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Genetic variation and spatial structure in sugar maple (*Acer saccharum* Marsh.) and implications for predicted global-scale environmental change

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Abstract

Current ecosystem model predictions concerning the effects of global temperature increase on forest responses do not account for factors influencing long-term evolutionary dynamics of natural populations. Population structure and genetic variability may represent important factors in a species' ability to adapt to global-scale environmental change without experiencing major alterations in current range limits. Genetic variation and structure in sugar maple (*Acer saccharum* Marsh.) were examined across three regions, between two stands within regions, and among four to five open-pollinated families within stands (total $N = 547$ genotypes) using 58 randomly amplified polymorphic DNA (RAPD) markers. Differences within open-pollinated families account for the largest portion of the total variation (29%), while differences among regions represent less than 2% of the total variation. Genetic diversity, as indicated by estimates of percent polymorphic loci, expected heterozygosity, fixation coefficients, and genetic distance, is greatest in the southern region, which consists of populations with the maximum potential risk due to climate change effects. The high level of genetic similarity (greater than 90%) among some genotypes suggests that gene flow is occurring among regions, stands, and families. High levels of genetic variation among families indicate that vegetational models designed to predict species' response to global-scale environmental change may need to consider the degree and hierarchical structure of genetic variation when making large-scale inferences.

Symbols: $F_{st}, \theta =$ fixation coefficient, $H_s =$ mean expected heterozygosity, $P_p =$ percentage polymorphic loci

Keywords: gene flow, genetic variation, global warming, population structure, RAPDs, sugar maple

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Introduction

Current models of global-scale environmental change predict a doubling of atmospheric carbon dioxide in the next century and with it an average surface temperature increase of 2–4 °C (IPCC 1996). The rate of such a temperature change is unprecedented and thus the consequences, specifically to the 300 million hectares of forested land in the United States, are largely unknown. Since temperature is recognized as a primary determinant of plant growth and survival (Berry & Björkman 1980), one of the more important consequences of temperature increase would be the predicted northward redistribution of forest tree species (Houghton & Woodwell 1989; Winjum & Neilson 1990). Northern migrations of 600–700 km for spruce, sugar maple, and other species (Tirpak 1990) would have an enormous impact on current environmental and economic systems.

Theoretical climate-induced changes in species' distributions remain the foundation for models of vegetational migration. These models are often limited by the assumption that climate is the only factor controlling range limits, and by a misinterpretation of differences in

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fundamental vs. realized niches that could alter under conditions of global change (Loehle & LeBlanc 1996). Many models are based on a hypothetical response of an 'average tree' without regard to fluctuations in temperature across the current distribution (Musselman & Fox 1991) and/or without an understanding of the role that acclimation and genetic adaptation may have in a species' response to predicted climate regimes. Failure to consider genetic structure may limit the reliability of model-based predictions of climate change-induced forest redistribution.

From a physiological standpoint, adjustments to environmental stress associated with climatic warming may be more likely to occur in peripheral populations that are subject to more extreme environmental fluctuations and unpredictable selective pressures. Selection and/or drift can increase the frequency of rare or favourable alleles in proportions of a population that are isolated from the continuous distribution. With environmental changes, genotypes containing these rare alleles may have a higher potential adaptive value than do those genotypes lacking the rare alleles. In any event, populations that are genetically variable would have a greater likelihood of maintaining alleles that could contribute to phenotypic plasticity, and, although selection is unlikely to act on a single allele, it may act in a manner that maintains a stable polymorphism (Grant 1991). If the effects of climatic warming are most severe at the edges of a species' range, then the ability of peripheral populations to adapt to altered temperature and rainfall patterns will be important (Geber & Dawson 1993; Hoffmann & Blows 1993). If these populations have a greater capacity for adjustment to higher temperatures, and if they are not constrained by complete genetic isolation from other populations, then the effects of global warming will probably be less severe than what may be predicted from a simple temperature–response curve applied without regard to spatial or temporal genetic variation. In most forest tree species, genetic variability is not uniform among populations, and can be related to the capacity for adaptive adjustments (Bennett 1970). An evaluation of this variability could indirectly facilitate an assessment of the capacity for adaptation to increased temperature.

