strong for those from the Taygetos and the Parnassos in general.

Several morphological characteristics of the needles, lateral branch and buds were studied. They were chosen in relation to their potential value as indicators of drought adaptation (stomata on the upper side of the needle, apex shape indicative of cuticular thickness, etc.) or of hybridization with *Abies alba* (pubescence of annual lateral branch). All do not have the same value. The frequency of individuals with pointed apexes is higher in the south of the native region, but does not show a regular geographical evolution. However, the frequency of individuals with a low stomatal density on the upper side of the needle increases regularly from the southern to the northern part of the range; in the same way the frequency of pubescent individuals passes from 6% in the Menalon stands (Peloponnesos) to 33% in those from the southern Pindos.

Flushing, pubescence of lateral branch and stomatal density on the upper side of the needle are stable characteristics with age. Notable in the juvenile stage, the variability in apex shape seems to disappear over time. Height growth, measured at the juvenile stage in nursery, gives little information on later growth. The search for early selection criteria for firs remains a problem of primary importance.

Individual variation and the frequency of pubescent individuals makes it possible to measure the degree *Abies alba* has introgressed into different stands. Although much more noticeable in the northern part of the region studied (Pindos mountains), which is traditionally recognized as the southern limit of the chosen area of the hybrid fir *Abies borisii-regis*, this introgression remains visible to a lesser extent all the way into the southern Peloponnesos.

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Sources of Allozymic Variation in Thuja occidentalis in Southern Ontario, Canada

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Summary

Allozyme variation at 11 loci for seven enzyme systems was studied in three swamp and three cliff populations of *Thuja occidentalis* L. in southern Ontario. Overall genetic variability was extremely small, with 82% of loci monomorphic for all samples. Inbreeding coefficients indicated that no significant inbreeding occured at any site. χ^2-tests showed no significant differences in allele frequencies among the six stands; unbiased genetic distances among all stands were very small (average 0.0015), and no correlation between genetic and geographic distance was found. Of the total variability, 96.9% was among trees within stands, 1.9% among stands from the same habitat, and only 1.2% between habitat types. No variability was found when several branches from the same tree were compared. The number of effective migrants between

cliffs and swamps per generation was estimated as 21, and between sites as 12. It was concluded that the patterns of intraspecific variability, at the allozyme level, of *T. occidentalis* in southern Ontario are not adequately described by the concept of "wet" and "dry" ecotypes.

Key words: ecotypes, cliffs, swamps, isoenzyme variation, *Thuja occidentalis.*

Zusammenfassung

Die Variationsmuster von 11 Isoenzym-Loci, die für 7 Enzyme codieren, wurden in drei Sumpf- und drei Kliffbeständen von *Thuja occidentalis* L. in Südontario untersucht. Die genetische Variation war gering: 82% der Loci waren monomorph in allen untersuchten Bäumen. Die Inzuchts-Koeffizienten zeigten, daß in keinem der Bestände signifikante Inzucht stattgefunden hatte. χ^2-Tests bewiesen, daß sich die Allelhäufigkeiten an den 6 Standorten nicht unterschieden. Der genetische Abstand zwischen den 6 Beständen war sehr gering (im Durchschnitt 0,0015) und nicht mit der geographischen Entfernung korreliert. 96,9% der gesamten Variation befand sich zwischen den Bäumen innerhalb eines Bestandes, 1,9% zwischen den Beständen des gleichen Typs und nur 1,2% zwischen den Sumpf- und Kliff-Bestandstypen. Mehrere Zweige von dem gleichen Baum zeigten keine genetische Variation. Es wurde berechnet, daß pro Generation 21 erfolgreiche Übersiedlungen zwischen Sümpfen und Kliffs und 12 zwischen verschiedenen Standorten stattfinden. Die genetischen Variationsmuster innerhalb der Art *T. occidentalis* in Südontario lassen sich daher nicht mit dem Konzept von Feucht- und Trocken-Ökotypen erklären.

Introduction

The concept of ecotypes has been important historically in the study of intraspecies genetic variability in plants (Turesson, 1922a, b; Gregor, 1944). As defined by Davis and Heywood (1967), the term "ecotype" refers to any population which is differentiated from other populations with respect to any feature which can be attributed to the selective action of environmenal factors. Ecotypic variation is distinguished from variation at the species level by the presence of gene flow; from the products of this gene exchange, each environment then sorts out those genotypes which are best fitted to survice (Gregor, 1944). A large body of literature exists demonstrating the existence of ecotypes in certain forest trees (Zavitkovsky and Ferrell, 1968; Teich and Holst, 1974; Unterscheutz et al., 1974; O'Reilly et al., 1985; Stutz and Mitton, 1988).

