Table 2. — Paternal and maternal influence on height growth of Douglas-fir.

Source	1966 Crosses			1968 Crosses		
	Height*	S^+	$n^\ddagger$	Height*	S^+	$n^\ddagger$
POLLEN						
Southern Oregon	372	7.2	67			
British Columbia	400	9.6	35			
Open-pollinated	400	6.2	105	146	3.3	48
Provenance C				141	8.8	6
Provenance D				136	6.3	12
Provenance K				141	10.7	4
Provenance L				144	5.9	15
Provenance O				147	5.7	16
SEED TREE						
Provenance A	383	14.6	12	122	11.2	3
Provenance B	369	15.0	12	156	18.5	1
Provenance C	360	16.1	11	121	4.4	24
Provenance D	389	12.7	19	130	6.0	11
Provenance E	430	25.5	4			
Provenance F	415	24.4	8	123	7.0	8
Provenance G	406	11.3	24	131	4.1	30
Provenance H	391	12.7	17	132	4.2	20
Provenance I	403	10.1	26	134	8.7	5
Provenance J	393	12.6	16	156	11.1	3
Provenance K	388	16.5	9			
Provenance L	425	12.9	15	175	13.3	2
Provenance M	407	25.0	4	137	5.9	12
Provenance N	352	15.0	11	171	13.3	2
Provenance O	377	17.6	8			
Provenance P	365	15.0	11	177	18.5	1

* Mean height (cm) estimated using least squares.
+ Standard deviation of the mean height.
‡ Number of plots.

nificant at P = 0.01 *(Table 2)*. The least significant difference (LSD) can show the importance of the difference in mean height of two pollen sources. In general, this is given by $2\sqrt{S_1^2 + S_2^2}$, where S_1 and S_2 are standard deviations of two sources. For example, the 95 percent LSD between 1966 southern Oregon and British Columbia crosses is approximately $2\sqrt{51.84 + 92.16}$, where 51.84 and 92.16 are the squares of the standard deviations 7.2 and 9.6. This is an approximation because lack of independence among comparisons is not accounted for in calculating the variance of difference; however, the approximation is adequate for most purposes. Progenies of the open-pol-

linated lot and of those obtained with pollen from the plus tree of British Columbia had equal height growth, but those of the southern Oregon pollen source had trees almost 30 cm shorter, a significant difference as judged by the 95 percent LSD.

In 1966 crosses, the differences among mean height of progeny was influenced by both male and female sources, each significant at P = 0.01 *(Table 1)*. In 1968 crosses, height was influenced by male and female sources at the P = 0.05 and P = 0.01 levels of significance, respectively.

Interaction (specific combining ability) of male and female sources was not significant at P = 0.05 for any of the crosses, which suggests that general combining ability is the major source of genetic variability in height growth.

The correlation of 1966 and 1968 crosses for estimated mean height of the female effect is disappointingly low (r = —0.20) but not surprising considering the relatively large standard deviation of some mean heights. Large standard deviation may imply unreliable ranking of the female origin that results in attenuation of the correlation. Male-by-female or female-by-year interaction could also explain the low correlation. We discount the importance of male-by-female interaction because interaction mean squares were small compared to main effects, but because different individuals were represented each year, a female-by-year interaction could result, which would have the same effect as experimental.error on attenuating the correlation. Thus, we believe the most plausible explanation of the low correlation is large experimental error affecting ranking (Hinz *et al.* 1977).

In future studies, ranking of male and female sources can be made more accurate by reducing standard deviations of the means. This can be achieved by increased replication and by experimental design that reduces the influence of environmental variation.

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CHING, K. K., and BEVER, D.: Provenance study of Douglas-fir in the Pacific Northwest region. Silvae Genet. 9 (1): 11—17 (1960). — HINZ, P. N., SHORTER, R., DUBOSE, P. A., and YANG, S. S.: Probabilities of selecting genotypes when testing at several locations. Crop Science 17: 325—326 (1977).

Postglacial Migration Pathways of Quercus rubra L., Northern Red Oak, as Indicated by Regional Genetic Variation Patterns[1])

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Summary

Intraspecific genetic variation in *Quercus rubra* L. has been achieved by a combination of selection, gene flow, and possibly genetic drift processes acting upon ancestral genotypes. Initial differences in ancestral genotypes of advancing post-Wisconsinan *Quercus rubra* populations were further accented by differential selection regimes effecting a present day discontinuous pattern of diversity. Explanations of genetic variation in *Quercus rubra* initiated hypotheses of post-Wisconsinan plant movement in the Great Lakes region of North America. Central Canada was initially colonized by plants advancing from the upper peninsula of Michigan. Major initial advancements into mideastern Canada were from the lower peninsula of Michigan and lower New York into southern Ontario between the pluvial Great Lake basins of Huron, Erie, and Ontario. Later advancements into eastern Canada occurred further north after the early St. Lawrence River receded.

Key words: Quercus rubra, northern red oak, genetic variation, postglacial migration, Quaternary plant distribution.

Zusammenfassung

Bei *Quercus rubra* L. wurde mittels einer Kombination von Selektion, Gene flow und möglichen genetischen Strömungsprozessen, die sich nach Stammgenotypen richtet, die intraspezifische genetische Variation erreicht. Ursprüngliche Unterschiede bei Stammgenotypen von *Quercus rubra*-Populationen, die vom Standort Wisconsin aus weiter vorgedrungen sind, waren ferner durch differenzierte Selektionsverfahren bestimmt, die bis heute ein diskontinuierliches Muster der Verschiedenheit verursacht haben. Erklärungen der genetischen Variation bei *Quercus rubra* ließen die Hypothese entstehen, daß die Verschiebung von Pflanzen aus Wisconsin in die Great Lakes Region von Nordamerika später erfolgte. Zentralkanada wurde ursprünglich von Pflanzen besiedelt, die von der Upper Peninsula von Michigan aus dorthin gelangten. Die Hauptursache für die Ausbreitung in den Mittelosten Kanadas lag in der Verschiebung von der Lower Peninsula von Michigan und Lower New York aus nach Südontario zwischen die niederschlagsreichen Großen-Seen-Becken von Huron, Erie und Ontario. Spätere Ausbreitungen nach Ostkanada ereigneten sich weiter nördlich, nachdem der frühe St. Lorenz-Strom zurücktrat.

Introduction

The initial analyses of a *Quercus rubra* L. provenance test revealed that much of the genetic variation cannot be explained by conventional statistical analyses (SCHLARBAUM and BAGLEY, 1981). Therefore, a multivariate analysis was utilized to obtain additional information about origins of intraspecific variation patterns.

