Genetic Structure of Populations and Differentiation in Forest Trees

Raymond P. Guries and F. Thomas Ledig

Abstract: Electrophoretic techniques permit population biologists to analyze genetic structure of natural populations by using large numbers of allozyme loci. Several methods of analysis have been applied to allozyme data, including chi-square contingency tests, F-statistics, and genetic distance. This paper compares such statistics for pitch pine (Pinus rigida Mill.) with those gathered for other plants and animals. On the basis of these comparisons, we conclude that pitch pine shows significant differentiation across its range, but appears to be less differentiated than many other organisms. Data for other forest trees indicate that they, in general, conform to the pitch pine model. An open breeding system and a long life cycle probably are responsible for the limited differentiation observed in forest trees. These conclusions pertain only to variation at allozyme loci, a class that may be predominantly neutral with respect to adaptation, although gene frequencies for some loci were correlated with climatic variables.

During the last 40 years, a considerable body of information has been assembled on genetic variability in forest tree species. Measurements of growth rate, cold-hardiness, phenology, and related traits have provided tree breeders with much useful knowledge, and have indicated in a general way how tree species have adapted to a spatially variable habitat (Wright 1976). Most information has come from studies designed to assess relative differences in metric traits among provenances representing a wide geographic range. When the identification of suitable seed sources for use in reforestation is a primary objective, provenance tests (that is, common garden studies) may be indispensable. However, such studies are expensive to conduct, require large areas of land, yield useful data only after many years, and use traits of unknown inheritance.

The development of electrophoretic techniques during the last two decades provided an alternative to common garden techniques for estimating levels of genetic variation in natural populations (Lewontin 1974). Electrophoretic techniques are now widely used in studies of plant and animal populations and have produced a large body of data on the levels and patterns of genic variability characteristic of many species. Although the difficulties inherent in the large size and late reproductive maturity of trees somewhat delayed their study, there is in recent years a rapid accumulation of useful data from the application of electrophoretic techniques to several conifers.

Population Structure

A common notion among foresters is that most tree species are divided into relatively small breeding populations because of limited pollen or seed dispersal. Most matings are considered to be among near neighbors, leading in time to the division of a large population into numerous, small "neighborhoods." Other factors such as physical isolation, breeding system, population demography, natural selection, and random genetic drift accentuate such subdivision. The sum total of the ecological and genetic relationships among individuals and the populations they comprise is termed "population structure" (Jain 1975).

Of special interest to tree breeders are the genetic consequences of population structure. Several measures of the genetic structure of populations have been proposed, including assessments of (a) gene diversity in the average population, (b) levels of diversity in different populations, and (c) degree of differentiation among populations (Brown 1978). All these measures are amenable to allozyme analysis, and recent explorations have begun to probe the genetic structure of forest trees.

Our approach in this paper is to compare estimates of various parameters of population structure obtained from pitch pine (Pinus rigida Mill.) with those of other species. Rigorous comparisons are seldom possible because of variation in methods of data collection and analysis; therefore, we use them here only for purposes of general description.

Chi-Square Analysis of Heterogeneity

The subdivision of populations may lead to a heterogeneity of gene frequencies among subpopulations as a result of selection or drift. Variation in genic proportions

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can be subjected to a contingency chi-square analysis to determine the existence or extent of any heterogeneity (Workman and Niswander 1970). A major advantage of the technique is ease of calculation; however, the analysis does not identify the forces responsible for any observed heterogeneity. For pitch pine, chi-square was calculated using the technique of Snedecor and Irwin (1933):

$$\chi^2 = 2N\sum \frac{\sigma^2}{p_i}$$

in which N is the total number of individuals, \(\sigma^2\) is the variance in allele frequency, and \(\overline{p}_i\) is the weighted mean frequency.