Sugar maple (*Acer saccharum* Marsh.) is a good candidate for assessment of genetic variability because it has a large but relatively restricted range, long-distance gene flow among populations, and moderate inter- and intrapopulation genetic structure (Perry & Knowles 1991). In addition, sugar maple exhibits adaptation to altitudinal gradients (Ledig & Korbobo 1983), spatial-scale genetic structure (Young *et al*. 1993), genetic variability in response to temperature/moisture stress (Kriebel 1957), and its predicted response to climate change is prominent in existing vegetation models (Pastor & Post 1988; Davis & Zabinski 1992; Solomon & Bartlein 1992).

Using molecular genetic techniques, we have evaluated population-level genetic structure as an indirect indicator of the capacity for response to environmental change in order to address the following questions: Are peripheral populations genetically distinct from a continuous population? If so, what is the degree of relatedness (gene sharing) among populations? How might population structure relate to sugar maple's capacity to survive climate-induced stress? Finally, what are the implications for global-scale environmental change forest response modelling and eco-physiological research?

Random amplified polymorphic DNA (RAPD) markers (Williams *et al*. 1990) were used to evaluate genetic structure within and among sugar maple populations from three geographical locations representing a N–S gradient of the species' current distribution. The resulting evaluation allowed us to speculate on whether peripheral populations have a greater potential for adaptation to novel environments than do populations from the centre of the range based on the amount of genetic variability present within those populations, and whether population structure may have implications for experimental design related to global climate change.

Materials and methods

Material collection and DNA extraction

Seeds were collected from four to five open-pollinated mother-trees representing families in each of two stands in northern Wisconsin, northern Illinois, and eastern Tennessee. These sites were chosen to represent northern, central, and southern latitudinal regions within sugar maple's current distribution (Godman *et al*. 1990). Seedlings collected from a single mother tree are at least half-siblings, and some are likely to share paternal alleles as well, hence the use of the term 'family' to underscore their genetic similarity when compared to nonrelated genotypes. The term 'stand' defines a recognizably distinct group of trees that is often, but not consistently reproductively isolated from other stands. Seeds were harvested from mature trees within stands that were at least 1 km apart at the University of Wisconsin Kemp Biological Station and at the Northern Highland/American Legion State Forest near Lake Tomahawk, WI (45° 48′ N, 89° 35′ W); at two sites at the Fermi National Accelerator Laboratory near Batavia, IL (41° 51′ N, 88° 22′ W); and at two sites on the Oak Ridge Reservation near Oak Ridge, TN (36° 35′ N, 84° 55′ W). Seeds were dewinged, surface sterilized for 20 min in 10% (v/v) H_2O_2

Table 1. Descriptive measures of genetic variability across 58 loci for 27 sugar maple open-pollinated families from six stands within three regions.

Region/ Stand/Family	Sample size	% polymorphic loci [1]	Mean expected heterozygosity [2]
Northern/			
Kemp Station/1	14	55.2	0.220 ± 0.028
Kemp Station/2	16	56.9	0.201 ± 0.027
Kemp Station/3	21	62.1	0.249 ± 0.027
Kemp Station/4	22	55.2	0.215 ± 0.027
Kemp Station/5	17	58.6	0.231 ± 0.028
State Forest/1	22	56.9	0.225 ± 0.028
State Forest/3	21	58.6	0.216 ± 0.026
State Forest/4	22	62.1	0.241 ± 0.028
State Forest/5	18	62.1	0.210 ± 0.026
Central/			
Site 50/1	18	60.3	0.214 ± 0.027
Site 50/2	28	51.7	0.204 ± 0.026
Site 50/3	27	50.0	0.199 ± 0.027
Site 50/4	22	48.3	0.201 ± 0.028
Site 50/5	19	50.0	0.205 ± 0.029
Site 29/1	29	69.0	0.254 ± 0.025
Site 29/2	19	62.1	0.235 ± 0.027
Site 29/3	21	65.5	0.229 ± 0.025
Site 29/4	15	63.8	0.217 ± 0.025
Southern/			
Park City/2	22	50.0	0.211 ± 0.029
Park City/3	21	48.3	0.208 ± 0.028
Park City/4	22	60.3	0.245 ± 0.027
Park City/5	22	58.6	0.205 ± 0.025
Park City/6	16	46.6	0.197 ± 0.029
Walker Branch/1	21	46.6	0.208 ± 0.028
Walker Branch/3	11	46.6	0.180 ± 0.028
Walker Branch/6	20	55.2	0.205 ± 0.026
Walker Branch/7	21	51.7	0.206 ± 0.027