Population genetic studies based on electrophoretically detectable variation in isoymes have more recently revealed inadequacies in the ecotype concept. Such studies have made clear: 1. that intraspecific genetic variation is a universal phenomenon existing to some degree in nearly all species with a wide ecological distribution, and 2. that it exists simultaneously on a number of different spatial scales, from large-scale geographic or regional variation down to differences among clusters of individuals within local stands (Linhart et al., 1981; Loveless and Hamrick, 1984; Plessas and Strauss, 1986). The term "ecotype" has been used by different authors to describe variation on any one of these scales, usually without giving information about variability at other scales (Squillace and Bingham, 1958; Wells, 1964; Billings et al., 1971; Teich and Holst, 1974; Unterscheutz et al., 1974). For this reason some authors argue that the term is ambiguous and fails to provide a useful concept (Spurr and Barnes, 1980). A much more useful approach is that taken by a number of recent studies which partitioned the total genetic variation found within a species among the different spatial scales (Yeh and Layton, 1979; Yeh and O'Malley, 1980; Linhart et al., 1981; El-Kassaby and Sziklai, 1982; Fins and Seeb, 1986; Plessas and Strauss, 1986; Bousquet et al., 1987; Cheliak et al., 1988; Moran and Adams, 1989).

A frequently cited example (e. g. Krebs, 1972; Spurr and Barnes, 1980) for ecotypic differentiation in forest trees has been that of eastern white cedar (*Thuja occidentalis* L.). Throughout its range, this species is found both in very dry ("upland", old field or rock outcrop) and very wet ("lowland" or swamp) locations (Habeck, 1958; Blanchet, 1982). Based mainly on differences in root growth between upland and lowland seedlings when grown in different soils, Habeck (1958) and Musselman et al. (1975) concluded that *T. occidentalis* shows local ecotypic differentiation with respect to drought adaptation. However, the design of the above experiments did not take into account the variation among individual stands and trees, and therefore conclusions regarding the presence or absence of ecotypes within this taxon may be premature. The present study used electrophoretic techniques to examine variability in allozyme patterns between and within habitats (cliff and swamp "ecotypes") local stands, and individual trees of *T. occidentalis* in southern Ontario. Allozyme variation within and among *T. occidentalis* populations has been previously studied in northwestern Ontario (Perry et al., 1990), but no distinction between wet and dry habitats was made.

Methods

Sample collection

Thuja occidentalis was sampled at three dry (cliff) and three wet (swamp) sites typical of similar ones found extensively throughout southern Ontario (*Fig. 1*). *T. occidentalis* was the dominant canopy forming species at all sites.

One shoot of the current year's growth was collected in the fall of 1987 from a total of 162 trees (between 16 and 54 trees per stand, except for Campbellville Swamp, where only six trees were sampled). *T. occidentalis* shows exten-

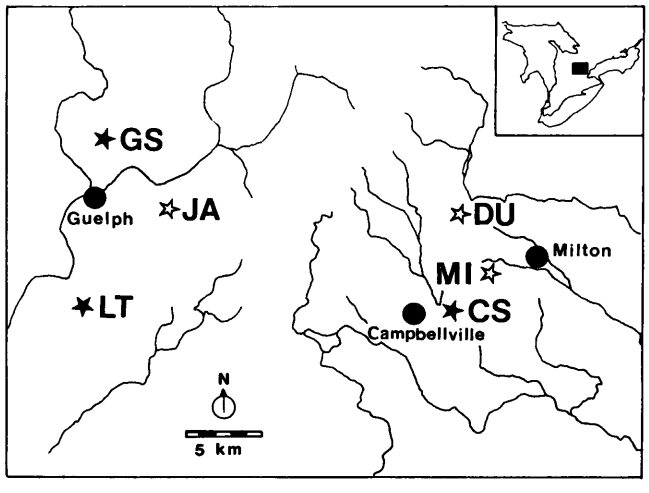

Figure 1. — Relative locations of the six stands sampled in southern Ontario. Cliff stands (open stars); MI, Milton; DU, Dufferin; JA, Jail. Swamp stands (solid stars): GS, Guelph Swamp; CS, Campbellville Swamp; LT, Little Tract.

sive vegetative reproduction by layering (POTZGER, 1937), and distances between sampled trees were large enough to ensure that no vegetatively reproduced shoots from the same individual were included. To estimate the likelihood that some of the genetic variability found was present within individuals and due to somatic mutations, multiple samples (consisting of six different growing tips) were taken from a total of 14 trees at four sites.