A significant amount of heterogeneity is apparent at most of 21 loci in 11 populations of pitch pine (Table 1). Considering the wide range over which pitch pine samples were collected (from Quebec to North Carolina), differential selection in varying environments is one possible explanation. Distribution of allele frequencies was observed to be heterogeneous over relatively short distances in ponderosa pine (Pinus ponderosa Dougl. ex Laws.), perhaps because of differential selection on slopes of varying aspect (Mitton and others 1977). However, Neale (1978) found no evidence of allelic heterogeneity among populations of balsam fir (Abies balsamea [L.] Mill.) occurring along an elevational gradient in New Hampshire, although differences in growth and physiological processes were observed and related to environmental variation along the same transect (Fryer and Ledig 1972).

Genetic drift could also produce heterogeneity. In pitch pine, certain populations (for example, one in St. Chryso-stome, Quebec) are isolated from the main body of the species range. If such populations were founded by a small number of individuals, genetic drift could account for much of the observed heterogeneity. Genetic drift was a possible explanation for observed heterogeneity of gene frequencies among three small populations of Table Mountain pine (Pinus pungens Lamb.) in Virginia (Feret 1974). In any event, the large range in chi-square values among loci in pitch pine suggests that different loci are probably responding independently to whatever factors are responsible for the heterogeneity.

### F-STATISTIC ANALYSIS OF POPULATION STRUCTURE

The structure of a subdivided population can also be analyzed by F-statistics (Wright 1951, 1965, 1969; Kirby 1975; Nei 1977). F-statistics were originally devised to examine structuring in hierarchical populations by using the correlation between uniting gametes within and among subpopulations and for the population as a whole. Wright (1965) advanced three parameters "in terms of a total population (T), subdivisions (S), and individuals (I). \(F_{ST}\) is the correlation between gametes that unite to produce the individuals, relative to the gametes of the total population. \(F_{IS}\) is the average overall subdivisions of the correlation between uniting gametes relative to those of their subdivision. \(F_{IT}\) is the correlation between random gametes within subdivisions, relative to gametes of the total population. The list can be extended if there are further subdivisions. The above three F-statistics are not independent."

These statistics have as a common focal point the fixation index, F, which represents the total deviation from Hardy-Weinberg proportions because of the joint effects of finite population size, selection, inbreeding, and other factors. The estimate of \(F_{IS}i\) for the \(i^{th}\) subpopulation was calculated as:

$$F_{IS} = 1 - H / \left(1 + 2N - 1\right) \sum p_i q_i$$

in which \(H\) is the observed number of heterozygotes in the \(i^{th}\) subpopulation and the denominator is the expected number corrected for finite population size (Kirby 1975).

\(F_{IS}\) represents the average deviation of the population's genotypic proportions from Hardy-Weinberg equilibrium for a locus and is calculated as the weighted mean of the F values for all populations:

$$F_{IS} = \sum \frac{N_i}{N} p_i q_i F_{IS} / \sum \frac{N_i}{N} p_i q_i$$

A negative \(F_{IS}\) value represents an excess of heterozygotes. It is worth noting that \(F_{IS}\) not equivalent to the coefficient of inbreeding except in the unlikely event that inbreeding