[1]Significant at $P < 0.05$.
[2]Unbiased estimate (Nei 1978) ± SE

and 0.5% (v/v) Tween-40 (polyoxyethylene 20 sorbitan monopalmitate) and stratified in moist paper towels at 4 °C for 90–120 days. Germinating seedlings were transferred to individual pots and grown for 30–60 days in the greenhouse under 16-h days. For most samples, approximately 50 mg leaf tissue were collected by punching four 1.0-cm diam. leaf discs using the lid of a micro centrifuge tube. Some samples were processed from whole cotyledons minus the seed coat. Genomic DNA was extracted from leaf or cotyledon tissue following a modified CTAB protocol previously developed for aspen population studies (Tuskan *et al*. 1996). DNA was quantified fluorometrically and diluted to 1 ng μL^{-1} for use in the RAPD polymerase chain reaction. A total of 547 genotypes from 27 half-sib families were examined in this study (Table 1).

Genetic data

RAPD reactions were set up under the following conditions: Each reaction contained 50 mM KCl, 10 mM Tris-HCl pH 8.0, 1 mL L^{-1} Triton X-100, 2.5 mM $MgCl_2$, 200 µM each deoxynucleotide triphosphate, 0.5 U *Taq* polymerase (Promega Corp., Madison, WI), 100 µg mL^{-1} bovine serum albumin, 1 ng template DNA, and 10 ng decanucleotide primer (Operon Technologies, Inc., Alameda, CA and University of British Columbia, Vancouver, BC) in a 10 µL volume. Amplification reactions of all genotypes by a single primer were set up with aliquots of an identical mastermix that contained all components except template DNA. Negative controls (reactions containing mastermix but no template) and internal positive control standards were used across reaction sets. Thermoreactions consisted of 35 cycles of denaturation at 94 °C for 5 s, annealing at 36 °C for 30 s, and polymerization at 72 °C for 1 min. Amplified DNA fragments were electrophoresed on 1.5% (w/v) agarose gels in 0.5X TBE at 5 V cm^{-1} and visualized with ethidium bromide (0.1 µg mL^{-1}). Gels were photographed under UV light and scored for presence or absence of DNA fragments representing amplified DNA markers.

Analysis of RAPD markers

The analysis of RAPD marker polymorphisms as alleles assumes (i) Mendelian segregation (ii) Hardy–Weinberg allele frequencies, and (iii) that dominant (marker present) alleles and recessive (marker absent) alleles, respectively, are identical in state among individuals (Apostol *et al*. 1996). Markers which occurred at a frequency greater than 0.995 for all three regions were discarded (Lynch & Milligan 1994), as were individual genotypes missing marker data due to amplification failure for greater than 15% of the data points.

