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# Variation in Leaf Morphology among Disjunct and Continuous Populations of River Birch (Betula nigra L.)

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### Abstract

Leaves from disjunct and continuous populations of river birch *(Betula nigra* L.) were sampled in each of four regions. Analyses based on 18 attributes revealed no apparent morphological trends across the species' range. However, half the attribute means were significantly different among regions and all the attributes were significantly different among local populations. In only one case was an attribute mean significantly different between disjunct and continuous populations. Overall attribute variances were consistently greater than values reported for related species. In each region several attribute variances were significantly different between disjunct and continuous populations. In the Indiana-Illinois, Kansas-Missouri-Oklahoma, and North Carolina-South Carolina regions most of these variances were higher in continuous populations than in their disjunct counterparts. In contrast, the Pennsylvania-New York-Massachusetts region exhibited higher variation in disjunct populations than in the continuous populations. It was concluded that the factors which influence leaf morphology in this species may not be associated with macroclimatic gradients, and that the observed differences may be due largely to the effect of genetic drift in local populations.

*Key words:* marginal populations, phenotypic variation, *Betula nigra.*

### Zusammenfassung

Blätter der Flußbirke aus vier Regionen Nordamerikas wurden gesammelt und gemessen. Die Analyse von 18 morphologischen Merkmalen aller Populationen ergab keine klaren Trends über das untersuchte Verbreitungsgebiet. Es gibt in der Hälfte der Fälle Unterschiede zwischen Regionen und in allen Fällen zwischen örtlichen Populationen. Merkmalsunterschiede zwischen disjunkten und kontinuierlichen Populationen sind kaum zu finden: In nur einem Fall war der Unterschied statistisch gesichert. Die Variationsbreite der Merkmalsmittelwerte zwischen nah verwandten Arten ist durchaus größer als bisher berichtet wurde. In jeder Region gibt es Fälle, in denen die Variationsbreite zwischen disjunkten und kontinuierlichen Populationen unterschiedlich ist. In den Regionen Indiana-Illinois, Kansas-Missouri-Oklahoma und North Carolina-South Carolina ist die Variationsbreite der Merkmale durchschnittlich höher in den kontinuierlichen als in den disjunkten Populationen. In Pennsylvania-New York-Massachusetts wurden jedoch große Variationsbreiten in den disjunkten Populationen gefunden.

Es wird daraus geschlossen, daß Umweltfaktoren, welche die Blattmorphologie beeinflussen, nicht mit makroklimatischen Gradienten zusammen hängen. Die beobachteten Differenzen könnten in hohem Maße auf die Wirkung genetischer Drift in lokalen Populationen zurückgeführt werden.

### Introduction

Populations on the margins of a species' range, exhibiting varying degrees of spatial isolation, are important to several models of speciation (Cook 1961, Lewis 1962, Raven 1964, Grant 1971). While it is generally accepted that these marginal populations differ genetically and ecologically from centroid populations, there is little documentation of this in forest trees. In *Pinus taeda* L., van Buijtenen (1966) found marginal populations to be highly variable with respect to needle length, cone size, and drought resistance when compared to centroid populations. However, Stern and Roche (1974) state that most observations point to less genetic variation in marginal populations than in more centroid populations.

River birch *(Betula nigra* L.), the focus of this study, is an intolerant, pioneer hardwood species common on bottomland sites in eastern North America. Eighteen disjunct populations were reported to exist along the margins of the species' natural range (Little 1971). The objective of the present study was to determine if these populations exhibited less variation than populations within the continuous, more centrally located segments of the range.

### Materials and Methods

Using Little's (1971) map of the distribution of river birch, a search for the 18 disjunct populations was initiated. The existence of only four of the eighteen populations was confirmed and served as the basis for sampling *(Table 1)*. The degree of disjunctness of each area from the continuous range varied from 31 km in the Kansas-Missouri-Oklahoma region to 257 km in the Pennsylvania-New York-Massachusetts region. The elevation of sample sites was also highly variable- ranging from 3 m at a site in Massachusetts to 610 m at a site in North Carolina.

