPPERSON and CHUNG, 2001; PARKER et al. 2001; CHUNG and CHUNG, 2004).

As part of a larger project investigating spatial and temporal genetic structure in populations of *Quercus* species (Fagaceae) in South Korea, CHUNG et al. (2002), using allozyme loci, examined the spatial genetic structure in three undisturbed local populations of *Q. acutissima* Carruth, a deciduous broad-leaved tree, at a landscape scale (15 ha, 250 x 600 m) on Oenaro Island, South Korea. The authors did not detect any spatial genetic structure within populations, probably due to extensive competitive thinning among genetically related seedlings or juveniles coupled with overlapping seed shadows and/or substantial gene flow among local populations. In contrast, a preliminary spatial autocorrelation analysis of 413 individuals in a disturbed inland population (hereafter referred to GNU, a 200 x 300 m area) revealed significant, positive fine-scale genetic structure extending from 10 m to 50 m (CHUNG et al., 2002). CHUNG et al. (2002) suggested the effects of habitat disturbance on seed dispersal and recruitment as explanatory factors for the greater internal genetic structure observed in the disturbed GNU population relative to Oenaro Island populations. The GNU stand is located near Gyeongsang National University in Jinju, South Korea, and is located about 500 m – 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 GNU and the 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 observed within GNU, in contrast to Oenaro Island, indicating that regeneration may be enhanced by higher light levels resulting from local disturbance such as cutting trees for firewood. Comparison of 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 several factors, including the effects of habitat disturbance on seed dispersal and recruitment (“disturbance-based hypothesis”; HAMRICK et al., 1993). As only one disturbed inland population was examined, more genetic studies of disturbed populations would be necessary to test the hypothesis.

In this study multilocus allozyme genotypes were mapped and sampled from two disturbed populations of *Q. acutissima* occurring in southern Korea. Spatial autocorrelation statistics, RIPLEY’S (RIPLEY, 1976, 1977) *L*-statistics, and WRIGHT’S *F*-sta-

tistics were then calculated to examine the distribution of individuals and spatial genetic structure both within and between populations. Finally, our estimates were compared to the previous study on undisturbed and disturbed populations of the species in southern Korea (CHUNG et al., 2002).

Materials and Methods

Quercus acutissima is a large deciduous tree of hillsides ranging from South Korea to Japan and is commonly planted as an ornamental in North America. 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 et al., 1993). Acorns of *Quercus acutissima* consistently mature in the second season and ger-