Measures of genetic diversity within and among regions, stands and families were generated by analysing data with the computer programs RAPDFST, RAPDBIOS, RAPDDIST (Black 1997), BIOSYS-1 (Swofford & Selander 1981), and PHYLIP 3.5C (Felsenstein 1993). rapdfst was used to calculate modifications of Wright's F_{ST} (Wright 1951), defined as the ratio of the observed variance in allele frequencies among regions, stands, and families in a nonhierarchical fashion to maximum variance in allele frequencies in the overall population. Modifications include the calculation of Weir & Cockerham's (1984) Theta (θ), which is a jack-knife (numerical resampling technique that estimates bias and variance for genetic parameters) estimate of Wright's F_{ST} adjusted for small, unequal sample size, and Lynch & Milligan's (1994) F_{ST}, which is based on estimates of excess heterozygosity expected when using RAPD markers. These estimates were used preferentially for analysis of RAPD data over standard F_{ST} to avoid error associated with the difference in using dominant RAPD markers vs. codominant isozyme or RFLP markers (Apostol *et al*. 1996). RAPDBIOS was used to estimate the frequency of the A and B alleles representing presence and absence, respectively, of the markers and to produce a datatype = 3 data set for biosys-1. The Lynch & Milligan (1994) correction for small sample size option was not used, since preliminary analysis showed slight or nonsignificant differences in allele frequency reporting using that method. Hierarchical estimates of variance components and Wright's (1978) standard fixation coefficients (F_{ST}) were calculated using the STEP HIERARCHY option of BIOSYS-1.

Goodness-of-fit of allele frequencies was measured using a contingency χ^2 analysis at each locus under the null hypothesis that allele frequencies were equal among subpopulations (Sokal & Rohlf 1981). Genetic variation within families was measured in terms of mean expected heterozygosity (H_s, the mean frequency of heterozygotes under Hardy–Weinberg expectations) and percent polymorphic loci (P_p, the proportion of genetic loci having greater than one allele). Variation among populations was assessed using Nei's (1972) genetic distance:

$$D = -\ln [N_{AB} / (\sqrt{N_{AA} N_{BB}})],$$

where N_{AB} is the probability that two alleles are identical across populations A and B; N_{AA} is the probability that two alleles chosen randomly from population A are identical, and N_{BB} is the probability that two alleles chosen randomly from population B are identical. RAPDDIST was used to compute 1000 bootstrap (resampling method where some number n observations are drawn at random, with replacement, so that each observation has an equal chance of being drawn, in order to obtain information about the distribution of estimates) pairwise distance matrices among families which were input into NEIGHBOUR (Felsenstein 1993), a neighbour-joining algorithm (Saitou & Nei 1987), in order to examine relationships of genotypes among families, stands, and regions.

Results

Three-hundred-and-six primers were initially screened using a bulked subsample of DNA templates from each regional population. Out of these primers, 22% (67/306) produced no amplification products, or amplified only faint, unscoreable markers. Thirty-two percent (98/306) amplified products that were essentially monomorphic, occasionally producing 1–2 faint markers that were polymorphic. Forty-six percent of the primers (141/306) amplified products that displayed interpopulation polymorphisms. Many of these primers produced excessive numbers of markers that were difficult to separate. Nine primers producing a total of 58 clearly discernable polymorphic markers with minimal background amplification were selected for population analysis. Primer sequences and marker descriptions are available from the authors.

Several markers representing unique alleles were observed in regional populations. One marker, $OPA15_{1125}$ (so designated by the name of the RAPD primer from which it was derived and by the molecular weight of the DNA marker fragment), is unique to the northern region, occurring in nine individuals representing four families and two stands. Otherwise, unique alleles were observed in the southern region only. $OPC7_{2100}$ is unique to the Walker Branch stand, occurring in 55% and 29% of individuals in two families. $OPA15_{1075}$ is common in the Park City stand, occurring in 18% to 63% of individuals in all five families. This marker is also present in three individuals representing two families in the Walker Branch stand. $OPH5_{1400}$ occurs exclusively in four Park City families, at frequencies ranging from 32% to 64%. $OPH5_{1025}$ is remarkable for its absence from the southern region, although it is present in 14% of northern and 20% of central region

Table 2a. Estimates of θ (jackknife) and F_{ST} (± SD) averaged over all loci across genotypes within and between sugar maple stands.