Sample preparation and electrophoresis

Approximately 50 mg of shoot tip tissue were placed in a chilled ground-glass test tube together with 1 ml of extraction buffer (pH 7.0; 0.1 M Tris, 0.5 M sucrose, 12 mM Cysteine HCl, 2% ascorbic acid, 1% Tween 80; developed by L. DAISLEY, G. BUCHERT and K. FISCHER, Ontario Tree Improvement and Forest Biomass Institute, pers. comm.) and homogenized using a motor-driven ground-glass pestle. Isozyme variation was assessed by horizontal starch gel electrophoresis, following standard procedures (HARRIS and HOPKINSON, 1976). The following gel/electrode buffer system was used throughout (developed by L. DAISLEY, G. BUCHERT and K. FISCHER, Ontario Tree Improvement and Forest Biomass Institute, pers. comm.): electrode buffer: 0.04 M citric acid (monohydrate), 0.084 M Tris, adjusted to pH 6.7 using N-(3-aminopropyl)morpholine; gel buffer: 0.134 M Tris, 0.065 M Histidine, adjusted to pH 7.0 with HCl. Two standards whose banding patterns were known (a known genotype of *Silene latifolia* POIRET) were run on each gel to allow cross-comparison of bands between different gels. Each sample was run in duplicate or triplicate on different gels.

A total of 14 enzyme systems were initially assayed. Seven of these (Aldolase (ALD), Esterase (EST), Glyceraldehyde-3-phosphate dehydrogenase (GAPDH), Glutamate dehydrogenase (GDH), Aspartate aminotransferase (AAT), Peroxidase (PER), and Phosphoglucomutase (PGM)) produced faint or blurry phenotypes that were not consistently scorable and were subsequently omitted. The seven systems used for analysis are listed in *Table 1*, along with the number of loci scored for each, the number of loci that were variable, and the number of alleles observed at each variable locus.

Table 1. — Enzyme systems assayed; references for stain recipes; number of loci identified; number of variable loci, and number of alleles observed at each variable locus (in parentheses).

Enzyme (Abbreviation)	reference[a]	loci	var.loci (alleles)
Diaphorase (DIA)	1	1	0
Glucose-6-phosphate dehydrogenase (G6P)	2	1	0
Isocitric dehydrogenase (IDH)	3	1	0
Leucine aminopeptidase (LAP)	2	1	0
Malate dehydrogenase (MDH)	2	3	1 (3)
Phosphoglucose isomerase (PGI)	4	2	0
6-phosphogluconic dehydrogenase (6PGD)	3	2	1 (3)

[a]) 1 = HARRIS and HOPKINSON, 1976
2 = ROOSE and GOTTLIEB, 1976
3 = SHAW and PRASAD, 1970
4 = GOTTLIEB, 1973

Table 2. — Allele frequencies for the two polymorphic loci at the three cliff stands (Milton — MI, Dufferin — DU, Jail — JA) and the three swamp stands (Guelph Swamp — GS, Little Tract — LT, Campbellville Swamp — CS); inbreeding coefficient, F_{IS}; and χ^2-values and associated probabilities from the tests comparing observed genotype frequencies at each stand with HARDY-WEINBERG expectations[a]).

Locus	Allele	MI	DU	JA	GS	LT	CS
MDH	1	0.94	0.91	0.83	0.84	0.97	1.00
	2	0.06	0.09	0.17	0.16	0.03	0.00
F_{IS}		0	-0.19	+0.39	-0.14	0	-
χ^2		0.001	0.18	2.29	0.15	0.006	-
p		0.97	0.67	0.13	0.70	0.94	
6PGD	1	0.77	0.87	0.78	0.94	0.89	0.92
	2	0.23	0.13	0.22	0.06	0.11	0.08
F_{IS}		-0.14	-0.09	+0.18	-0.09	-0.10	-
χ^2		0.55	0.07	0.62	0.04	0.06	0.01
p		0.46	0.79	0.43	0.84	0.81	0.92

[a]) No χ^2-test was performed when observed and expected frequencies were identical.

Calculations

Allele frequencies were calculated for each stand as well as for each habitat. For each stand where 16 or more trees were sampled, the inbreeding coefficient

F_{IS} = 1 — (observed % heterozygotes / expected % heterozygotes) was calculated. F_{IS} substantially greater than zero indicate inbreeding, while F_{IS} of or near zero characterize random-mating populations (WRIGHT, 1931). Contingency χ^2-tests were performed to compare allele frequencies among individual stands.