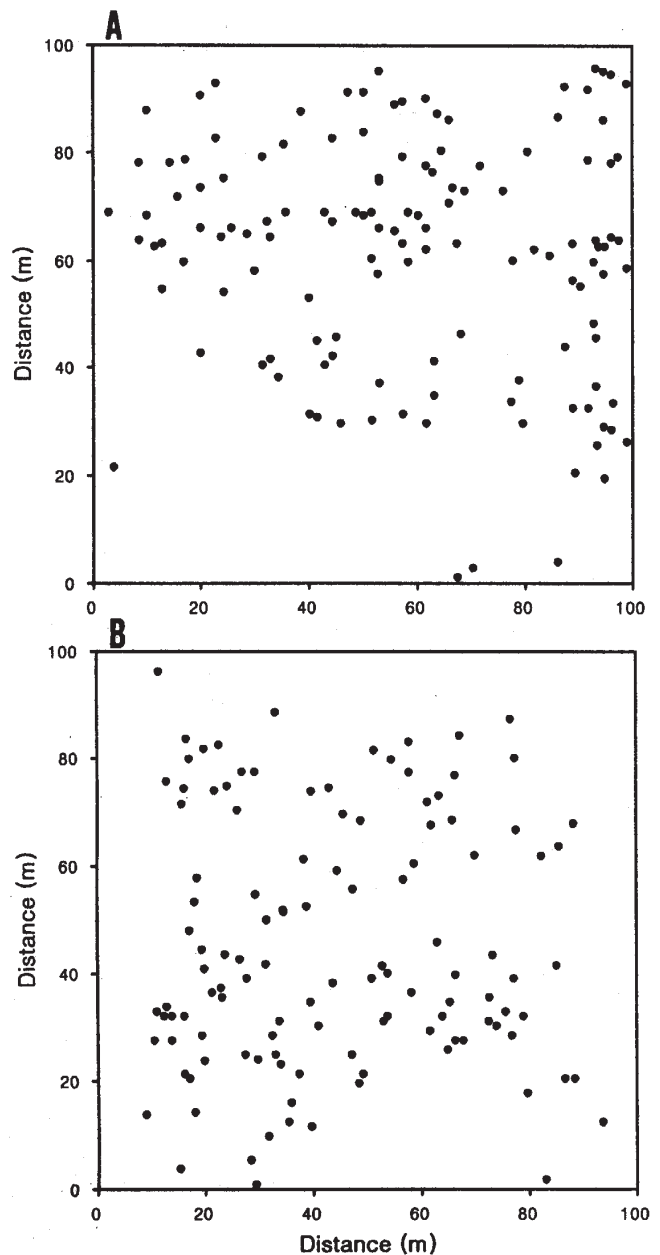


Figure 1. – Distribution of individuals in two populations of *Quercus acutissima*. Population A ($N = 134$) is located in Leebansung-myeon and population B ($N = 118$) is in Shinan-myeon, Province Gyeongsangnam-do, southern Korea.

minate in the spring ("biennial fruit maturation": BORGRARDT and NIXON, 2003). 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).

In April 2003, 252 visually identified individuals as larger than 15 cm diameters at breast height (dbh) were mapped and leaf samples were collected from two disturbed populations in southern Korea. The first stand (population A, a 100 x 100 m area, 134 individuals, Fig. 1) is located on a south-facing hillside behind a traditional Korean rural village (Leebansangmyeon, Jinju city, Province Gyeongsangnam-do). Approximately, northwestwardly 38.8 km, the second stand (population B, a 100 x 100 m area, 118 individuals, Fig. 1) is located on a south-facing hillside behind a traditional Korean rural village (Shinan-myeon, Shanchung-gun, Province Gyeongsangnam-do). Population B is approximately 196 km from Oenaro Island and population A is approximately 176 km from Oenaro Island. Near the two stands, there were traditional Korean farm houses, rural roads, and paddy fields which were created at least several hundred years ago. Traditionally, oak-dominant hillsides behind farm houses in southern Korea have been often used as a playground for children and other living purposes of farmers (e.g., places for drying sweet potato shoots and other cereal crops). Like GNU stand, we considered populations A and B to be disturbed. In these two stands, *Q. acutissima* is the dominant species with several seedlings and juveniles growing into the canopy. Beyond the stands, there is a typical hillside type of southern Korean forests: *Pinus densiflora* is the dominant species with a few seedlings of *Q. acutissima* and other shrubs such as *Rhus* spp. and *Lespedeza* spp. One leaf was collected from each individual of *Q. acutissima* and stored at 4°C until enzymes were extracted.

The leaf material was cut into small pieces and crushed with a mortar and pestle. A potassium phosphate extraction buffer (MITTON et al., 1979) was added and the crushed extract was absorbed onto 4 x 6 mm Whatman 3 mm chromatography paper (Whatman International, Maidstone, England). The wicks were stored at -70°C until needed for electrophoretic analysis. Electrophoresis was performed using 12% starch gels. The enzyme/buffer systems and stain recipes were the same as the previous study (CHUNG et al., 2002). 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 were designated sequentially with the most anodally migrating alleles designated with superscript *a*. Of the nine loci examined, five were polymorphic while the *F1,6-1*, *F1,6-2*, *Idh*, and *Pgi-1* were monomorphic.

To assess the spatial distribution of *Q. acutissima* individuals (15 cm dbh) in two populations, we used RIPLEY's *L*-statistics (RIPLEY, 1976, 1977; e.g., PARKER et al., 1997). RIPLEY's *L*(*d*) is calculated from the number of point pairs within concentric circles of increasing radii (*d*) around each plant. As use of

circles with a radius greater than half the shortest plot side introduces excessive bias due to edge effects, we selected radial distances 1 to 50 m for each population (PARKER et al., 1997). The expectation for *L* at the radial distance, $d[L(d)]$, is zero when the dispersion pattern is random at the scale of *d*; $L(d) > 0$ for aggregation; $L(d) < 0$ for hyper-dispersion (i.e., a regular distribution). To assess statistical significance, *L*(*d*) values were compared observed values with envelopes generated by the 5% and 1% highest and lowest values generated from 199 Monte Carlo simulations of a randomly distributed population. All calculations and simulations were performed using a program developed by P. ALDRICH (Smithsonian Institution, National Museum of Natural History, USA) and E. BERG (Kenai National Wildlife Refuge, AK, USA).