Previous results indicated that patterns of genetic variation are, in part, associated with environmental factors (SCHLARBAUM and BAGLEY, 1981). Explanation of variation patterns by selection in response to provenance environment, however, would be unrealistic with the possible exceptions of winter leaf retention and fall phenological characteristics. Apparently gene frequencies in *Q. rubra*, as expressed by tree growth and phenological characteristics, are primarily affected by inheritance of ancestral genotypes of trees initially colonizing sites after the last glaciation and secondarily by processes governing genetic equilibrium.

In order to hypothesize relationships of presentday genotypes to ancestral genotypes and possible pathways of gene flow with the *Q. rubra* populations, an understanding of the time and place of origin of the species and extent of its range during the glacial and interglacial stages of the Pleistocene is necessary. The genus *Quercus* is known from examination of the Dakota Sandstone of Cretaceous age (80 to 100 million years ago) (KNOLTON, 1898). The time that *Q. rubra* became a distinct species is not known, but it probably had become differentiated by early in the Pleistocene Epoch, now thought to have begun 2.5 to 3.0 million years ago (BOELLSTORFF, 1978). Most of the vegetation

records of the Pleistocene are based on pollen rather than leaves, seeds, or wood, and even though *Quercus* pollen has been recognized in early Pleistocene sediments, it has not been identified as to species. The oldest sediments from which macroscopic remains of *Q. rubra* have been recovered are the Don beds of Toronto, Ontario (COLEMAN, 1941), which are generally recognized to be Sangamonian in age, and a pre-Wisconsinan site near Milford, Nova Scotia (PREST, 1970). Identification of the species at these locations indicates that prior to the last glaciation (Wisconsinan), *Q. rubra* had a range at least as extensive as its present one.

Even though BRAUN (1951) and KINSEY (1929) suggested that a mixed hardwood-conifer forest, including *Quercus*, existed close to the margin of the Wisconsinan glacier in Ohio and Indiana, pollen spectra (KAPP and GOODING, 1964) and fossil wood recovered from nonglacial and proglacial sediments in those states indicated that *Quercus* did not exist near the ice margin during the Wisconsinan glacial maximum *(Fig. 1)*. From geomorphic and fossil mollusk data, WAYNE (1967) suggested that the northern limit of deciduous forest, including *Q. rubra*, in Indiana probably was south of the 38 parallel. GRÜGER (1972a, b), however, found *Quercus* pollen to be continuously present, though greatly diminished in numbers, during Wisconsinan time in sediments that filled a kettle on the Illinoian till plain 60 km southwest of the Wisconsinan glacial limit in Illinois. During the Wisconsinan glaciation, and undoubtedly during earlier glaciations as well, severe climatic and environmental conditions at the ice margin in the eastern United States caused *Quercus rubra* to retreat to refugia 50 to 100 km or farther south of the ice sheet. The abrupt climatic warming about 10,000 years ago ended the dominance of the more northerly spruce-fir-pine forest cover, and the oak hickory assemblage migrated rapidly into the area that had been occupied by the ice sheet (BERNABO and WEBB, 1977).

The post-Wisconsinan topography in eastern North America encountered by advancing plant communities was similar to present day topography except for the Great Lakes area and upstate New York (HOUGH, 1958; FLINT, et al., 1959). The Great Lakes varied in dimensions throughout much of postglacial time, and Lake Champlain and prehistoric Lake Albany were larger than their present day size for some time after the ice disappeared from the region.

Most of the *Q. rubra* populations sampled by this study had been destroyed by the effects of the Wisconsinan ice sheet and were replaced through northward migration of the species during the last 8,000 to 13,000 years. Origins of variation patterns among provenances, unexplained by the previous paper (SCHLARBAUM and BAGLEY, 1981) could indicate pathways of *Q. rubra* colonization into the northern part of its present distribution and corresponding ancestral genotypes.

Materials and Methods

The experimental material and characteristics observed in this study are described in detail by SCHLARBAUM and BAGLEY (1981). Twenty-seven population samples consisted of open pollinated progenies from an average of eight mother trees *(Fig. 2)*. Trees of provenance No. 31, from seed collected from an artificial planting, were deleted from this analysis because of the uncertain heritage. Nine growth and spring and fall phenological characteristics were observed over a number of years. No distinctions

were made for different planting dates in the analysis.

Principal coordinate analysis was utilized to show associations among population samples in hyperspace. Detailed methodology of principal coordinate analysis can be found in GOWER (1966, 1967) and WILLIAMS et al. (1971). Analysis of variance for each trait, ignoring replication, was used to obtain F ratios for character weighting. Character weight was defined as the F ratio minus 1, which is an effective method of character weighting for principal coordinate analysis (ADAMS, 1975, 1977). Character weights were used to compute a weighted, ranged Gower metric matrix (GOWER, 1971; ADAMS, 1972, 1975) to obtain similarity measures among provenances which were then used as input for the principal coordinate analysis .

The principal coordinate analysis factored the similarity matrix into major coordinates (axes) of variation, arranged in n-dimensional space. Using coordinate loadings of each seed source, a contour map of each principal coordinate was constructed to examine regional trends in variation (ADAMS, 1970, 1977).

The contour maps show provenance location and illustrate geographic patterns of variation explained by each principal coordinate. Patterns of the contours can be interpreted in different ways. Contours could illustrate gene flow pathways, present day or ancestral population genetic structure, environmental characteristics, or random cause variables such as bias data measurements which are regarded as "noise".
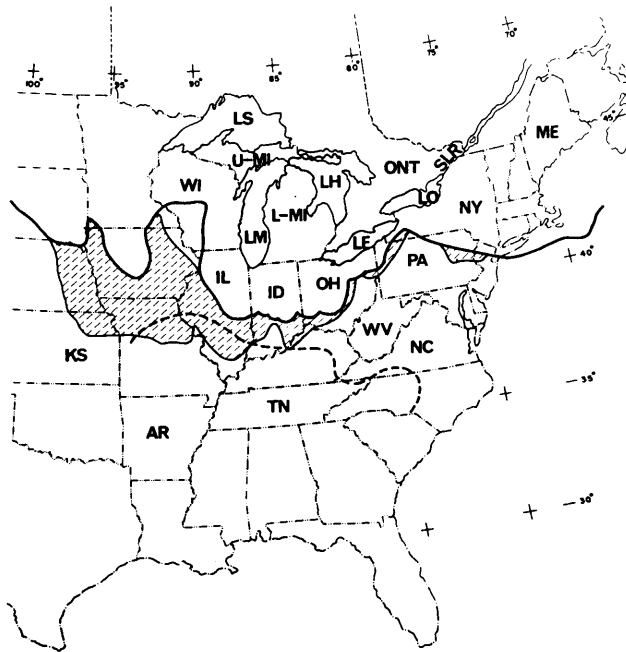