Gene diversity analyses (NEI, 1973; CHAKRABORTY, 1980) were performed separately for each polymorphic locus to partition H_T (the overall allozyme variation among all *T. occidentalis* sampled in this study), into its components, H_S (the genetic diversity within habitats) and D_{ST} (the genetic diversity between habitats). H_S was further subdivided into H_C (the genetic diversity within stands within habitats) and D_{CS} (the genetic diversity among stands within habitats). The proportion of the total variation attributable to differences between habitats, $G_{ST} = D_{ST} / H_T$, was then calculated, as was the proportion of the total variation attributable to differences among stands within habitats, $G_{CS(T)} = D_{CS} / H_T$. This approach has been outlined by ALDEN and LOOPSTRA (1987).

NEI's (1978) unbiased genetic distance was calculated between all pairs of stands. The unbiased genetic distance was preferred over the standard genetic distance (NEI, 1972) because it corrects for small sample sizes. The effective number of migrants per generation, N_em (where N_e is the effective population size, and m is the rate of migration; CROW, 1986) was estimated as

$$N_em^{stand} = (1 - G_{ST}) / (4\ G_{ST})$$

for migrants between stands, and

$$N_em^{habitat} = (1 - G_{CS\,(T)}) / (4\ G_{CS\,(T)})$$

for migrants between habitats. Averages over the two polymorphic loci were used.

Results

Genetic variation within T. occidentalis

Of the 11 loci that were consistently scorable, nine (or 82%) were monomorphic in all six stands sampled (*Table 1*). One locus (6PGD) was polymorphic in all populations, and one locus (MDH) was polymorphic in all but the Campbellville Swamp population (where the number of individuals sampled was very small).

Table 2 shows the allele frequencies for the two scorable polymorphic loci. Inbreeding coefficients near or smaller than zero were found for all but the Jail population. The χ^2-tests showed observed genotype frequencies to agree with those expected under HARDY-WEINBERG equilibrium.

Genetic differentiation between habitats and among stands

The gene diversity analysis gave very similar results for both of the polymorphic loci (*Table 3*). Of the total genetic diversity present in the 162 samples, an average (over both loci) of 96.9% was present among the individuals within a stand. Only 1.9% of the variability distinguished stands within habitats, and only 1.2% was attributable to differences between swamps and cliffs. Samples taken within the same tree or from different stems of a vegetatively produced cluster were identical at all loci without exception. The number of effective migrants between different stands each generation, N_em^{stand}, was estimated as 12.3 and the number of migrants between swamp and cliff, $N_em^{habitat}$, as 20.6.

Unbiased genetic distances between pairs of stands were very small, ranging from 0 to 0.0033 with a mean of 0.0015 (*Table 4*). This limited degree of differentiation among stands was further substantiated by the results of the χ^2-tests that showed no significant differences in allele frequency among stands for both of the polymorphic loci (6PGD: $\chi^2 = 8.443$, df = 5, p = 0.133; MDH: $\chi^2 = 11.034$, df = 5, p = 0.051). There was no significant correlation between genetic and geographic distances for all pairs of stands (r = —0.0066, p>>0.05). The average genetic distance between all pairs of cliff sites was 0.0005, as compared to 0.0007 for all swamp pairings.

Discussion

There was little variability in the allozyme markers studied among the six local stands, and very little differentiation between populations from contrasting cliff and swamp habitats despite their classification into ecotypes by previous workers (HABECK, 1958; MUSSELMAN et al., 1975). Habitat type accounted for only 1.2% of the total variability in enzyme markers, while 97% was present among individuals within stands. The unbiased genetic distances between stands were small when compared with published literature values for other conifers (e.g. FINS and SEEB, 1986; CHELIAK et al., 1988). This and the absence of significant differences in allele frequencies among stands suggests that all the trees studied, regardless of stand or habitat type, were members of a larger homogeneous population. If a species is abundant and common and its stands not well isolated from each other geographically, as is the case for *T. occidentalis* in southern Ontario, it possible for populations to be genetically linked by gene flow through a network of stands (BOUSQUET et al., 1987). Our results agree with those of PERRY et al. (1990), who found little heterogeneity in allozyme patterns among six northwestern Ontario populations of *T. occidentalis*.