<table>
<thead>
<tr>
<th>Locus</th>
<th>(X^2)</th>
<th>df</th>
<th>(P&lt;)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MDH-1</td>
<td>45.76</td>
<td>10</td>
<td>0.005</td>
</tr>
<tr>
<td>MDH-2</td>
<td>107.77</td>
<td>10</td>
<td>0.005</td>
</tr>
<tr>
<td>IDH</td>
<td>95.43</td>
<td>10</td>
<td>0.005</td>
</tr>
<tr>
<td>FUM</td>
<td>18.22</td>
<td>10</td>
<td>.1</td>
</tr>
<tr>
<td>PGM-1</td>
<td>9.39</td>
<td>10</td>
<td>.5</td>
</tr>
<tr>
<td>PGM-2</td>
<td>42.22</td>
<td>10</td>
<td>.005</td>
</tr>
<tr>
<td>GPI-1</td>
<td>16.60</td>
<td>10</td>
<td>.1</td>
</tr>
<tr>
<td>GPI-2</td>
<td>28.07</td>
<td>10</td>
<td>.005</td>
</tr>
<tr>
<td>6-PGD-1</td>
<td>166.36</td>
<td>10</td>
<td>.005</td>
</tr>
<tr>
<td>6-PGD-2</td>
<td>52.58</td>
<td>10</td>
<td>.005</td>
</tr>
<tr>
<td>G-6-P</td>
<td>39.66</td>
<td>10</td>
<td>.005</td>
</tr>
<tr>
<td>LAM</td>
<td>51.91</td>
<td>10</td>
<td>.005</td>
</tr>
<tr>
<td>LAP-2</td>
<td>37.97</td>
<td>10</td>
<td>.005</td>
</tr>
<tr>
<td>GOT-1</td>
<td>44.39</td>
<td>10</td>
<td>.005</td>
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<tr>
<td>GOT-2</td>
<td>34.59</td>
<td>10</td>
<td>.005</td>
</tr>
<tr>
<td>ACP</td>
<td>54.92</td>
<td>10</td>
<td>.005</td>
</tr>
<tr>
<td>ACO</td>
<td>131.04</td>
<td>10</td>
<td>.005</td>
</tr>
<tr>
<td>GDH</td>
<td>31.72</td>
<td>10</td>
<td>.005</td>
</tr>
<tr>
<td>ADH</td>
<td>3.64</td>
<td>10</td>
<td>.95</td>
</tr>
<tr>
<td>ALD-1</td>
<td>30.00</td>
<td>10</td>
<td>.005</td>
</tr>
<tr>
<td>ALD-2</td>
<td>148.57</td>
<td>10</td>
<td>.005</td>
</tr>
</tbody>
</table>
alone is responsible for departures from Hardy-Weinberg equilibrium. \( F_{IS} \) can be averaged across all loci. The extent of differentiation among subpopulations is measured by \( F_{ST} \), the correlation between random gametes within subdivisions, and was calculated as Nei's (1975) \( G_{ST} \):

\[
G_{ST} = \frac{D_{ST}}{H_{T}}
\]

in which \( H_{T} \) is the gene diversity in the total population, \( D_{ST} \) is the average gene diversity among subpopulations.

\[
H_{T} = 1 - \sum_{k} \left( \frac{\sum_{i} p_{ik}^2}{S} \right)^2, \quad \text{and}
\]

\[
D_{ST} = \sum_{i} \left( \frac{\sum_{k} p_{ik}^2}{S} \right) - \sum_{k} \left( \frac{\sum_{i} p_{ik}^2}{S} \right)^2.
\]

in which \( p_{ik} \) is the frequency of the \( k \)th allele in the \( i \)th subpopulation and \( S \) is the number of subpopulations.

For gene loci with only two alleles, \( F_{ST} \) was also calculated as:

\[
F_{ST} = \frac{\sigma_{jk}^2}{\bar{p}_{j} \bar{p}_{k}},
\]

in which \( \sigma_{jk} \) is the weighted sum of squared deviations of the individual subpopulation gene frequencies from the mean gene frequency, divided by the number of subpopulations, and \( P \) and \( q \) represent weighted mean frequencies.

\[
\sigma_{jk} = \frac{\sum_{i} N_{i}}{N} (p_{ji} - \bar{p}_{j})(p_{ki} - \bar{p}_{k}),
\]

\[
\bar{p}_{j} = \frac{\sum_{i} N_{i} p_{ji}}{N}, \quad \text{and}
\]

\[
\bar{p}_{k} = \frac{\sum_{i} N_{i} p_{ki}}{N},
\]

where \( p_{ji} \) and \( p_{ki} \) are the \( j \)th and \( k \)th alleles in the \( i \)th population. \( F_{ST} \) for multiple alleles must be calculated for each combination of alleles. For pitch pine, differences between Nei's \( G_{ST} \) and Wright's \( F_{ST} \) were negligible, and Nei's calculation was preferred.

The overall fixation index, \( F_{IT} \), represents the correlation between uniting gametes relative to the gametes of the total population and was calculated from \( F_{IS} \) and \( F_{ST} \) as:

\[
F_{IT} = F_{IS} + (1 - F_{IS}) F_{ST}.
\]

Like \( F_{IS} \), \( F_{IT} \) may be positive or negative, with a negative value indicative of excess heterozygotes. If all populations are in Hardy-Weinberg equilibrium, \( F_{IS} = 0 \) and \( F_{IT} = F_{ST} \). However, even if Hardy-Weinberg proportions are obtained, differentiation because of differing allele frequencies in subpopulations can lead to significant \( F_{ST} \) and \( F_{IT} \) values.