The spatial distributions of allozyme polymorphisms were analyzed using a pairwise estimate of genetic correlation, f_{ij} (a "coancestry" coefficient; sensu KALISZ et al., 2001), which measures the correlation between the frequency of a random allele from one individual with that of a random allele from another (COCKERHAM, 1969). The f_{ij} was estimated between all pairs of individuals within each population at a given distance interval following the methods of KALISZ et al. (2001). Mean values of f_{ij} were obtained for distance intervals (lags) of 10 m by averaging over all pairs of individuals located within that interval. This measure of coancestry has expected value of $f_{ij} = 0$ when there is no genetic correlation between the frequencies of alleles in individuals at the spatial scale of interest, $f_{ij} > 0$ when individuals in a given distance class are more closely related than expected by chance, and $f_{ij} < 0$ when 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. D. NASON (Iowa State University, USA).

Several parameters commonly used to estimate genetic diversity were calculated for each of the two populations using the programs POPGENE (YEH et al., 1999) and FSTAT (version 2.9.3 by GOUDET, 2001): the proportion of polymorphic loci (%*P*) among nine loci used, mean number of alleles per locus (*A*), observed (H_o) and expected (H_e) heterozygosity or Nei's unbiased gene diversity. For each population, fixation indices (*F*) and a 95% bootstrap confidence interval (95% CI) were calculated using the program GDA (LEWIS and ZAYKIN, 2001). WRIGHT's (1965) F_{IS} and F_{ST} were calculated using WEIR and COCKERHAM's (1984) multilocus estimators f and θ 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}) and inbreeding due to each local population subdivision (F_{ST} , an indicator of the degree of differentiation among local populations). 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_{IS} and F_{ST} ; observed mean F_{IS} and F_{ST} were considered significant when confidence intervals did not overlap zero. These calculations were made using the program FSTAT.

Results

The results of RIPLEY's *L*-statistics indicated significant aggregation of individuals at interplant distances extending from 2 m (population A at 95% CI) or 4 m (population B at 99% CI) to 50 m ($P < 0.01$) (Fig. 2).

Relative to 99% confidence limits, autocorrelation analysis for population A showed that mean coancestry values (f_{ij}) calcu-

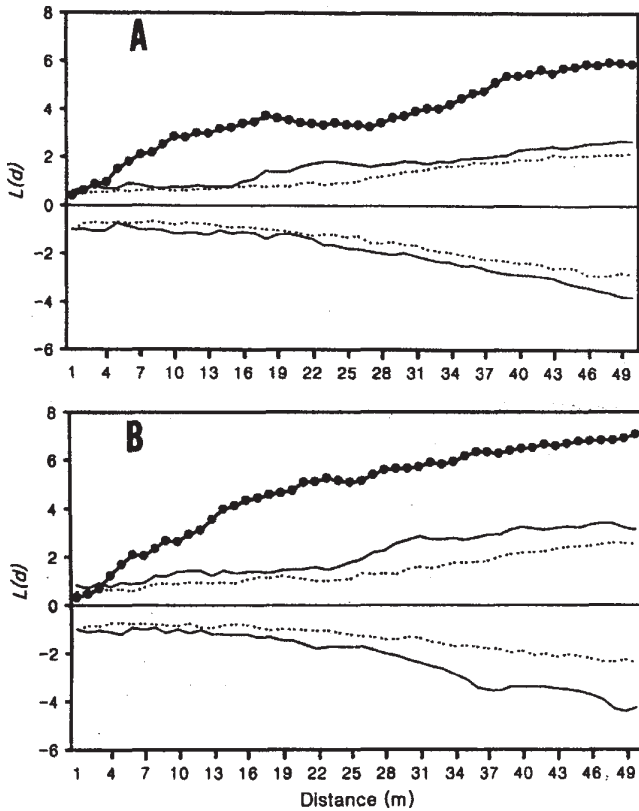


Figure 2. – Observed $L(d)$ values for univariate RIPLEY analysis of individuals of *Quercus acutissima* for populations A and B (closed circles with solid lines) and envelopes defined by the 5% (dashed lines) and 1% (solid lines) highest and lowest values generated from 199 Monte Carlo simulations of a randomly distributed population. $L(d) > 0$ indicates aggregation.