The estimated number of effective migrants between cliffs and swamps each generation was 21. Migration of this magnitude would require intense selective pressure for genetic differences between habitats to be maintained, considering that as few as one migrant every other generation may be sufficient to obscure any differentiation due to genetic drift (WRIGHT, 1931; BOUSQUET et al., 1987). For *T. occidentalis*, our results indicate that gene flow outweighs the differential selective forces in the two contrasting environments. Gene exchange between adjacent sites can be accomplished by both pollen and seeds, both of which are wind-dispersed in *T. occidentalis* (CAULKINS, 1967). CAULKINS (1967) found that the seed dispersal of this species was limited to 50 m to 60 m by the short height of the trees and the density of the stands; however, this limitation is unlikely to apply to the exposed trees at the upper edge of cliffs in our study. Wind-borne pollen is known to travel distances much greater than those separating our cliff and swamp sites (SPURR and BARNES, 1980; BRIGGS and WALTERS, 1984). Previous studies have documented that wind-pollinated species tend to show little genetic differentiation among populations (LOVELESS and HAMRICK, 1984). The maintenance of large amounts of genetic variation among individual trees within populations has been found for other coniferous trees such as lodgepole pine (*Pinus contorta* DOUGL.; YEH and LAYTON, 1979), Monterey pine (*Pinus radiata* D. DON; PLESSAS and STRAUSS, 1986), Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO; YEH and O'MALLEY, 1980; EL-KASSABY and SZIKLAI, 1982), white spruce (*Picea glauca* (MOENCH) VOSS; ALDEN and LOOPSTRA, 1987), and tamarack (CHELIAK et al., 1988). Such variability may be due to selection in spatially and tem-

Table 3. — Results of gene diversity analysis for the two polymorphic loci.

Source of variability	Gene diversity parameter	MDH	6PGD	Average
Total	H_T	0.169 (100%)	0.278 (100%)	0.223 (100%)
Between habitats	D_{ST} (G_{ST})	0.001 (0.8%)	0.004 (1.6%)	0.003 (1.2%)
Within habitats	H_S	0.167	0.273	0.220
Among stands within habitats	D_{CS} ($G_{CS(T)}$)	0.005 (2.8%)	0.003 (1.2%)	0.004 (1.9%)
Within stands within habitats	H_C	0.163 (96.4%)	0.270 (97.2%)	0.216(96.9%)

Table 4. — Estimates of NEI's (1978) unbiased genetic distance (x 10^{-4}; below diagonal) and geographical distances (km; above diagonal) between six stands of *Thuja occidentalis*.

Stand[a]	MI	DU	JA	GS	CS	LT
MI	-	4.3	21.3	26.0	3.5	26.3
DU	480	-	18.5	23.0	6.0	24.8
JA	462	603	-	6.0	19.3	8.3
GS	2844	52	1379	-	24.5	10.8
CS	1462	16	3285	1168	-	23.0
LT	799	275	2089	882	0	-

a) See *Table 2* for stand codes.

porally heterogeneous environments and provide the potential for migration and adaptation to new habitats (ALDEN and LOOPSTRA, 1987).

Our allozyme based results contradict earlier studies on *T. occidentalis* by HABECK (1958), based on seed germination and seedling growth, and MUSSELMAN et al. (1975), who found evidence for clear genetic differentiation into "wet" and "dry" ecotypes of *T. occidentalis*. However, their studies did not determine the relative extent of differentiation within and among individual stands of each habitat type. MUSSELMAN et al. (1975) investigated two pairs of adjacent wet and dry stands separated by a larger geographical distance. They found ecotypic differentiation only for seedlings grown from seed collected at one of these locations, leading them to the conclusion that ecotypic differentiation was localized. However, since their collections at this pair of stands involved only four trees per stand (the sample sizes were larger for the pair of stands where no differentiation was found), and since they were unable to reproduce their findings with rooted cuttings from the same stands, their differences could have been due to within-stand variability. Habeck (1958) collected seed from a larger sample of approximately 12 trees at each of 26 stands and found clear differences in seedling root growth (the seed germination differences he reported are less convincing). However, he then pooled all collections from each habitat type, so that the relative amount of variability present within each stand is not known. It should also be noted that the conclusions of both HABECK (1958) and MUSSELMAN et al. (1975) were based mainly on rooting habit, which is known to be a particularly plastic trait in many forest trees (SPURR and BARNES, 1980).

