GENETIC STRUCTURE OF FOREST TREE POPULATIONS: MEASUREMENT AND INTERPRETATION

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Abstract.--The population genetic structure of forest trees is reviewed in the context of forest stand development. The effects of variation in mating system parameters, seed production and dispersal, and survival and early growth on population genetic structure in forest stands are discussed. In general, forest tree populations are considered to be relatively unstructured due to their large effective population size, outcrossing breeding system and long-life cycle. However, much of what is known about the population structure of trees is based upon results from studies of conifers, and our perspectives could change as more woody angiosperms are studied.

Additional keywords: F-statistics, gene diversity, silvicultural implications, population subdivision.

Forest trees typically occur in extensive populations distributed across the landscape in a mosaic of age classes and species mixtures. A popular view is that such populations are subdivided into smaller "neighborhoods" within which mating occurs among related individuals. This arrangement of populations into a collection of hierarchical units is called population genetic structure, a term which conveys the image of a spatial or temporal organization of genotypes and sub-populations. A variety of genetic models (see Wright 1969 for a review) have been proposed for the analysis of subdivided populations, and a variety of measures of within- and between-population differentiation have been used to assess population structure.

The forester's interest in the subdivision of a large population of trees into smaller "neighborhoods" is primarily a silvicultural one. The quality as well as the abundance of natural regeneration is important in assessing the success of various silvicultural systems. For example, it may be of interest to know the size of a locally adapted population when making decisions about the size of a harvest so that future regeneration needs are satisfied by seed from well-adapted individuals. The extent to which individuals within a population are mating "at random" may also be important in choosing a silvicultural system so that outcrossing may, for example, be favored. Tree breeders may also wish to know the degree of sub-structuring so that "candidate trees" selected from wild stands are not drawn from the same "neighborhood".

In all the above instances, we need techniques to measure and subsequently interpret population genetic structure in trees. It is also important to consider what genetic and ecological factors give rise to such structure. In what follows, I have tried to identify and assess a number of potentially important factors/mechanisms which could give rise to appreciable levels of genetic structure within a population of trees. For simplicity, I have identified several major features of forest stands and how each may affect the development of population structure: 1) distribution of parental genotypes, 2) mating system dynamics, 3) seed dispersal, and 4) survival and growth during the early stages of stand development.

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Measuring Population Structure

In principle, any set of genetic traits could be used to assess population genetic structure, although the approach would vary considerably between different sets of traits. In practice, traits such as allozymes for which gene frequencies can be enumerated are favored, in part because so much of population genetics theory is couched in terms of gene frequencies. Two related analyses, gene diversity statistics (Nei 1973) and F-statistics analysis (Wright 1951, 1965), are commonly employed in studies of population genetic structure. Both focus upon the hierarchical nature of population subdivision across landscapes and differ primarily in estimation procedures which emphasize genotype arrays (F-statistics) or gene frequency arrays (gene diversity analysis). The availability of a variety of software packages together with the technical simplicity and speed of allozyme analysis has led to the rapid expansion of our knowledge in this area of forest biology.

Metric traits can also be utilized as analysis of variance techniques can partition genetic variances into within- and among-population components. Many provenance/progeny test reports have partitioned variation into among tree, stand and region components. However, cross-comparisons among studies of different species, or even different populations of the same species, are not commonly made based upon metric traits because test environment is a major factor in the partitioning of variance components. Thus, estimates of population genetic structure may vary considerably from year to year or site to site as variance components change. For example, Clausen (1973) noted that stands may represent a large proportion of total variation in height growth in yellow birch in one year, while family effects dominate in the next year. In red maple, Townsend and Harvey (1983) noted that stands generally represented a greater source of variation than families for height, diameter and other traits, but differences in the apportionment of this variation varied several-fold depending upon test environment. In some conifers there appears to be more consistency, at least for height growth, with several reports indicating that stands account for about twice as much variation as families within stands (Wright et al. 1976, des Bordes and Thor 1979, Thor and Gall 1978). However, the large environmental effects common to most field studies, together with the large differences in sampling strategies and field designs make it very difficult to assess population genetic structure based upon metric traits.