Figure 1. — Solid line indicates laurentide ice sheet position St. Lawrence River. (Figures 1, 2, 6, 7, 8, 9, 10 and 11 based on in-(18,000 B.P.). Shaded area represents maximum extent of pre-Wisconsinan glaciations. Dashed line indicates estimated northern limit of Q. rubra ca. 18,000 B. P. Abbreviations: AR-Arkansas, ID-Indiana, IL-Illinois, KS-Kansas, ME-Maine, L-MI-Lower Michigan, U-MI-Upper Michigan, NC-North Carolina, NY-New York, OH-Ohio, PA-Pennsylvania, TN-Tennessee, WI-Wisconsin, WV-West Virginia, ONT-Ontario, Canada, LE-Lake Erie, LH-Lake Huron, LM-Lake Michigan, LO-Lake Ontario, LS-Lake Superior, SLR-St. Lawrence River.(Figures 1, 2, 6, 7, 8, 9, 10 and 11 based on information in BERNABO and WEBB (1977), BRYSON et al. (1969), GRÜGER (1972a, b), GRÜGER (1973), KAPP and GOODING (1964), MAXWELL and DAVIS (1972), PREST (1970), WAYNE (1967), and WHITEHEAD (1965) studies).
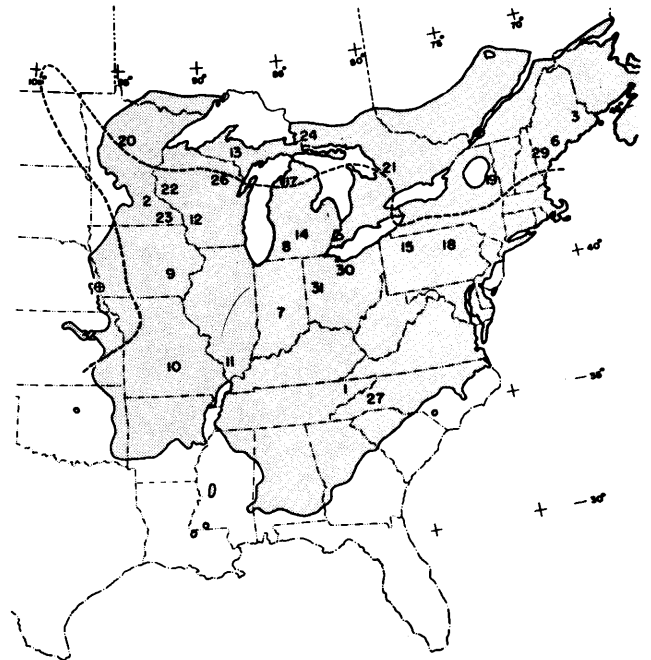
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Figure 2. — Shaded area represents present distribution of Q. rubra L. Numbers represent location of Q. rubra population samples. Crossed-circle represents location of plantation site. Dashed line represents present 10% Quercus isopoll.

Results

The principal coordinate analysis extracted 5 principal coordinates (PC) accounting for 76.06% of the variation present among provenances. Of the coordinates, only the contours of PC$_1$, PC$_2$, and PC$_3$ show meaningful patterns for interpretation of genetic or environmental variation. PC$_4$ and PC$_5$ probably represent some unknown "noise" and were disregarded.

Principal coordinate 1 (PC$_1$), accounting for 44 percent of the variation, shows two general groupings with several
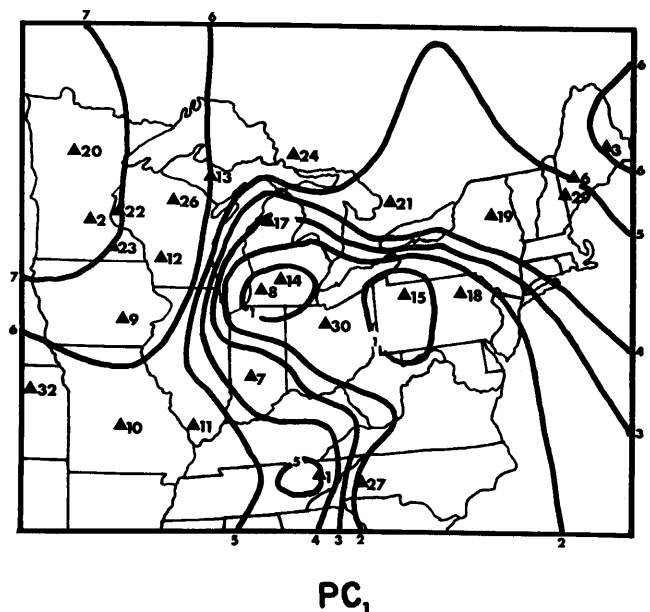

PC$_1$

Figure 3. — Contour map of the first principal coordinate which accounted for 44 percent of the variance among populations. The differentiation of the upper midwest and mideast populations from other populations is clearly shown. Contour levels range = —.57 to +.37.

populations intermediate *(Fig. 3* and *Table 1)*.

Population samples 15, 14, 8, 27, 30, and 18 form a distinct cluster. Trees from other remaining provenances show an east-west cline and a north-south cline with populations 7 and 17 being intermediate between the two clusters.

Principal coordinate 2 (PC$_2$), accounting for 14 percent of the variation, shows two general clusters of populations with trees from provenance 17 somewhat in between the clusters *(Fig. 4* and *Table 1)*. Trees from lower latitudes and the upper northeast, Nos. 6, 11, 29, 19, 21, 10, 7, and 1 are grouped together on principal coordinate 2 as shown by *Figure 4*. Within this group, the trees from the lower latitudes had slightly higher contour values than trees from the upper northeast. Trees from the remaining provenances grouped together, forming a southeast to northwest cluster.

Principal coordinate 3 (PC$_3$), accounting for 9 percent of the variation, shows two major groups *(Fig. 5* and *Ta-*

PC$_3$

Figure 5. — Contour map of the third principal coordinate which accounted for 9 percent of the variance among populations. The major trend is the differentiation of the upper Great Lakes populations (13, 24, 26) for the other populations. Contour levels range = −.29 to +.23.

ble 1). The major geographic pattern is the differentiation of the upper Great Lakes populations (13, 24, 26) from the other populations. The remaining populations are contained within lines of higher value with populations 1, 12, and 2 having relatively higher contour values.