F-statistics are arranged by increasing \( F_{ST} \) values for several species of plants and animals including human populations in Table 2. Two species of trees, pitch pine and balsam fir, for which estimates are included in Table 2, were both characterized by relatively small \( F_{IS} \) values, an indication that populations are at or near Hardy-Weinberg equilibrium. This may or may not indicate that inbreeding is insignificant, because a tendency toward increasing \( F_{IS} \) values by way of inbreeding could be offset by such factors as migration or differential fertility. In fact, opposing forces probably counter-balance each other in many instances, with the net result that \( F \) (and, therefore, \( F_{IS} \)) is near zero (Workman 1969).

For both tree species, \( F_{ST} \) values were also small, relative to other organisms. Balsam fir, which did not show allelic heterogeneity in contingency chi-square tests (Neale 1978), has a value of \( F_{ST} \) about one-half as large as pitch pine. However, the range sampled in pitch pine was much larger, more than 1000 km in both north-south and east-west directions, while balsam fir was sampled on a single mountainside. \( F_{ST} \) values have been calculated for a variety of other organisms not given in Table 2, but including the house mouse (\( F_{ST} = 0.024 \), one barn; Selander 1970), Drosophila robusta (\( F_{ST} = 0.055 \), Eastern United States; Prakash 1973), and the brown snail (\( F_{ST} = 0.116 \), a city

Table 2—F-Statistics from plant, animal, and human populations

<table>
<thead>
<tr>
<th>Groups of plant, animal, and human populations</th>
<th>Loci</th>
<th>( F_{IS} )</th>
<th>( F_{ST} )</th>
<th>( F_{IT} )</th>
<th>Sampling unit</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Japanese</td>
<td>1</td>
<td>0.002</td>
<td>0.001</td>
<td>0.003</td>
<td>All Japan</td>
<td>Nei and Imaizumi 1966</td>
</tr>
<tr>
<td>Monarch butterfly</td>
<td>6</td>
<td>.008</td>
<td>.009</td>
<td>.017</td>
<td>Eastern United States</td>
<td>Eanes and Koehn 1978</td>
</tr>
<tr>
<td>Balsam fu</td>
<td>7</td>
<td>.001</td>
<td>.012</td>
<td>.013</td>
<td>New Hampshire mountainside</td>
<td>Neale 1978</td>
</tr>
<tr>
<td>Papago Indians</td>
<td>7</td>
<td>-.005</td>
<td>.023</td>
<td>.009</td>
<td>10 reservation districts</td>
<td>Workman and Niswander 1970</td>
</tr>
<tr>
<td>Pitch pine</td>
<td>21</td>
<td>.009</td>
<td>.029</td>
<td>.034</td>
<td>Eastern United States</td>
<td>Guries and Ledig (in preparation)</td>
</tr>
<tr>
<td>Bluegill</td>
<td>3</td>
<td>.012</td>
<td>.029</td>
<td>.024</td>
<td>Within reservoirs</td>
<td>Avise and Felley 1979</td>
</tr>
<tr>
<td>Yanomama Indians</td>
<td>8</td>
<td>.028</td>
<td>.064</td>
<td>.045</td>
<td>37 villages in Venezuela</td>
<td>Neel and Ward 1972</td>
</tr>
<tr>
<td>Cylindric blazing-star</td>
<td>15</td>
<td>.407</td>
<td>.469</td>
<td>.426</td>
<td>1/8 acre</td>
<td>Schaal 1975</td>
</tr>
<tr>
<td>Phlox (3 species)</td>
<td>4 to 6</td>
<td>.503</td>
<td>.200</td>
<td>.643</td>
<td>Central Texas</td>
<td>Levin 1978</td>
</tr>
</tbody>
</table>
block; Selander and Kaufman 1975). Geographic differentiation for pitch pine across its range is roughly no larger than that observed among bluegill populations within a single lake or Indian settlements on a single Indian reservation. The estimates for pitch pine are considerably smaller than those obtained for brown snails within the narrow confines of a city block or the herbaceous plant, cylindric blazing-star (Liatis cyindracea Michx.), growing on a plot of only 1/8-acre. Although population differentiation has occurred in pitch pine as indicated by the chi-square contingency test, it has not developed to the degree characteristic of many other organisms.