Almost all of the available information on population genetic structure in forest trees is of recent origin (post-1975), employs biochemical polymorphisms, and focuses upon conifers. Procedures are more or less standardized here, and different studies of the same species typically yield comparable results (e.g., Dancik and Yeh 1983, and Wheeler and Guries 1982, for lodgepole and jack pines). Gene diversity analyses consistently indicate that for tree species studied to date 90% or more of the total allozyme variation is apportioned within populations, the remainder being attributable to between population differences (Guries 1984, and others). Basically, almost all populations of a given species share the same allozymes at approximately the same frequency. Rare alleles may occur but, by definition, they account for very little of the total diversity and have little effect on most diversity statistics analyses.

Comparisons of the extent and patterning of allozyme and quantitative traits are tempting because they appear to provide opportunities for a thorough understanding of population structure. And if the genetic organization of both sets of traits were similar, it would seem to suggest that one (the easiest to measure) could replace the other in studies of genetic architecture. However, I know of no evidence which indicates that allozyme and quantitative trait loci can be considered as analogs for population structure studies. Indeed, Lewontin (1984) cautions against just such comparisons because of the difficulties involved in demonstrating significant differences between gene frequencies and the means of metric characters. Thus, while the patterning of variation for morphometric and allozyme traits may be similar in many ways (e.g., Wheeler and Guries 1982), there are also well-studied species in which no useful pattern relationships are apparent (e.g., Merkle and Adams 1987). At present, there is no simple formula by which the extent and patterning of genetic variation as assessed by metric characters versus allozymes can be used to produce recommendations on seed transfer, choice of silvicultural system, or related problems. Analyses of both kinds of data are useful for enhancing our understanding of genetic processes in forest stands, but management recommendations demand that we favor interpretations that best reflect patterns of adaptive variation.

Several recent reviews of population genetic structure in plants in general (Hamrick et al., 1979; Loveless and Hamrick, 1984) and forest trees in particular (Namkoong, 1983; Guries, 1984) indicate that in terms of allozyme diversity, forest tree populations are highly polymorphic, exhibit relatively little population subdivision, and appear to be essentially panmictic in terms of mating behavior. These are rather sweeping generalizations and exceptions do exist, many of which are interpretable in terms of mating system, seed dispersal mechanism or other life history features. In addition, it is important to note that most analyses of forest tree population structure involve spatial rather than temporal variation, and most analyses involve only a single generation. Thus, while we would prefer to have a more dynamic assessment of the current situation, we are limited to a static one, somewhat akin to a "snapshot". From this "snapshot", we have some idea of what features characterize the population structure of a typical conifer but we cannot tell how rapidly or in which direction it might change.

Interpretation of Population Structure

Stage 1: Genetic Structure in the Mature Population

The array of genotypes which comprises the mature stand represents the very small pool of survivors of a once much larger number of seedlings and saplings. Both stochastic and directional factors have influenced the development of each population. Unfortunately, we virtually never have pedigree information on individuals in such populations, and the extent to which these breeding trees are (or are not) randomly distributed can influence the potential levels of subdivision in future generations.

A number of studies of the genetic structure of (mostly) conifer populations have been conducted during the past 10 years, and collectively have yielded a portrait of a typical conifer population. In general, populations of reproductive individuals conform to Hardy-Weinberg proportions, with F_{IS} values at or near zero for many conifer species (Guries and Ledig 1982, Dancik and Yeh 1983, Knowles 1984, Boyle and Morgenstern 1987, and others). For other species, small departures from H-W proportions, either as excesses or deficiencies, of heterozygotes (5-15% range) suggest modest levels of sub-structuring and have usually involved situations where favorable microsites might favor survival and growth of families (Linhart et al. 1981), where seed caches could give rise to clusters of related individuals (Furnier et al. 1987), where extreme environments might favor a narrow set of genotypes (Neale and Adams 1985), or similar situations which could be expected to lead to aggregation of related individuals. However, the average degree of relatedness in virtually all of these studies is considered to be much less than that of half-sibs.