From June to August of 1979 leaf samples were obtained from trees within each disjunct area and from adjacent areas within the continuous range of the species. Fifty trees were sampled in each of one to three local populations within each disjunct area, depending on its size, and three within each adjacent continuous (non-disjunct) area, for a total of 21 populations (*Table 1*). Samples within the continuous range were collected as close to each disjunct area as possible in order to eliminate the effects of differences in macroclimate on between-population variation.

At least five short or spur shoots, each bearing two leaves, were collected from the inside lower crown of each tree, pressed and dried (Sharik and Barnes 1971). On each short shoot the leaf with the greatest number of teeth and veins, usually the longer of the two leaves, was selected for measurement. Seventeen of the 18 attributes used to define leaf morphology were those used in similar investigations of related birch species (Sharik and Barnes 1971, Dancik and Barnes 1972). L20, the leaf base angle in degrees, was added in the present study to more adequately characterize leaf base shapes found in river birch. Attributes L1 and L12 of Shark and Barnes (1971) were not applicable to the present study and were therefore dropped.

Overall population means and variances were calculated for each of the 18 leaf attributes, utilizing the entire data set of 5,250 observations in 21 populations. Means and coefficients of variation were also calculated for each attribute by region, by range (disjunct and continuous populations within each region), and by individual local population (replicate).

Analysis of variance (ANOVA) was performed to determine levels of significance among region, range, and replicate means for each attribute. The basic design was unbalanced, completely nested (hierarchical), with a single variable of classification. The analysis of variance performed on the entire data set was used to determine the significance of region and replicate effects. A separate ANOVA was performed on each region to determine the effect of range (disjunct versus continuous) within the region.

A multivariate analysis of variance (MANOVA) was also performed to determine significance among regions, and between disjunct and continuous populations within each region. These tests excluded the synthetic attributes L14—L19 as they were considered redundant. In order to perform the multivariate tests the nested design had to be modified to provide an error matrix with sufficient degrees of freedom. This was done by eliminating the range and replicate effects for the test of region, and eliminating the replicate effect for the test of range. Tests were performed both with and without the discrete attributes.

In addition to tests of significance for various mean effects, an F test was used to determine significance for magnitudes of variation between disjunct and continuous populations for each attribute by region (Dixon and Massey 1969). Significance between disjunct and continuous populations was also determined multivariately, with the equality of the variance-covariance matrix tested according to Morrison (1967).

Although attributes L2, L9, L10, L11, and L13 were included in most of the analyses, some difficulty was foreseen in interpreting the results due to the discreteness of these attributes. Therefore, a chi-square test of homogeneity or independence was also used to test their significance for the various effects (Dixon and Massey 1969).

All tests of statistical significance were made at an alpha level of .05 or greater.

## Results

The coefficients of variation (CV) for most of the attributes were on the order of 15—25 percent. However, both of the attributes expressing base symmetry, L9 and L11, had much higher CV's (*Table 2*). Except for L10, which was almost constant, L17, the blade width to blade length ratio, had the lowest CV. L3, the number of pairs of lateral veins, also had a CV that was somewhat lower than the other attributes.

ANOVA tests for differences among the means of the 21 local populations were significant for all attributes (Coyle 1981). The ANOVA tests for region indicated significant differences for nine of the 18 attributes (*Table 2*). All of the attributes showing significance except L8, number of

*Table 1.* — Location of sample populations.