As a result of a low fixation index within populations (low $F_{IS}$) and a lack of extensive differentiation among populations (low $F_{ST}$), the total fixation index, $F_{IT}$, in pitch pine is also low. The two estimates for herbaceous plants included in table 2 have $F_{IT}$ values from 10 to 20 times greater than pitch pine, a feature probably indicative of a high degree of inbreeding in the herbs.

**ANALYSIS OF GENETIC DISTANCE**

Perhaps the most widely applied index of genetic differentiation is that of genetic distance (Nei 1972). This method was developed to use isozyme data as a measure of the accumulated number of gene substitutions per locus and is defined by:

$$D = -\log I$$

in which $I$ represents the normalized identity of genes. If two populations have the same alleles in the same frequency, $I = 1$; when two populations have no alleles in common, $I = 0$.

Estimates of genetic distance among populations within a species (or among species) are available for a number of plants and animals (see reviews of Avise 1974, Gottlieb 1977). Estimates of the mean genetic distance among conspecific populations for a number of species indicate that divergence among populations of tree species has been rather limited relative to that found in other organisms over much smaller areas (table 3). Results are consistent with $F_{ST}$ values presented earlier. It should be noted that all tree species for which such estimates are available are outbreeding and anemophilous, and gene flow may be substantially greater than for trees that use animals as pollen vectors.

Comparisons of genetic distance with geographic distance have frequently been useful in determining whether differentiation can be explained on the basis of isolation by distance. For example, genetic distance in cylindric blazing-star (table 2) was strongly correlated with geographic distance and "neighborhoods" became well-differentiated over distances of several meters (Schaal 1974).

To test whether a significant relationship exists between genetic and geographic distance for populations of pitch pine, a product-moment correlation was calculated and proved to be nonsignificant ($r = 0.263; 0.1 > P > 0.05$). By contrast, a significant correlation was noted between genetic and geographic distance for Douglas-fir ($Pseudotsuga mariesii$ [Mirb.] Franco) populations in coastal British Columbia.4 However, it appears that much of the differentiation observed in Douglas-fir was the result of differences between island and mainland populations.5

**RELATIONSHIP TO ENVIRONMENTAL GRADIENTS**

Geographic distance per se may not be the most useful parameter by which to measure isolation, especially if the loci in question are under selection pressure. Therefore, product-moment correlations between the frequency of the most common allele and several climatic variables were calculated for the 11 most polymorphic loci in pitch pine (table 4). Significant correlations were noted for six of the 11 loci. Although such correlations are not evidence for the operation of natural selection, they parallel clinal patterns

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5Personal communication from D. M. O’Malley, University of Wisconsin, Madison, July 1979.

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**Table 3**—Mean genetic distance estimates, $D$, for a number of species and sampling units with estimates arranged in order of increasing $\bar{D}$