Discussion

The patterns of variation of PC$_1$ are interpreted as illustrating the colonization pathways of *Q. rubra* into the northern portion of the present day range after the Wisconsinan glacial retreat. Advancement of the species from the midwestern states, Kansas through Illinois, was probably due north. In eastern states, colonization pathways probably expanded from Appalachian mountain areas in West Virginia and lower Pennsylvania *(Fig. 1)*. The different environmental conditions of the areas colonized, i.e. prairie versus lower Great Lakes region, caused different selection pressures to be applied to existing genotypes resulting in diverse genotypes of *Q. rubra* in these areas. The intermediacy of population sample 7 is probably the result of gene flow between western and eastern genotypes which combined in the Indiana area *(Fig. 1)*.

The association of population 1 from Tennessee with more western populations was unexpected. This relationship may originate from gene flow between sympatric western and eastern populations or similar selection regimes acting upon ancestral genotypes initially colonizing the region. Evidence of a somewhat linear east to west relationship is shown by similarity measures of population sample 1 with populations 10 and 11, 0.92 and 0.87 respectively, which are higher than values involving other populations.

In all analyses of the provenance test, population 27 was shown to be similar to populations from the lower Lake States (Pennsylvania, Ohio, lower peninsula of Michigan) (Schlarbaum and Bagley, 1981). Provenance 27 is located 762—1006 meters above sea level in the Appalachian mountains. It is unlikely that the association with lower Lake States' populations is based upon present day gene flow
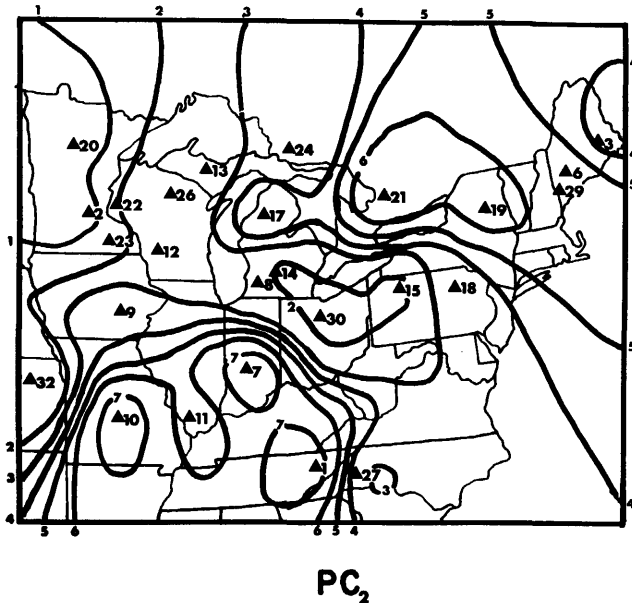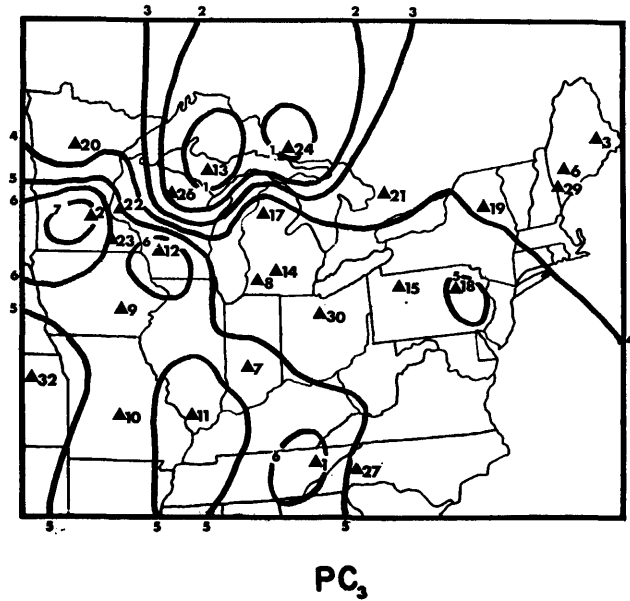

PC$_2$

Figure 4. — Contour map of the second principal coordinate which accounted for 14 percent of the variation among populations. The major trend shows a northwest-southeast grouping with disjunct similarities between the southwest and northeast populations. Contour levels range = −.25 to +.30.

Table 1. — Coordinate loadings of provenances determined by principal coordinate analysis.

Provenance	Principal Coordinate 1	2	3
1	.12	.38	.17
2	.48	−.35	.35
3	.25	−.01	−.09
6	.06	.18	−.08
7	−.14	.35	.07
8	−.62	−.14	.01
9	.25	.02	.09
10	.08	.34	.08
11	.19	.19	.01
12	.38	−.14	.24
13	.21	−.12	−.35
14	−.65	−.19	.01
15	−.67	−.18	.02
17	−.28	.14	.04
18	−.46	.01	.06
19	.04	.23	−.03
20	.40	−.27	−.07
21	.05	.26	−.04
22	.35	−.11	−.01
23	.35	−.17	.11
24	.20	−.05	−.30
26	.30	−.09	−.25
27	−.58	−.10	−.01
29	.00	.21	−.05
30	−.52	−.18	.01
32	.19	−.22	.01

as mountain top genotypes are often virtually isolated in their respective environments (Löve, 1959; Wynne-Edwards, 1937, 1939).

The disjunctive characteristics of trees from provenance 27 are attributed to post-Wisconsinan selection against genotypes adapted to cold temperatures in the lower elevations. When the Laurentide ice sheet was at a maximum *(Fig. 1)*, environmental conditions at the vicinity of provenance 27 were generally colder and more harsh than present day climate. The high elevation sites were likely devoid of oak species, while lower elevations were inhabited by various tree species probably including *Q. rubra* (Whitehead, 1965). Because of different environmental pressures than those currently existing, selection regimes were also different, selection favoring trees less likely to be injured by early spring and fall frosts and generally adapted to a cooler year around climate. As the ice retreated and advancement of the oak-hickory community into high elevation sites began, selection once again favored genotypes adapted to warmer environments in lower elevations. Only in the higher elevations of mountain tops did selection regimes resemble those prevalent when the Laurentide ice sheet was at a maximum. The end result of the differential selection was that genotypes adapted to cold climates survived only in isolated, high elevation pockets in the Appalachian mountains. This theory is supported by range maps based on morphological characteristics of *Q. borealis* (Michx.) F. and *Q. borealis maxima* (Marsh) Sarg. (Munns, 1938), the two previously recognized northern red oak subspecies. Trees in the highlands of North Carolina, Tennessee, and Arkansas exhibit characteristics of *Q. borealis*, the northern subspecies, and trees of the lower elevations are characteristic of *Q. borealis maxima*, the southern subspecies. Kriebel *et al. (1976)* also indicated evidence of isolation of northern genotypes of *Q. rubra* in the Arkansas highlands.