Region/Stand	Weir and Cockerham's θ [1]	Lynch and Milligan's F_{ST} [2]
Northern/	0.025 ± 0.009	0.024 ± 0.042
Kemp Station	0.170 ± 0.030	0.181 ± 0.144
State Forest	0.282 ± 0.038	0.272 ± 0.185
Central/	0.058 ± 0.018	0.071 ± 0.080
Site 29	0.173 ± 0.038	0.218 ± 0.178
Site 50	0.223 ± 0.025	0.271 ± 0.156
Southern/	0.105 ± 0.016	0.101 ± 0.081
Park City	0.246 ± 0.030	0.273 ± 0.180
Walker Branch	0.350 ± 0.045	0.366 ± 0.233
Across regions	0.077 ± 0.010	0.086 ± 0.057

[1]Weir & Cockerham (1984)
[2]Lynch & Milligan (1994)

Table 2b. Variance components and *F* statistics (Wright 1978) combined across 58 RAPD loci representing genetic differences among (i) families within stands (ii) stands within region and (iii) across regions.

Within source	Among source	Component	F_{ST}
Family	Stand	3.90221	0.238
Family	Region	4.70928	0.273
Family	Total	5.04702	0.287
Stand	Region	0.80707	0.047
Stand	Total	1.14482	0.065
Region	Total	0.33775	0.019

Table 3. Nei's Genetic Distance (*D*) coefficients (Nei 1972) summarized for four to five families in two stands in each of three regions for a total of 547 sugar maple genotypes.

Between regions

Regions	(*D*)
Northern/Central	0.0137
Northern/South	0.0290
Southern/Central	0.0493

Between stands within regions

Region	(*D*)
Northern	0.0335
Central	0.0373
Southern	0.0474

Among families within stands within regions

Region	Stand	(*D*)	Range (*D*)
Northern	Kemp Station	0.07	0.0361 to 0.1045
	State Forest	0.0953	0.0688 to 0.1279
Central	Site 50	0.0824	0.0366 to 0.1331
	Site 29	0.1218	0.0939 to 0.1490
Southern	Park City	0.1042	0.0634 to 0.1534
	Walker Branch	0.1111	0.0939 to 0.1353

Among families across stands within regions

Region	(*D*)	Range (*D*)
Northern	0.0898	0.0361 to 0.2001
Central	0.1083	0.0366 to 0.1685
Southern	0.1248	0.0634 to 0.2310

genotypes. Four additional markers are present only in southern populations but had to be discarded due to scoring difficulties or unacceptably low frequency in the populations (Lynch & Milligan 1994). The probability of not detecting an allele within a particular stand at a frequency greater than or equal to 5% [$(1-0.05)^N$ where N = number of uncorrelated gametes sampled per stand)] ranged between 0.2% and 1.6%, with an average of less than 1%.

Genetic variability metrics among regions only indicate that the southern region has the highest average percent polymorphic loci ($P_p = 91.4$) and mean expected heterozygosity ($H_s = 0.300$) compared with the northern ($P_p = 81.0$, $H_s = 0.298$) and central ($P_p = 77.6$, $H_s = 0.288$) regions. However, among families across regions, the southern region has the lowest average number of polymorphic loci and expected heterozygosity ($P_p = 51.2$, $H_s = 0.207$), while the northern region has the highest ($P_p = 58.6$, $H_s = 0.223$)(Table 1).

Independent estimates of fixation indices (θ and F_{ST}) across genotypes within stands are significantly higher for the southern region than for northern and central regions, and indicate that approximately 25–35% of the total variation within the southern region is attributable to differences among families within stands (Table 2a). Both θ and F_{ST} produced comparable values; however, θ estimates were slightly but consistently lower. Since the standard deviation associated with F_{ST} is larger, we preferentially refer to θ in this discussion. The amount of variation attributable to differences between stands within regions is higher for the southern region (10.5%) than for the northern (2.5%) or central regions (5.8%). Among families across all regions, allelic differences account for 7.7% of the total variation (Table 2a). However, hierarchical *F*-statistics (Wright 1978) indicate that less than 2% of the total variation is attributable to allelic differences among regions (Table 2b). Differences within stands among regions account for less than 5% of the variance. The largest proportion of the total variation (29%) is attributable to allelic differences within families, with allelic differences among individuals accounting for