| Population[1] | State | County | Watershed | Latitude (Deg N) | Longitude (Deg W) | Elevation (meters) | Minimum Distance to Continuous Range (km) |
|---|---|---|---|---|---|---|---|
| 111 | IN | Bartholomew | White Creek | 39.06 | 85.92 | 177 | 0 |
| 112 | IN | Greene | Richland Creek | 39.03 | 86.91 | 155 | 0 |
| 113 | IN | Sullivan | Dugger | 39.07 | 87.29 | 149 | 0 |
| 121 | IN | Pulaski | Ryan Ditch | 41.16 | 86.90 | 213 | 233 |
| 122 | IN | Pulaski | unnamed swamp | 41.16 | 86.92 | 213 | 233 |
| 123 | IN | Jasper | Luken Ditch | 41.17 | 86.93 | 216 | 233 |
| 211 | KA | Cherokee | Spring River | 37.02 | 94.72 | 244 | 0 |
| 212 | KA | Cherokee | Fly Creek | 36.73 | 95.02 | 238 | 0 |
| 213 | OK | Osage | Sand Creek | 36.73 | 96.18 | 226 | 0 |
| 221 | KA | Chautauqua | Birch Creek | 37.03 | 96.00 | 235 | 31 |
| 222 | KA | Chautauqua | Coon Creek | 37.01 | 96.04 | 253 | 31 |
| 311 | PA | Pike | Delaware River | 42.21 | 78.84 | 110 | 0 |
| 312 | NY | Ulster | Esopus Creek | 41.97 | 74.00 | 43 | 0 |
| 313 | PA | Pike | Bushkill Creek | 41.09 | 75.00 | 110 | 0 |
| 321 | MA | Essex | Merrimack River | 42.76 | 71.04 | 3 | 257 |
| 322 | MA | Essex | Lake Cochichewick | 42.69 | 71.10 | 34 | 257 |
| 323 | MA | Essex | Lake Wenham | 42.59 | 70.89 | 12 | 257 |
| 411 | SC | Oconee | Ramsay Creek | 34.69 | 83.14 | 238 | 0 |
| 412 | SC | Union | Tyger River | 34.63 | 81.74 | 122 | 0 |
| 413 | NC | Buncombe | French Broad River | 35.51 | 82.58 | 610 | 0 |
| 421 | NC | Swain | Tuckasegee River | 35.44 | 88.38 | 549 | 75 |

[1] Code numbers signify: First digit, region (1 = IN — IL, 2 = KA — OK — MO, 3 = PA — NY — MA, 4 = NC — SC). Second digit, disjunction (1 = continuous, 2 = disjunct); Third digit, replicate (No. 1—3).

*Table 2.* — Attribute statistics for river birch and significance tests of means and variances among regions and between continuous and disjunct populations.

| | Population Statistics (n=21) | | | | | Significance Tests | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Between Continuous and Disjunct Population Variances | | | |
| Attribute[1] | Mean | Min. | Max. | Mean CV | Overall CV (n=5250) | Among Region Means | IN-IL | KA-MO-OK | PA-NY-MA | IN-IL |
| L2 | 0.94 | 0.89 | 1.00 | 24.7 | 25.5 | | | ** | ** | |
| L3 | 8.4 | 8.1 | 9.1 | 12.0 | 12.6 | | | | | |
| L4 | 49.4 | 41.9 | 54.8 | 14.6 | 16.2 | | ** | | | * |
| L5 | 11.0 | 7.9 | 13.7 | 22.6 | 25.6 | | ** | | | |
| L6 | 32.2 | 27.0 | 36.4 | 16.3 | 17.8 | | | | | |
| L7 | 19.0 | 16.6 | 22.0 | 20.9 | 22.6 | | ** | | ** | * |
| L8 | 29.5 | 24.6 | 34.6 | 18.8 | 21.1 | * | ** | ** | ** | |
| L9 | 0.19 | 0.03 | 0.43 | 241.0 | 209.5 | * | | ** | | ** |
| L10 | 5.0 | 4.9 | 5.0 | 1.8 | 2.2 | | ** | ** | ** | ** |
| L11 | 1.4 | 1.1 | 1.7 | 40.5 | 43.3 | * | | | | ** |
| L13 | 2.7 | 2.2 | 3.2 | 24.3 | 26.5 | ** | | | | ** |
| L14 | 0.173 | 0.158 | 0.199 | 13.4 | 14.9 | | ** | | ** | ** |
| L15 | 0.603 | 0.506 | 0.757 | 16.4 | 19.3 | * | | ** | ** | ** |
| L16 | 0.222 | 0.184 | 0.261 | 17.6 | 19.5 | * | ** | | ** | |
| L17 | 0.653 | 0.567 | 0.684 | 9.9 | 10.7 | ** | ** | | * | ** |
| L18 | 0.384 | 0.349 | 0.417 | 15.8 | 16.6 | ** | ** | | ** | |
| L19 | 3.5 | 2.9 | 4.0 | 14.7 | 17.2 | ** | | ** | ** | |
| L20 | 50.3 | 41.1 | 58.2 | 19.4 | 20.9 | | ** | | | ** |