In his study of budbreak, McGee (1974) sampled *Q. rubra* populations of varying elevations in the mountains of western North Carolina attributing existing clinal variation patterns to selection in response to environmental conditions. The differences among populations McGee observed were probably the genetic differences between genotypes adapted to warm temperatures and post-Wisconsinan refugia of genotypes adapted to more cooler temperatures and the results of gene flow between two genotypes. McGee's determination of an elevation-budbreak relationship within populations of the area studied may not be extended, with the possible exception of the Arkansas highlands, beyond this specific area. Other studies of budbreak in *Q. rubra*, involving a wide sampling base, have shown that with respect to seed source elevation, budbreak is nonclinal in variation (Gall and Taft, 1973; Kriebel *et al.*, 1976; Schlarbaum and Bagley, 1981).

The initial post-Wisconsinan colonization pathways of *Q. rubra* in the Great Lakes region can be hypothesized by relating the retreating Laurentide ice sheet position (Bryson *et al.*, 1969; Prest, 1970; Saarnisto, 1974), pluvial Great Lake morphology (Hough, 1958; Prest, 1970), and palynology investigations (Bernabo and Webb, 1977) with the regional genetic variation patterns of *Q. rubra* shown by the present study *(Figs. 6—11)*.

Prior to the discussion of colonization of this region, it is necessary to observe some minor discrepancies and problems which arose while relating the studies in the diverse fields of discipline. Hough (1958) provides an excellent review of the progression of the icemarginal and post-

glacial phases of the Great Lakes from 11,000 years B. P. (before present = before 1950) to the present. In a later
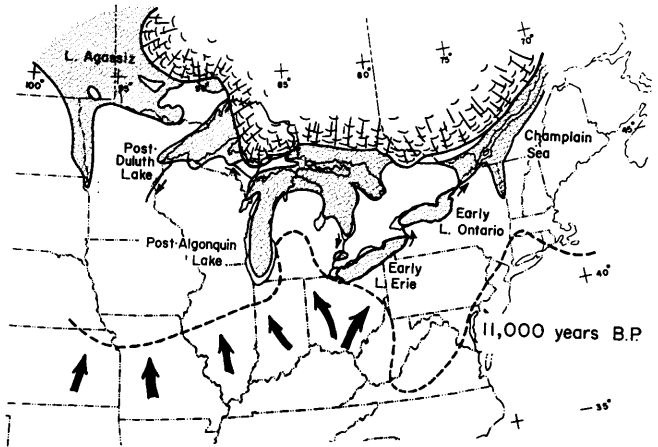

Figure 6. — Estimated advancement of *Q. rubra* ca. 11,000 B.P. Dashed line indicates 10% *Quercus* isopoll. Large arrows indicate *Q. rubra* migration. Small arrows indicate drainage from pluvial Great Lakes. Shaded areas represent pluvial Lake basins.
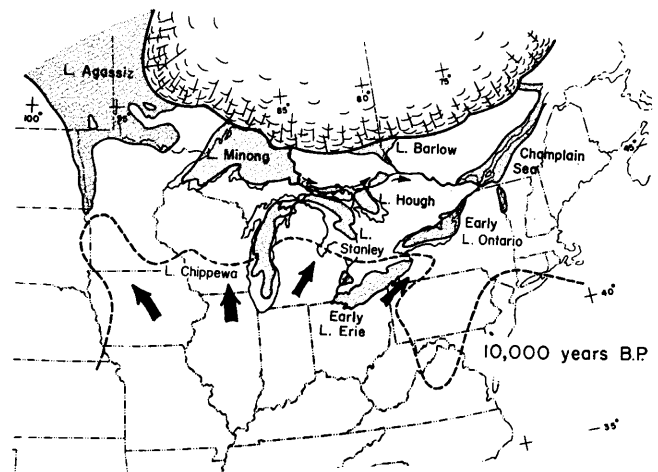

Figure 7. — Estimated advancement of *Q. rubra* ca. 10,000 B. P. Dashed line indicates 10% *Quercus* isopoll. Large arrows indicate *Q. rubra* migration. Shaded areas represent pluvial Great Lake basins. Small arrows indicate drainage from pluvial lakes.
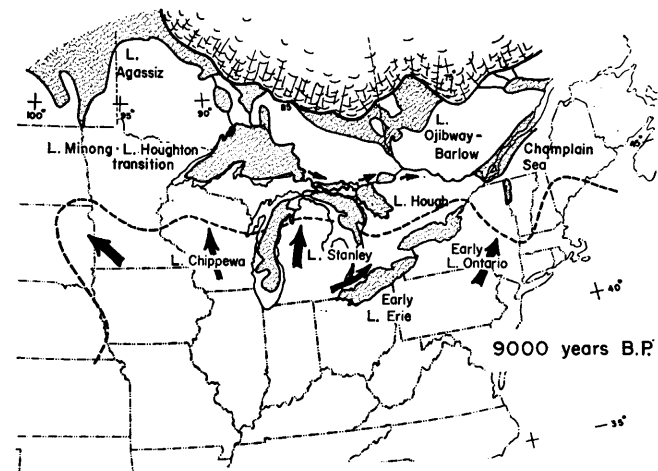

Figure 8. — Estimated advancement of *Q. rubra* ca. 9,000 B. P. Dashed line indicates 10% *Quercus* isopoll. Large arrows indicate *Q. rubra* migration. Shaded areas represent pluvial Great Lake basins. Small arrows indicate drainage from pluvial lakes.
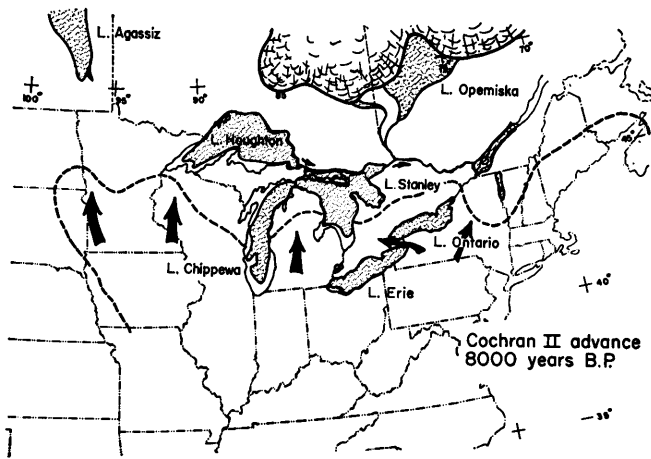
Figure 9. — Estimated advancement of Q, rubra ca. 8.000 B. P. (Cochran substage). Dashed line indicates 10% Quercus isopoll. Large arrows indicate Q. rubra migration. Shaded areas represent pluvial Great Lake basins. Small arrows indicate drainage from pluvial lakes.