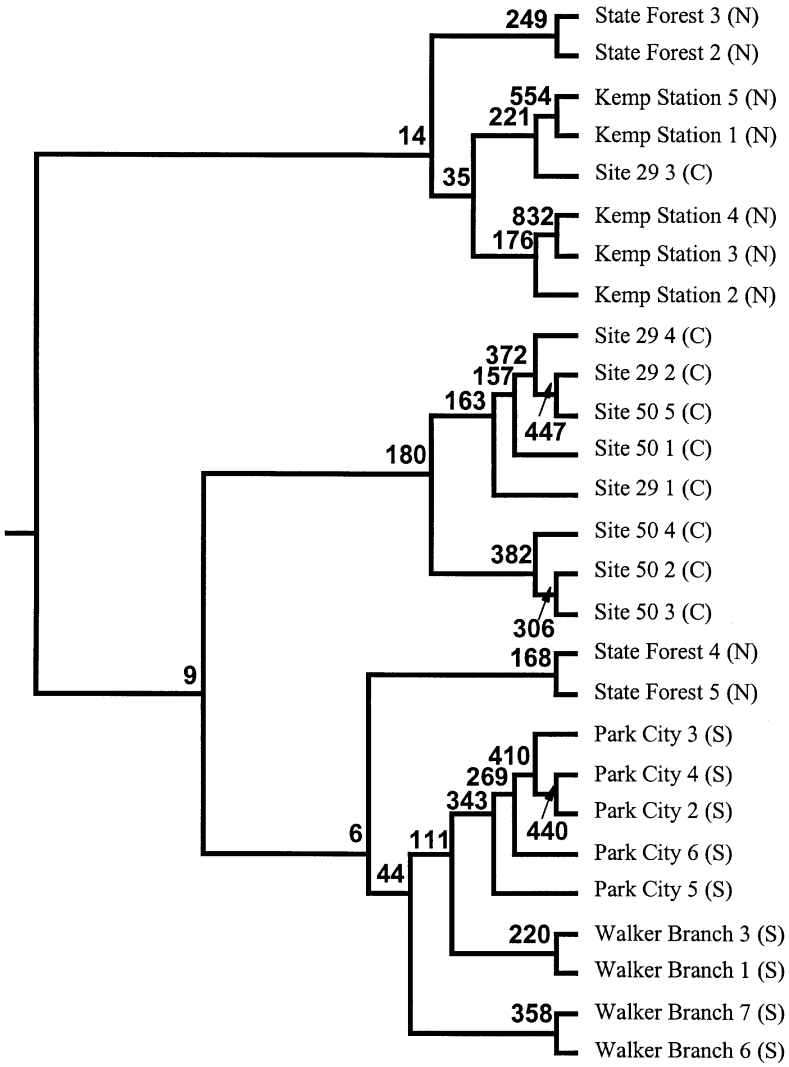

Figure 1. Neighbour-joining analysis of relationships among families across regions based on Nei's (1972) genetic distance matrices bootstrapped 1000 times. Numbers at the nodes indicate the number of times the group consisting of families to the right of the node are supported out of 1000 dendrogram topologies. N, northern region; C, central region; S, southern region.

the majority of the total variation across families, stands, and regions (Table 2b).

Allele frequencies at all but four loci are highly significantly different ($P < 0.001$) among regions according to contingency χ^2 analysis (data not shown). Allele frequencies between stands were not significantly different ($P < 0.05$) for 58%, 34%, and 29% of loci in northern, central, and southern regions, respectively. Among families within stands within regions, differences in allele frequencies are not significantly different for 33–43% (northern), 28–31% (central), and 26–28% of southern loci.

Pairwise comparison of genetic distance coefficients (Nei 1972) suggests decreasing similarity of genotypes from among regions, followed by similarity between stands within regions, and then similarity among families within stands within regions (Table 3). Average genetic distance among regions is low, especially between northern and central regions ($D = 0.0137$), indicating that, on average, genotypes within these regions shared nearly 99% of the sampled alleles. Average genetic distance between stands within regions is only three to four percent. Families within stands within regions share an average of 98% to 93% of their alleles (Table 3). The widest degree of similarity among genotypes is found in the southern region, where similarity estimates among genotypes within families range from 77% to 94%.