<table>
<thead>
<tr>
<th>Species</th>
<th>Loci</th>
<th>$\bar{D}$</th>
<th>Sampling unit</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Douglas-fir</td>
<td>21</td>
<td>0.004</td>
<td>Coastal British Columbia</td>
<td>Yeh and O’Malley (in preparation)</td>
</tr>
<tr>
<td>Pitch pine</td>
<td>21</td>
<td>0.007</td>
<td>Eastern United States</td>
<td>Guries and Legid (in preparation)</td>
</tr>
<tr>
<td>Silver spot butterfly</td>
<td>3</td>
<td>0.13</td>
<td>Northern California</td>
<td>Brittacher and others 1978</td>
</tr>
<tr>
<td>Norway spruce</td>
<td>4</td>
<td>0.14</td>
<td>Sweden</td>
<td>Lundkvist and Rudin 1977</td>
</tr>
<tr>
<td>House mouse</td>
<td>41</td>
<td>0.14</td>
<td>Single barn</td>
<td>Selander, Hunt and Young 1969 (see Nei 1972)</td>
</tr>
<tr>
<td>Phlox</td>
<td>20</td>
<td>0.19</td>
<td>Central Texas</td>
<td>Levin 1978</td>
</tr>
<tr>
<td>Mosquitos</td>
<td>18</td>
<td>0.42</td>
<td>Coastal Kenya</td>
<td>Tabachnick and others 1979</td>
</tr>
<tr>
<td>American Indian tribes</td>
<td>6</td>
<td>0.53</td>
<td>Northern South America</td>
<td>Ward and others 1975</td>
</tr>
<tr>
<td>Topminnow</td>
<td>25</td>
<td>0.19</td>
<td>Northwestern Mexico</td>
<td>Vrijenhoek and others 1977</td>
</tr>
<tr>
<td>Pocket gophers</td>
<td>23</td>
<td>0.14</td>
<td>Southwestern United States</td>
<td>Patton and Yang 1977</td>
</tr>
<tr>
<td>Newts</td>
<td>35 to 40</td>
<td>0.292</td>
<td>River drainage in California</td>
<td>Hedgecock 1978</td>
</tr>
</tbody>
</table>
of phenotypic variation noted in wood specific gravity (Ledig and others 1975) and cone serotiny (Ledig and Fryer 1972), and genetic variation in height growth revealed in a common garden study (Ledig and others 1976). In all of these studies patterns of variation were well correlated with ecological variables considered important to growth or survival. In the present study, for four of six loci, significant correlations between allele frequencies and climatic variables involved winter temperature or snowfall, which perhaps, reflect environmental stress; conditions which tend to reduce survival and limit reproductive rate in pitch pine.

**DISCUSSION**

The overall picture of pitch pine emerging from these analyses is one of a weakly differentiated series of populations. Although isolation by distance appears to be an important aspect of differentiation in herbaceous plant species, it is only mildly so in pitch pine. The lack of significant barriers to gene flow may be one important reason for the relatively undifferentiated status of pitch pine with regard to allozyme loci. Although the range of pitch pine includes disjunct populations, no major geographic barriers to gene flow exist, and the time since pitch pine migrated from its glacial refugium to occupy its present range has been brief, less than 100 to 300 generations. Furthermore, pitch pine, like most north-temperate tree species, is anemophilous, and wind can be an effective pollen vector for long distance transport (Koski 1970). In addition, pitch pine shows a dramatic depression when subjected to inbreeding (Wright 1962); therefore, selection reduces the impact of inbreeding and favors a strong tendency to outbreeding. For genetic distance, the estimates for pitch pine and other tree species (table 3) are similar and smaller than similar comparisons with inbreeding herbaceous species. The characteristic long generations and open breeding systems shared by tree species may act to distinguish them from herbaceous species.

Nevertheless, the data are insufficient to determine whether the results observed for pitch pine are really typical of other forest trees. Our current opinion is that they will prove to be reasonably typical of many other eastern conifers. Similarities in breeding system, demography, range, time since post-Pleistocene recolonization, and other factors all suggest that patterns paralleling that of pitch pine might be expected. Conifers such as eastern hemlock (Tsuga canadensis [L.] Carr.), which is a late successional species, red pine (Pinus resinosa Ait.), which has limited genetic variability (Fowler and Morris 1977), or jack pine (Pinus banksiana Lamb.) with an extensive range, may differ from the pitch pine model. Conifers of the Western United States may be relatively more differentiated than pitch pine, especially those that have extensive and fractionated populations in mountainous areas where opportunities for differential selection are great. In mountainous areas population structure in its spatial aspects conforms to an island model, and is conducive to differentiation among populations. Some hardwoods, those that are insect-pollinated, may also deviate considerably from the pitch pine model, but most anemophilous hardwoods should parallel pitch pine. Electrophoretic studies of these and other species will undoubtedly increase our knowledge of the genetic structure and differentiation characteristic of forest trees. Results from such studies should be of great interest and value to population biologists and tree breeders alike.

Acknowledgments

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