Figure 10. — Estimated advancement of Q.rubra ca. 7.000 B. P. Dashed line indicates 10% Quercus isopoll. Large arrows indicate Q. rubra migration. Shaded areas represent pluvial Great Lake basins. Small arrows indicate drainage from pluvial lakes.

Figure 11. — Estimated advancement of Q. rubra ca. 4.000 B. P. Dashed line indicates 10% Quercus isopoll. Large arrows indicate Q. rubra migration. Shaded areas represent pluvial Great Lake basins. Small arrows indicate drainage from pluvial Great Lakes.
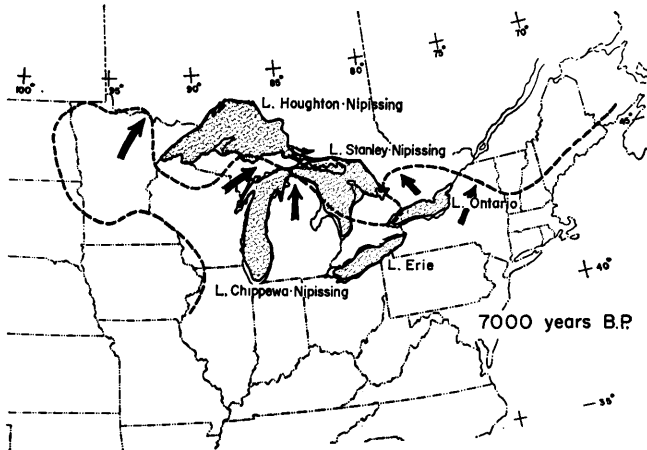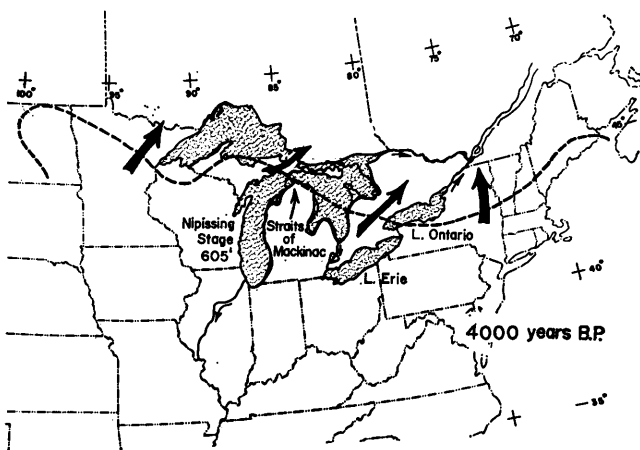
study, Bryson et al. (1969), using many radiocarbon dates that had not been available to Hough, suggested positions

of the ice sheet that differed considerably. Other studies (Saarnisto, 1974; Prest, 1970), using similar basic data, suggest still other ice positions during the final retreat of the Laurentide ice margin. Figures 6—12 are based primarily on the detailed series prepared by Prest (1970, Figs. 16 a—z), in which he has interpreted ice marginal positions and the development of the Great Lakes and Lake Agassiz at intervals of a few hundred years from 14,000 to 6,000 years B. P. The 10% Quercus pollen isopolls were taken from the maps by Bernarbo and Webb (1977).

The positions of the pollen isopolls in Figures 6—11 are probably not an accurate indication of the foremost advancement of Q. rubra nor does it define the real abundance of proportional distribution of any particular Quercus species because different oak species pollen are indistinguishable. Pollen rain, however, does give a valid general idea of the presence or absence of a genus as a significant element of the surrounding forest. The relationship between the 10% Quercus isopoll today and the present range of Q. rubra is shown in Figure 2.

Although Quercus pollen is indistinct, it is unlikely that Q. rubra was present at the northern isopoll maxima until approximately 8000 B. P. in the Great Lakes region and 6000 B. P. in the western region proximal to the Great Lakes. The initial postglacial environmental conditions at the isopoll positions were probably more suitable for other species of Quercus with different environmental requirements than Q. rubra (Wright, 1971). Thus in the western prairie regions, the isopoll probably reflects the advancement of Quercus macrocarpa Michx., bur oak, and in the wetter eastern region. Quercus bicolor Willd., swamp white oak, and other bottomland oak species probably precluded Q. rubra. The isopoll positions, therefore, will be utilized to give relative estimates of the advancement of Q. rubra. By 8000 B. P. the Quercus isopoll was at its northernmost position in the Great Lakes region and had been essentially stable for 1000 years (Figs. 8—9). In the western area, the northward isopoll maximum was attained at 7000 B. P. and maintained throughout 4000 B. P. The authors believe that during the years of stabilization of the environment, as indicated by the unchanging isopoll positions, Q. rubra would have advanced to at least the isopoll maximum, in the respective areas, and begun, with environmental fluctuations and topography permitting, to extend to its present day range limits which are further northward (Harlow et al., 1978).

The Laurentide ice sheet attained its maximum southward extension from approximately 20,000 B. P. to 15,000 B. P. then began to recede with intermittent readvancement. The last major readvancement, the Valders glacial substage, reached southern maximum extension at approximately 11,800 B. P. Post-Valders ice sheet movement receded rapidly from 11,000 until about 8500 years B. P. and Quercus migrated northward steadily during this time. The Cochrane advance, about 8000 years ago (Fig. 9), slowed the migration briefly and was the last change in the Laurentide ice sheet to affect the distribution of Quercus. The 10% Quercus isopoll position at 11,000 B. P. suggests the advancement of Q. rubra into the lower peninsula of Michigan from the West Virginian region with slower advancement in the proximal western and eastern regions (Fig. 6).