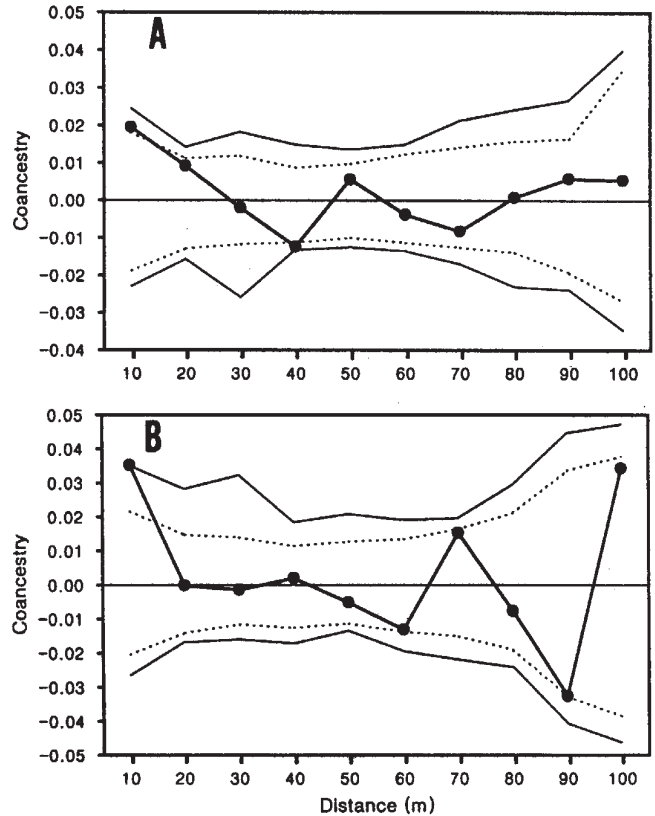


Figure 3. – Correlograms of estimated coancestry (f_{ij}) for two populations A and B in southern Korea. Closed circles with solid lines indicate mean coancestry values for successive distance classes. The solid and dashed lines represent upper and lower 99% and 95% confidence envelopes, respectively, around the null hypothesis of $f_{ij} = 0$.

lated for shorter distance intervals were not significantly different from zero (Fig. 3). At the 95% level, in contrast, a significant but weak positive value ($f_{ij} = 0.020$) at 10 m was found in population A (95% CL = 0.018) (Fig. 3), while a significant but weak negative coancestry values ($f_{ij} = -0.012$) was observed at 40 m in population A (95% CL = -0.011). Overall, similar results were found in population B, but at the 99% level, a significant but weak positive value ($f_{ij} = 0.036$) at 10 m was observed (95% CL = 0.035) (Fig. 3). Except this, there were no significant values across distances at either level.

The mean percentage of polymorphic loci within local populations was 55.6% (Table 1). There were no significant differences in genetic diversity (A and H_e) between the two stands (WILCOXON signed rank test). Genetic diversity was moderate at the local population level ($H_e = 0.149$). Within each population, mean fixation indices (F) and the 95% confidence intervals (95% CI) showed a significant deficit of heterozygosity in both populations (Table 1). In calculating F_{IS} over populations, a significant deficit of heterozygosity was found ($F_{IS} = 0.090$; 95% CI = 0.071, 0.172). Finally, allele frequencies were significantly different between populations for all loci but *Skdh-1*. We found that about 97% of the total variation in the study area resides within populations, but 95% CI (0.007, 0.037) about the mean F_{ST} (0.029) showed that differentiation among the two populations was significantly different from zero.

Discussion

Weak but significant positive fine-scale genetic structure at 10 m distance was detected in the two disturbed populations, which is consistent with the structure found in the disturbed

population (GNU) near Gyeongsang National University ($f_{ij} = 0.028$ at 10 m with a significant, positive fine-scale genetic structure extending from 10 m to almost 50 m: CHUNG et al., 2002).

In the two disturbed stands examined in the present study, *Q. acutissima* is the dominant species with several seedlings and juveniles growing in the many small gaps within the two stands resulting from local disturbance. As *Q. acutissima* could be able to regenerate in gaps formed under current conditions (S. YAMAMOTO of Nagoya University, Japan, personal communication), formation of small gaps, probably due to human-mediated disturbance, may be of importance for regeneration of *Q. acutissima* (YAMAMOTO, 1989). These small gaps provide light conditions favorable to the germination and establishment of

Table 1. – Summary of allozyme variation and mean F -values observed within two populations of *Quercus acutissima*.^{a)}

Population	N	%P	A	H_o (SE)	H_e (SE)	F (95% CI)
A	134	55.6	2.00	0.134 (0.209)	0.150 (0.232)	0.111 (0.076, 0.110)
B	118	55.6	1.89	0.134 (0.202)	0.147 (0.211)	0.092 (0.046, 0.186)
GNU ^{b)}	413	55.6	2.00	0.120 (0.187)	0.140 (0.222)	0.142 (0.072, 0.160)
Mean ^{c)}	156	66.7	2.00	0.139 (0.004)	0.151 (0.005)	0.079

^{a)} Abbreviations: N , sample size; %P, percentage of polymorphic loci; A , mean number of alleles per locus; H_o , observed heterozygosity; H_e , HARDY-WEINBERG expected heterozygosity or genetic diversity; SE, standard error; and F , fixation index.