[1] Linear measurements are in millimeters. L2, vein alignment: 0 = paired, 1 = unpaired; L3, number of pairs of lateral veins; L4, blade length; L 5, petiole length; L 6, blade width;L7, point of maximum blade width; L8, number of teeth; L9, base symmetry: 0 = symmetrical, 1 = asymmetrical; L10, base shape: 1 = cordate (> 2 mm depth), 2 = subcordate (0—2 mm depth), 3 = rounded to obtuse, 4 = truncate, 5 = cuneate to acute; L11, coincidence of base symmetry in leaf pairs: 1 = symmetrical both leaves, 2 = asymmetrical one leaf, 3 = asymmetrical both leaves; L13, serration type: 1 = single, 2 = single to slightly double, 3 = double, 4 = extremely double; L 14, relative number of pairs of lateral veins (L3/L4); L15, relative number of teeth (L8/L4); L16, relative petiole length (L5/L4); L17, blade width/blade length (L6/L4); L18, blade shape (L7/L4); L19, average number of teeth between lateral veins (L8/L3); L20, base angle in degrees; * alpha = 0.05, ** alpha = 0.01; CV = coefficient of variation. Note: IN - IL should read NS - SC.

teeth, were either discrete or synthetic attributes. MANOVA tests for differences among regions were significant both with and without the discrete attributes.

Each set of tests by region showed at least some differences between disjunct and continuous populations (*Table 2*). Attribute L7, point of maximum blade width, was the only attribute mean that was significant between disjunct and continuous populations in any of the four regions. However, in each region at least six attributes showed significant differences in variance. Only variances of L3 and L6 were not significantly different between disjunct and continuous populations in at least one region. None of the attribute variances was consistently significant across all four regions. In the Indiana-Illinois (IN-IL) region L7 means were significantly different between disjunct and continuous populations (*Table 2*). Ten of the attributes also showed significant differences in variances between disjunct and continuous populations. The variance of nine of the 18 attributes was greater in the continuous populations than in the disjunct populations. Only one of the attributes was significantly more variable in the disjunct area. In the Kansas-Missouri-Oklahoma (KA-MO-OK) region six attribute variances were significantly different between continuous and disjunct populations (*Table 2*). The trend was similar to that of the IN-IL region with four attribute variances greater in the continuous and two greater in disjunct populations. The Pennsylvania-New York-Massachusetts (PA-NY-MA) region showed significant differences in variances between continuous and disjunct populations for ten attributes (*Table 2*). Though the differences in variance were again pronounced, the trend was the reverse of the IN-IL region. Here nine of the ten attributes showing significance had higher variances in the disjunct area than in the continuous part of the range. In the North Carolina-South Carolina (NC-SC) region ten attribute variances were significantly different between disjunct and continuous populations (*Table 2*). Again, like the IN-IL and KA-MO-OK regions, most (seven of ten) of these attributes exhibited higher variances in the continuous part of the range than in the disjunct area.

Although in only one instance did the ANOVA tests show a significant difference in attribute means between disjunct and continuous populations, MANOVA tests between disjunct and continuous populations were significant in each of the four regions. However, the significance of the MANOVA tests may have been due to the use of the among-trees sum of squares in the error term, rather than the among-replicate populations sum of squares which was used in the ANOVA tests.