Neighbour-joining analysis based on these same distance coefficients suggests a loose association of families and regions (Fig. 1). However, the probability of the regional associations being statistically meaningful is low. Bootstrap support is high for some, but rarely all, families within stands. For example, although the node consisting of all five Park City families is supported in 34% of 1000 possible topologies, this is the only case where an entire stand is clustered into a single group with greater than 25% bootstrap support. Generally,

support is strongest for two to three families within a stand. For example, the node consisting of individuals derived from mothers Kemp Station 3 and 4 is supported in 83% of the topologies, and the node consisting of Kemp Station 1 and 5 individuals is supported 55% of the time.

Discussion

In their review of isozyme diversity in plant species, Hamrick & Godt (1990) suggest that there is little influence of regional distribution in levels of genetic variation found within plant populations. We did not expect significant genetic differentiation within regions given the high level of gene flow among sugar maple stands (Gabriel & Garrett 1984; Foré *et al*. 1992). Our study suggests that most of the variability is among individuals within families within stands, and this finding agrees with previous reports in the literature (Ledig & Korbobo 1983; Foré *et al*. 1992). It is apparent from the high number of shared alleles among regions that peripheral populations are not genetically isolated from the continuous population. However, overall diversity (as indicated by fixation coefficients within families, between stands, and within region; genetic distance among genotypes; and differences in allele frequencies) is highest in the southern region and lowest in the northern region. In the south, at least, where several unique alleles were observed, selection pressures may be acting on peripheral populations in a way that favours genotypic diversity. Although we expected to see a similar effect in our survey of northern genotypes, we recognize that the northern population may not be the best representative of the periphery of sugar maple's range. Northern genotypes were collected at 45°N, although the northern distribution of maple extends to nearly 49°N. Therefore, this population has a buffer zone of greater than 150 km. On the other hand, the southern population was probably more representative of a peripheral population, since maple's range rarely extends below 35°N, and the genotypes used in this study were collected at 36°N.

Using isozymes, Young *et al*. (1993) observed genetic structure in sugar maple among populations across the species range, among stands within a single region, and among individuals within stands. They found that the easternmost population sampled had the lowest heterozygosity of the regional populations and a low percentage polymorphism. They speculated that it could either be the result of genetic drift and/or selection at the eastern limit of the species range. However, Perry & Knowles (1989) found levels of variation in sugar maple at the northern limit of its range to be consistent with variation found in other hardwoods: $P_p = 38.2$ and $H_s = 0.110$. In our study, heterozygosity and percentage polymorphic loci are higher in the southern region when compared to the central and northern regions, but when compared as families across regions, overall heterozygosity and percentage polymorphic loci are lower in southern families. This suggests that there is less gene flow occurring among families within the southern region than among families within other regions, most likely because population structure is different in the south. Sugar maple is soil-site specific in the south, but found on a wide variety of soil types in the north; therefore, at the southernmost edge of the range sugar maple occupies smaller, more widely separated areas (Godman *et al*. 1990). It is evident, however, from the high degree of similarity among genotypes across regions that gene flow is not severely restricted.

In our study of RAPD markers, estimates of percentage polymorphism (Table 1) are higher than in the Perry & Knowles's (1989) study; however, this result was expected because the number of markers generated from a single RAPD primer is generally much higher than the number of alleles at most isozyme loci (Weising *et al*. 1995). Since there is a positive relationship between the amount of polymorphism and the degree of heterozygosity, the overall mean expected heterozygosity across families ($H_s = 0.216$) is higher than, but consistent with, heterozygosity estimates based on isozymes in other hardwoods (Hamrick & Godt 1990). F_{ST} estimates using isozymes indicate that approximately 3% of the observed variation occurs among stands (Perry & Knowles 1989). This estimate is consistent with estimates derived from RAPD data (Table 2b), which demonstrate that variation among stands accounts for approximately 6.5% of the total variation. Overall fixation coefficients across regions ($\theta = 0.077$; Table 2a) were similar to those observed by Young *et al*. (1993) ($F_{ST} = 0.049$) using allozyme data. However, Young *et al*. (1993) indicated that genetic variation among stands was lower than among regions. This is in contrast to RAPD data that suggest there is more variation among stands than among regions (Tables 2a and b).