Pollen rain distributions (Bernabo and Webb, 1977; Figs. 6—11) indicate that distinct colonization pathways characterized Quercus advancements in eastern North America. Advancement in the eastern Great Lakes region was

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in the area between the pluvial Great Lakes basin and a natural barrier formed by the Appalachian and Adirondack mountain ranges and prehistoric Lakes Champlain and Albany which partitioned a separate coastal migration route. The mountainous area between the two pathways, excepting the Adirondack range where *Q. rubra* does not occur, was probably colonized with genotypes from each respective pathway in the same manner of the lower Appalachian mountain colonization in the vicinity of population 27, as previously discussed. The coastal migration route will be discussed later in this paper.

Figure 7 illustrates the steady advancement of *Quercus* northward. In the western region *Q. rubra* appears to be steadily advancing due north, to roughly the 42nd parallel. Advancement in the eastern Great Lakes region was in the proximal area of pluvial Lake Stanley (Huron basin) and early Lake Erie. Advancement in lower Michigan probably stabilized in response to the inability of preceding plant communities to advance further northward and adverse environmental conditions.

BERNABO and WEBB (1977) show an isopoll position in lower Ontario at 10,000 B. P. This was apparently drawn as an extrapolation from the isopoll position in lower Michigan and lower New York, both based upon actual data. Because of the low levels of pluvial Lake Stanley *(Fig. 7)*, the authors feel that it would have been possible for *Quercus*, probably *Q. bicolor*, to be present in southern Ontario in this time period. It is unlikely though, that *Q. rubra* had migrated into Ontario as early as 10,000 B. P.

By 9000 B. P. *(Fig. 8) Quercus* was rapidly advancing northward in the eastern region (BERNABO and WEBB, 1977) with *Q. rubra* probably entering lower Ontario between pluvial Lake Stanley and early Lake Erie and perhaps between early Lake Ontario and early Lake Erie. Western advancement of *Q. rubra* is estimated to be between the 43rd and 44th parallel.

The 10% *Quercus* isopoll stabilized at about 8000 B. P. as a result of the Cochrane ice advance *(Fig. 9)*. Advancement into Canada in the eastern Lake Ontario basin area probably did not take place as the early St. Lawrence River may have remained a barrier at this time. Western advancement probably continued with *Q. rubra* likely advancing to the 44th parallel.

Figure 10 illustrates the advancement of *Q. rubra* around the eastern end of pluvial Lake Payette (Michigan and Huron basins) and the extensive intrusion of *Q. rubra* into upper Michigan, and further western regional advancement. The topographic possibility for advancement into upper Michigan by lower Michigan *Q. rubra* populations across the present day straits of Mackinac area probably existed. However, the authors believe the advancement of *Q. rubra* into upper Michigan and Canada from lower Michigan, or vice versa, did not occur in amounts that would alter the diverse lower Lake States and western genotypes. This opinion is based upon the site requirements of *Q. rubra* for establishment (FOWELLS, 1965; HARLOW et al., 1978) and the observed differential genetic variation between upper and lower Michigan *Q. rubra* populations and other forest trees. The Mackinac area was probably very wet and in portions, swamplike, due to the low elevation of the region as compared with the surrounding area. *Q. rubra* is not well adapted to very wet or swamp sites and probably did not advance into the area. Additional evidence to support this hypothesis is based upon the similarity of population samples 13, 24, and 26 from upper Michigan and Western Ontario as contrasted to this dissimilarity

with population 17 *(Fig. 3)* (SCHLARBAUM and BAGLEY, 1981) and the differences observed between upper and lower Michigan trees (AREND et al., 1961; CANAVERA and WRIGHT, 1973; YAO et al., 1971).

Based upon the topography shown by *Figure 10,* the authors believe that by 6000 B. P. *Q. rubra* populations began to advance into Canada in the proximal western Lake Superior area and to possibly circumvent Lake Superior. Colonization probably continued into Ontario with populations expanded northward along pluvial Lake Huron basin shorelines.

Intersection between the advancing western and lower Lake State genotypes probably occurred prior to 4000 B. P. as *Q. rubra* progressed further along in each respective pathway *(Fig. 11)*.

Gene flow along all pathways illustrated in *Figure 10* probably continued from 6000 B. P. to the present as topography shown by *Figure 11* and present day topography *(Fig. 2)* indicates that pathways remained unobstructed. With the recession of the early St. Lawrence River, advancement of *Q. rubra* populations across the St. Lawrence River into Canada occurred. High water levels in the Superior, Michigan, and Huron basins formed a water barrier between upper and lower Michigan, eliminating possibilities of northward gene flow between the two peninsulas.

The four-mile-wide Straits of Mackinac still provides an effective barrier to prevent south to north gene flow between the peninsulas. Gene flow, via pollen, from south to north is probably prevented by the four mile separation (ARCHIMOWITSCH, 1949; COLWELL, 1951) and the predominantly southeastern wind directions over the Straits of Mackinac (National Weather Service, 1975). These facts, coupled with the previous discussion and evidence, support a hypothesis of the singular upper Michigan ancestry of *Q. rubra* in this area.

Although the hypothesis explains why trees of population 17 resemble lower Lake State trees more than western trees, it does not explain the tendency toward intermediacy of the population. This can be accounted for by the fact that the principal coordinate analysis was partially based upon fall phenological characteristics dates, which are under genetic control and were selected in response to provenance photoperiod. Population 17 is highest in latitude of all lower Lake State population samples and therefore is more similar to high latitude western populations with respect to dormancy processes.

As previously mentioned, there was a distinct Atlantic coastal migration route of *Q. rubra* as indicated by pollen rain distributions (BERNABO and WEBB, 1977; cf. *Figs. 1—6*). The northward advancement of *Quercus* in this region was probably more rapid than the continental advancements because of a different environment along the coast. Unfortunately, the ancestral genotypes of the coastal populations are unknown as this study lacks samples of the lower portion of the region. The authors believe it is unlikely that the ancestral genotypes of the coastal region were similar to western genotypes because of the vastly different environmental conditions which must have influenced selection regimes in the region. The original oak populations of this area probably exhibited a closer affinity with lower Lake State genotypes because of the closer proximity of the populations and subsequent gene flow.

The preceding paragraph hypothesizes initial colonization of the upper northeast by trees with, generally, lower

Lake State genotypes. However, genotypes of trees from provenances of this region are more similar to western tree genotypes than lower Lake State tree genotypes (Fig. 3). Genotypes of present day populations, as represented by population samples 3, 6, 19, 21 and 29, are probably the results of initial colonization by lower Lake State type genotypes, intersection and gene flow from western genotypes advancing from the inter-Great Lake region, and subsequent selection regimes which, in part, favored genes from western populations.