A smaller body of data, mainly for white spruce, suggests that neighboring individuals are highly related as measured by the production of apparently inbred individuals from matings among closely spaced trees (Coles and Fowler 1976, Park

Fowler and Coles 1982). Trees within some stands are viewed as being related at the level of half-sibs (r = 0.25) with progeny arrays related at much higher levels.

Such contrasting viewpoints are vexing, and seem to beg that investigators line up along opposing sides. In truth, I believe the actual levels of relatedness among trees in forest stands lie somewhere between the two. Allozyme studies probably underestimate the true level of relatedness due to sampling errors (misclassification) and the fact that F-statistics analysis is a single-generation approach with cumulative effects of mild inbreeding not measured. The alternative approach favored by Fowler and co-workers is inclusive in its estimation of inbreeding via controlled crosses and progeny analysis, but overestimate relatedness by assigning a coefficient of relatedness of r = 1 to selfed full-sibs. In my opinion, a modest coefficient of relatedness (r = 0.05-0.15) would be reasonably accurate for near neighbors in most forest stands.

Stage 2: Mating Systems

The question of mating system as a contributor to population structure in trees appears straightforward, perhaps because almost all of our efforts have focused upon conifers. In general, estimates of mating system parameters for conifers suggest that out-crossing rates are very high, typically 90% or higher, with the remainder of viable seeds attributed to self-pollination (El-Kassaby et al. 1981, Shaw and Allard 1982, Cheliak et al. 1985, Neale and Adams 1985, Furrier and Adams 1987, and others). While some variation in estimates of outcrossing occurs from year-to-year (Cheliak et al. 1985) the situation in conifers suggests that pollen dissemination in wild populations is widespread and the proportion of seeds due to selfing is small. Selection against these inbred progenies further reduces the contribution of the mating system to generation of population structuring in conifers.

Adaptations such as serotinous cones, and/or the ability to modify the level of investment made in male and female reproductive structures, could greatly modify population genetic structure in trees. Several studies of pollination and seed production in seed orchard settings have demonstrated that a relatively small number of males may be responsible for contributing the bulk of the male gametes to the seed produced in a given year (Muller-Starck and Ziehe 1984, Schoen and Stewart 1987). If this pattern of mating were common in wild stands for many species, effective population sizes could be greatly reduced in some years with attendant genetic drift effects. However, for species with serotinous cones (i.e., many *Pinus* species) the ability to release seed from many different seed crops following a fire could have the reverse effect. Thus, two strong but opposite forces may cancel one another with the result that little evidence of genetic drift or inbreeding is observed.

The role of the mating system in angiosperm trees in modifying population structure is likely to be rather different from that of conifers given the much larger array of flower structures, modes of pollination and occurrence of mechanisms such as incompatibility which exist in angiosperms. The eucalypts are probably the best studied angiosperm trees in this regard, and estimates of outcrossing for these animal-pollinated species are generally lower than those of conifers, typically in the range of 70-90% (Brown et al. 1984). Data for tropical tree species are almost non-existent and the only published report to date indicates that outcrossing rates also can be high for tropical species (O'Malley and Bawa 1987).

Stage 3: Seed Dispersal

As with mating system parameters, the preponderance of studies of conifers has colored our perspective of the importance (or lack thereof) of seed dispersal mechanisms in creating population structure. Virtually all conifers studied to date have wind dispersed seed which tends to be dispersed within restricted distances downwind from seed trees (Yocom 1968, and others). For most conifers, seed dispersal is leptokurtic with most seed deposited within a few hundred meters of the seed tree while smaller numbers are more widely dispersed.