Results of chi-square tests of independence for the discrete attributes L2, L9, L10, L11, and L13 are presented elsewhere (Coyle 1981). All five of the attributes were significant among regions, as compared to three of the same attributes which were significant in the ANOVA tests. While none of the ANOVA tests showed significance for these attributes between disjunct and continuous populations, chi-square tests showed significance for at least two attributes in all but the PA-NY-MA region. All five of the attributes were also significantly different among local populations, as they were in the ANOVA tests.

## Discussion

Little is known concerning variability among diverse populations of birches in general, and even less about variability in river birch specifically. A few studies have suggested that considerable variation within river birch exists (Wendling 1970, Roth 1971). Results from this study support earlier work to the extent that the observed coefficients of variation for leaf attributes were almost without exception higher in river birch than those for the same attributes as measured in sweet birch (*B. lenta* L.) and yellow birch (*B. alleghaniensis* Britt.) (Dancik and Barnes 1975, Sharik and Barnes 1979). The generally lower variances of attributes for river birch from disjunct populations in all but the PA-NY-MA region when compared to populations from the continuous part of the range may be the result of founder effects, drift, or more intense selection pressures operating in the disjunct areas. The relatively small number of attribute variances that were significantly different between disjunct and continuous populations in the KA-MO-OK region may be due to insufficient spatial isolation, as McGregor (personal communication) has indicated that river birch may not be truly disjunct from the continuous part of the species range in southeastern Kansas.

The high variances found in the disjunct area of the PA-NY-MA region compared to those in the continuous part of the range were contrary to the findings in the other regions, but are in agreement with studies involving other species (Ford 1975). Lewontin (1974) indicated that because of the temporal instability of marginal environments, variation in selection may result in highly variable marginal populations. Heslop-Harrison (1964) suggested that a species may possess greater variation near the edge of its range than at its center because of reduced interspecific competition in the former situation. According to Grant's (1971) theory of quantum speciation, higher variability in disjunct populations is possible where these populations have recently been established in suitable, but previously unoccupied areas. This may be the case in the New England area as there are reports that the river birch populations there are expanding rapidly (Koevenig 1975).

Mayr (1958) has suggested that an occasional marginal, disjunct population which succeeds in making an ecological shift and becomes adapted to a new niche, or even to a major new ecological zone, may expand rapidly under relaxed selection and start to accumulate additional genetic variability. Eventually the variation in this population may equal or even exceed that of centroid populations. The relatively high variation in disjunct populations of river birch from the PA-NY-MA region may be attributed to this phenomenon, although it is not clear that these populations occur in habitats which are markedly different from those in the main part of the species' range.

Unlike the relatively few differences found between attribute means of disjunct and continuous populations, nine of the 18 attributes in the present study showed significant among-region differences. Such regional differences among tree populations are commonly attributed to macroclimatic gradients (Stern and Roche 1974). However, previous investigations involving other North American dark-barked birches revealed an insignificant or weak relationship between climate and regional patterns of morphological variation (Clausen 1973, Dancik and Barnes 1975, Sharik and Barnes 1979). The possibility exists that at least some of the phenotypic differences observed in the present study are due to environmental rather than genetic differences, although Dancik and Barnes (1975) have argued that reasonable approximations of genetic variation in birches can be obtained from collections of plants in their native habitats.

The fact that more attributes exhibited significant differences among local populations than across regions or between disjunct and continuous areas, suggests that the factors which influence leaf morphology in river birch are not those associated with macroclimatic gradients. River birch is often absent from the floodplains of large rivers, but commonly occurs along the smaller tributary streams (Buell and Wistendahl 1955, McClelland and Ungar 1970, Cribben and Ungar 1974). Even the continuous portion of the range of the species may represent a mosaic of semi-isolated, local populations with differences in leaf morphology due mainly to the effect of genetic drift in local populations. This would be true especially if the genes which determine leaf morphology are nonadaptive, or only poorly adaptive, as seems to be the case for the attributes considered here and in studies of other dark-barked birches indigenous to North America.

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