High variation among families in the southern stands could have important implications in modelling species' responses to global climate change. Tirpak (1990) claims that forest productivity may increase in the north as hardwoods replace conifers, but emphasizes that the real threat to productivity is in the south, where forest mortality would be most severe due to reduced precipitation and increased evapotranspiration. However, in sugar maple there is evidence that southern genotypes may more easily tolerate temperature and moisture extremes (Kriebel 1957). Plants from habitats with large temperature variants over the growing season often possess greater acclimation potential over a wide

range of temperatures (Berry & Björkman 1980). Short-term physiological acclimation of this type has been noted in sugar maple (Gunderson *et al*. 2000), and the capacity for such adjustments may allow individuals to survive the episodic temperature stresses that occur more frequently at the periphery of their range. Over time, adaptations to environmental change are certain to occur (Orians 1996). The question is whether the rate of environmental change will exceed the species' ability to adapt to the predicted rapid increases in temperature, or whether selection is likely to act at all upon species which are already composed of broadly responding genotypes (Bazzaz 1996). Many models rely on a species' predicted response to elevated temperature, while others use temperature–response relationships based on current species' distribution and temperature-related determinants (e.g. growing degree days) of that distribution (Austin 1992; Solomon & Bartlein 1992). The GISS (Hansen *et al*. 1983) and GFDL (Manabe & Wetherald 1987) -based sugar maple range shift potentials, as described by Davis & Zabinski (1992), assume that a species grows only in a climate with temperature and precipitation identical to its current range. These models also assume a migration rate of 100 km per century, which is double the maximum rate ever recorded for temperate trees (Tirpak 1990).

Since most models assume that climate is the primary determinant of range limits, extreme range shift predictions could actually be an artifact of the model (Loehle & LeBlanc 1996). Although potential range shifts are high (up to 700 km per century), actual migration could be limited because of slow rates of seed dispersal. For example, range extension in sugar maple in response to glacial retreat in the Holocene varied from 10 to 20 km annually (Tirpak 1990).

What does this all mean in light of global-scale environmental disturbance? The broad genetic variability of sugar maple populations, in combination with the observed broad photosynthetic temperature response (Gunderson *et al*. 2000), suggests that sugar maple may be less affected by such disturbance than would less widely dispersed species with a more narrow genetic base. Population fragmentation, which can reduce genetic diversity and thus affect responses to environmental change, is expected to have a larger impact on species with broader geographical ranges, where the loss or isolation of some populations may affect the genetic structure of the species (Holsinger 1993). However, fragmentation does not seem to completely eliminate gene flow in sugar maple (Foré *et al*. 1992; Ballal *et al*. 1994), suggesting that gene flow mechanisms may buffer populations against loss of diversity. Furthermore, the high degree of variation within sugar maple implies that it may contain genetic mechanisms for adaptation given that natural selection can operate only in the presence of genetic variation. Finally, the amount of variation among families suggests that experiments relying on a few genotypes in growth chamber or open-top chamber experiments may not adequately represent the diversity present in the species. In this case, the number of individuals used may not be as important as is their representation of the range of genotypes present in natural populations. Many experiments attempt to limit genetic variation in order to detect a response; such methods, designed to select the 'average tree', could have very profound effects on models of forest migration. For sugar maple, the current data suggest that selecting representatives from different families would be more informative than selecting individuals from different regions or even from random genotypes. Experiments designed to predict species' response to environmental stresses would be more constructive if the degree and organization of genetic variation represented in the species is considered. By using genetic structure as a guide, researchers can be more definitive in making species-wide inferences from small-scale experiments.

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