A notable exception to this rule involves the seed caching of pinyon jays for species such as whitebark pine (Furrier et al. 1987). Because seed in a cache tend to be collected from one or a few trees, caches which germinate give rise to clusters of trees which are related. Similar situations could obtain for other species whose seed are cached by birds, squirrels or other animals.

Over 60% of the woody plant species of the eastern U.S. are dispersed by animals (Stapanian 1986). Scatterhoarding of nuts and eating fleshy fruits and defecating seeds are two principal mechanisms of seed dispersal and both have the potential to create population structure. Although these mechanisms are well-studied by ecologists, their impact upon population structure are poorly known (Hamrick and and Loveless 1986). Gravity dispersal, even with secondary dispersal (e.g., mammal seed caching) appears to lead to relatively high levels of population structure (Hamrick and Loveless 1986). This is consistent with the results of allozyme analyses of conifers where dispersal is largely by wind and levels of population structuring appear low. However, as more angiosperm trees are examined, I expect seed dispersal mechanisms unique to certain taxa to become recognized as important factors in creating population structure. Other interesting questions such as the effect of long-term, multi-year soil storage of seed (e.g., pin cherry, Marquis 1975) on population structure remain to be studied.

Stage 4: Survival and Early Growth

Several studies have indicated that populations of seedlings and/or saplings of trees appear to exhibit temporal variation in population structure. In sugar maple, genetically different cohorts of seedlings occur, either due to unequal representation of pollen and/or seed parents in different years, or because selective forces favor certain genotypes in certain years (Mulcahy 1973). Probably both stochastic and selective factors operate to reduce very dense seedling populations to a handful of ultimate survivors. In some situations it is apparent that the progeny populations are not identical to the parental populations (Tigerstedt et al. 1982, Roberds and Conkle 1984, Neale 1985), but over time progeny populations may come to closely resemble the original parental populations. A modest trend towards increasing heterozygosity over time via the loss of more homozygous (inbred?) individuals results in an apparent reduction in population structuring. How rapidly this may happen depends a great deal upon the complex of biological and physical features of a particular environment.

Excesses of homozygotes in the seed population actually decline over time (F_{IS} changes from positive to negative) apparently due to selection against inbred progeny (Shaw and Allard 1982, Tigerstedt et al. 1982, Yazdani et al. 1984, Plessas and Strauss 1986). Thus, although the seed/seedling population shows a moderate degree of relatedness among individuals, this degree of sub-structuring declines over time, perhaps to the low levels noted for mature stands of pitch pine (Guries and Ledig 1982), lodgepole pine (Dancik and Yeh 1983, Knowles 1984) and other species.

The genetic architecture of the progeny population should be an important consideration in the choice of a silvicultural system. Some silvicultural textbooks speculate upon the genetic implications of various silvicultural systems, but only limited experimental evidence is available on this point. When progeny arrays were examined in two Douglas-fir shelterwoods, Neale (1985) found little evidence that the density of "leave trees" affected the resultant structure of the progeny populations. Progeny populations appeared to be representative of surrounding stands. Marginally higher levels of inbreeding among seed crops were noted, but resultant seedling populations were not inbred. A similar situation was described for Pinus svlvesiris regeneration in Sweden following a seed-tree regeneration harvest (Muona et al. 1985). Seed collected from "leave trees" contained an excess of homozygotes compared to the adult population, but by age 10-20 this excess homozygosity had disappeared.

The very limited evidence available regarding the genetic implications of various silviculture systems on forest stands suggests that changes in population structure and levels of variation due to natural regeneration practices are slight. However, we cannot state this conclusion too strongly given the limited number of studies completed to date. Whether small, apparently insignificant, changes can accumulate each generation to result in dramatic long-term effects, or whether other silvicultural systems with other species can yield more pronounced changes is unknown. It is somewhat comforting that the few studies reported thus far have not detected major changes in gene frequencies or population structure characteristics but additional studies are needed before general recommendations can be made regarding the genetic impacts of silvicultural practices.

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