^{b)} Recalculated from disturbed GNU stand from CHUNG et al. (2002).

^{c)} Mean of three undisturbed populations (468 individuals) on Oenaro Island from CHUNG et al. (2002).

individuals adapted to establishment in small gaps, resulting in patches of similar aged individuals. We detected significant aggregation of individuals in the two populations. If favorable recruitment conditions translate into an increase in adult density, then the significant spatial genetic correlations at 10 m in the two populations examined in this study 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. *ochracea* (HAMRICK et al., 1993). Although significant, our estimate of near-distance f_{ij} in the two populations (0.020 and 0.036) 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 three disturbed populations including the GNU stand (CHUNG et al., 2002) on within-population spatial genetic structure appear to be similar to the previous studies on oaks. In Japan, UBUKATA et al. (1999) found a significant genetic structure in an old stand of *Q. mongolica* var. *grosseserrata* in Hokkaido. In northwest France, BACILIERI et al. (1994) examined fine-scale genetic structure in an adult stand of *Quercus petraea* and found significant genetic clustering within 20–50 m. In Canada, a weak but significant spatial genetic structure was also detected in a stand of *Q. macrocarpa* (GEBUREK and TRIPP-KNOWLES, 1994). These authors attributed the evidence of genetic structure primarily to the limited seed dispersal. The results from the disturbed populations, however, appear to be different from those for undisturbed populations of *Quercus acutissima* (CHUNG et al., 2002) and *Q. variabilis* in southern Korea (CHUNG and CHUNG, 2002) from which the authors also found little evidence of significant genetic structure across spatial scales of 100–200 m. The difference between our results and previous studies of oaks in southern Korea may reflect geographical variation in recruitment ecology or other controls on gene flow. Moreover, the comparison of the disturbed and undisturbed populations on southern Korean islands suggests that local variation in regeneration environments may underlie the development of different internal genetic structures.

The levels of genetic diversity within the two disturbed populations of *Q. acutissima* examined in this study were found to be comparable to the within-mean for other oak species ($H_e = 0.186$; HAMRICK et al., 1992) and the means for populations of other oak species in southern Korea ($H_e = 0.151$ in three undisturbed populations of *Q. acutissima*: CHUNG et al. [2002]; 0.147 in three undisturbed populations of *Q. variabilis*: CHUNG and CHUNG [2002]; 0.160 in two undisturbed populations of *Q. mongolica* var. *grosserrata*: CHUNG and CHUNG [2004]; and 0.140 in a disturbed population of *Q. acutissima*: recalculated from CHUNG et al. [2002]).

Significant deficits of heterozygosity were detected in both populations. These are consistent with a general conclusion that observed heterozygosity in oak populations is lower than the expected H-W equilibrium values (e.g., GUTTMAN and WEIGT, 1989; SCHNABEL and HAMRICK, 1990; BERG and HAMRICK, 1993, 1994; BACILIERI et al., 1994; GEBUREK and TRIPP-KNOWLES, 1994; SAMUEL et al., 1995; CHUNG and CHUNG, 2002; CHUNG et al., 2002). Significant deficits of heterozygosity within populations may be indicative of inbreeding and/or population substructure (HARTL and CLARK, 1997). Since selfing may be absent, certainly mating between related individuals would develop and be successful in the two stands. Our f_{ij} results showed that neighbor trees were related and several parent-offspring and sib mating would occur. This would even-

tually lead to an excess of homozygosity (not large if there is considerable pollen dispersal but present nevertheless) at the stand level. The Wahlund effects requires a more stringent spatial structuring which is less compatible with the data that showed relatively small spatial differentiation and little between stand differences (see below).

Low differentiation between the two disturbed populations of *Q. acutissima* parallels with those found for three populations of *Q. acutissima* on Oenaro Island (mean $F_{ST} = 0.010$; CHUNG et al., 2002), three populations of *Q. variabilis* on Dolsan Island ($F_{ST} = 0.023$; CHUNG et al., 2002), and two undisturbed populations of *Q. mongolica* var. *grosseserrata* on Mt. Jiri ($F_{ST} = 0.015$; CHUNG and CHUNG, 2004) in southern Korea. 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 (BERG and HAMRICK, 1993; DOW and ASHLEY, 1996, 1998; STREIFF et al., 1998).

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