As previously mentioned, there is a possibility that trees of western genotypes advanced into Canada around Lake Superior (Figure 11). The lack of similarity, of population 20 from northern Minnesota to northeastern trees, however, is not conclusive evidence against circumvention. Trees from Canadian and upper northeast locations were likely established and adapted to a lower latitude environment before introgression occured and probably would have caused heavy selection against invading northwestern genotypes.

Comparison of the contour map of PC$_1$ (Fig. 3) and the ranking of northern populations in the multiple range test of leaf flushing dates (SCHLARBAUM and BAGLEY, 1981) shows the close association of trends present in each figure. This relationship indicates that genetic differences among population samples in dates of initial leaf flush reflect differences present in ancestral genotypes which colonized respective provenance localities. Therefore, the genes controlling the initiation of spring growth in Q. rubra have probably not been selected for or modified by the influence of provenance environment to any great extent.

Genetic diversity within the western genotypic complex, encompassing populations 1, 2, 3, 9, 10, 11, 12, 13, 19, 20, 21, 22, 23, 24, 26, 29, and 32 is more prevalent than within the lower Lake States' Q. rubra populations as shown by Figure 3 and Table 1. The larger area inhabited by the western complex with a corresponding variety of environmental conditions influencing selection processes could explain the greater genetic diversity. The degree of affinity among populations is primarily based upon a combination of similarities in ancestral genotypes and, secondarily, environmental conditions influencing selection regimes. However, there are several situations in which unusual relationships among populations merit additional explanation.

Trees of population 2, while clearly originating from the same gene pool as trees of other western populations, somewhat appear as an independent entity (Fig. 3) (SCHLARBAUM and BAGLEY, 1981). The population is surrounded on three sides by other population samples and it is doubtful that environmentally based selection processes are responsible for the unique behaviour. The divergence of provenance 2 is probably due to either random genetic drift, which changed gene frequencies by chance fluctuations away from the population mean, or to sampling error.

Population 20 appears somewhat distinct from other western populations though not to the degree of population 2 (Fig. 3) (SCHLARBAUM and BAGLEY, 1981). Probably, as discussed previously, photoperiod-related fall characteristics injected bias into calculations of similarity measures causing a minor distortion in the relationships of population 20 with other population samples.

The major trend of PC$_2$ shows the divergence of trees from population 7, populations 1, 10, and 11 of the south and populations 6, 19, 21, and 29 of the upper northeast from the other population samples (Fig. 4). It is unlikely that the different regional environmental conditions caused parallel evolutionary processes to act on populations of

each area. PC$_2$ is probably indicative of regions of Q. rubra that are generally similar to western genotypes but also reflect the effects of gene flow from lower Lake States Q. rubra populations. As previously mentioned, gene flow between advancing postglacial populations probably accounts for the PC$_2$ separation of trees from upper northwest and population 7. Gene flow between sympatric lower Lake States and southern states populations is probably responsible for the PC$_2$ segregation of southern provenances. However, major alteration of gene frequencies of these respective populations by gene flow apparently is not occurring as the population samples show low degrees of similarity (Fig. 3).

PC$_3$ separates fast growing populations 1, 2, and 12 from slow growing populations planted in 1962-3 and No. 18 from slow growing lower Lake State provenances planted in 1964 (Fig. 5). This coordinate probably reflects differences in inherent growth potential as shown by the multiple range tests in the preceding paper (SCHLARBAUM and BAGLEY, 1981).

Conclusions

The results and discussion of analyses of this provenance plantation show that the intraspecific genetic variation of Q. rubra can be attributed to a combination of selection, gene flow, and possibly random genetic drift acting upon ancestral genotypes. Of these processes, selection influenced by environmental conditions was probably the primary agent in differentiating ancestral populations. Gene flow in colonizing post-Wisconsinan populations was probably important in changing gene frequencies only in the upper northeast and Indiana areas where genotypes from advancing western and eastern populations combined. Gene flow since initial intersection of different colonization genotypes appears to be relatively unimportant in changing population gene frequencies. The diversification of populations by selection rather than gene flow concurs with the theories of population differentiation of EHRLICH and RAVEN (1969) and ENGLER (1973). Intraspecific variation due to gene flow from isolated populations subjected to catastrophic selection, as described by LEWIS (1962), probably did not occur in Q. rubra. Random genetic drift could have occurred in one location, population sample 2, changing gene frequencies enough for the population to appear unique from adjacent populations but not enough to mask ancestral heritage.

As a means of explaining the origins of genetic variation in Q. rubra the principal coordinate analysis results initiated theories of plant advancement after the Wisconsinan glaciation. These hypotheses are based upon the study of the small number of populations sampled which are not representative of the entire area colonized. However, Q. rubra seems to be an excellent species to study for information about postglacial plant life advancements, since present day genotypes appear to be relatively unchanged from ancestral genotypes in certain regions. The theories of colonization pathways provide not only the explanation for patterns of intraspecific genetic variation in Q. rubra but can possibly be utilized for hypotheses concerning genetic diversity of other plant species in the Great Lakes area.

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Identification of Characteristic Traits of Two Varieties of Arizona Cypress

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Summary

Native trees and controlled plantings of two varieties of Arizona cypress were studied to identify morphological characteristics which are useful in classification of the varieties. Arizona cypress (*Cupressus arizonica* var. *arizonica*) and Smooth Cypress (*Cupressus arizonica* var. *glabra*) were studied both on an experimental planting in Alabama and in the wild in Arizona.

The two varieties were distinguishable primarily by bark texture and foliage resin gland occurrence. Other morphological traits appear to be affected to such a degree by the environment that they are not useful as classification variables.

Key words: Arizona cypress (*Cupressus arizonica* GREENE), morphology, breeding, variability.

Zusammenfassung

Es wurden autochthone Einzelbäume und kontrollierte Pflanzungen von 2 Varietäten von *Cupressus arizonica* untersucht, um morphologische Merkmale für eine brauchbare Klassifikation der Varietäten zu finden. *Cupressus arizonica* var. *arizonica* und *Cupressus arizonica* var. *glabra* wurden beide in einer Versuchspflanzung und am natürlichen Standort Arizonas untersucht. Die zwei Variatäten waren in erster Linie anhand ihrer Rindentextur und dem Auftreten von Blattharzdrüsen zu unterscheiden. Andere morphologische Merkmale scheinen in einem solchen Maße von der Umwelt beeinflußt zu sein, daß sie nicht als Unterscheidungsmerkmal zu benutzen waren.

Introduction

Arizona cypress (*Cupressus arizonica* GREENE) is a coniferous species indigenous to the southwestern United

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