A number of isozyme studies have been conducted on other conifers with similarly large ecological amplitudes as *T. occidentalis*. Among those, our results differ from those by STUTZ and MITTON (1988) on Engelmann spruce (*Picea engelmannii* (PARRY) ENGELM.), a species which also occurs on both dry and marsh sites. Even though adjacent dry and wet stands were close enough for both seeds and pollen to move between them, striking differences in genetic structure were found suggesting strong selective forces. For the same species, GRANT and MITTON (1977) found isozyme differentiation across a strong environmental gradient over small geographic distances at treeline. O'REILLY et al. (1985) found for black spruce (*Picea mariana* (MILL.) B.S.P.), another species analogous to *T. occidentalis* in its site preference, that upland and lowland stands could be distinguished using multivariate analyses on genotype frequencies. They also found a greater variability among upland stands than among lowland stands, which they explained by greater selective pressures on seedlings during establishment on dry upland sites. For *T. occidentalis*, in contrast, the average genetic distance between cliff sites was actually smaller than that between swamp sites. MORAN and ADAMS (1989) also found for Douglas-fir that north- and south-facing slopes did not differ in genetic structure, even though marked variation in quantitative seedling characters had been found previously between aspects.

With the exception of single stand, F_{IS} was negative or zero, and no evidence for inbreeding was found at any site. This agrees with the results of PERRY and KNOWLES (1990) for northwestern Ontario populations of *T. occidentalis*, where the proportion of heterozygotes agreed with HARDY-WEINBERG expectations when mature trees were sampled. The slight deficiency of heterozygotes in the Jail population could be due to its different age structure. The Jail site has only recently been colonized by *T. occidentalis*, with the oldest individuals about 45 years old and a high proportion of juveniles (LARSON, unpublished data); in contrast, the other cliff stands are old-growth with trees several hundred years old (LARSON, 1990). It has been shown that the proportion of heterozygotes may differ between different age classes due to the action of natural selection (PLESSAS and STRAUSS, 1986; STUTZ and MITTON, 1988; PERRY and KNOWLES, 1990).

The amount of genetic variability observed here was relatively small: only two of the eleven loci surveyed, or 18%, were polymorphic. Nine out of 18 loci, or 50%, were found to vary in northwestern Ontario populations of *T. occidentalis* (PERRY and KNOWLES, 1989; PERRY et al., 1990). Enzyme systems reported as polymorphic by these authors include 6PGD and MDH, as well as three other systems (AAT, PGM, and GDH) that showed signs of variability in our study, but could not be scored for all samples. Many other conifers, especially species which are widespread and common, harbor even larger amounts of variability (HAMRICK et al., 1979). For example, between 75% and 100% of all surveyed loci have been found polymorphic in *Pinus longaeva* BAILEY (bristlecone pine; HIEBERT and HAMRICK, 1983), *Pseudotsuga menziesii* (MERKLE and ADAMS, 1987; MORAN and ADAMS, 1989), and *Picea mariana* (O'REILLY et al., 1985). Low polymorphism has been reported for several other species with similarly large ranges as *T. occidentalis*, among them red pine (*Pinus resinosa* AIT.; FOWLER and MORRIS, 1977; SIMON et al., 1986), western larch (*Larix occidentalis* NUTT.; FINS and SEEB, 1986), and western red cedar (*Thuja plicata* DONN ex D. DON; COPES, 1981; YEH, 1988). In all three cases, a genetic "bottleneck" during the Pleistocene and regeneration of the present widespread population from a few individuals left during glaciation was suggested by the authors as a possible explanation for the low variability, and the same could apply to some degree to *T. occidentalis*. The relatively low genetic variability in this species could have restricted the possibilities for adaptive, local differentiation into ecotypes.

In conclusion, our results, based on allozyme variation, show that the patterns of genetic variation in *T. occidentalis* in southern Ontario are not consistent with previous classifications into "wet" and "dry" ecotypes (HABECK, 1958; MUSSELMAN et al., 1975). Plasticity of structure and function, rather than narrow genetic adaptation, may explain the wide ecological amplitude of *T. occidentalis*.

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Geographic Variation in Mississippi Loblolly Pine and Sweetgum

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Summary

Seed was collected along latitudinal transects from 575 loblolly pine (*Pinus taeda* L.) and 650 sweetgum trees (*Liquidambar styraciflua* L.) distributed throughout Mississippi and adjacent parts of neighboring states. Progenies were compared on the basis of various morphological and phenological traits both in the nursery and after 10 years in plantings in the southern, central, and northern parts of the study area. Patterns of variation are presented graphically on a series of maps.

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This paper is dedicated to the memory of Dr. Switzer.