GENETIC DIVERSITY IN CONIFER STANDS: EVALUATION, MAINTENANCE AND IMPROVEMENT

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Abstract.--Maintaining an "optimum" level of genetic diversity is often espoused as a reason to avoid plantation forestry as it is commonly practiced in the Southeast. Natural regeneration with selective harvesting is expected to yield a more diverse population than planting with seed orchard based seedlings and clearcutting. Whether or not this philosophy is valid is dependent upon the measure of diversity, the level of diversity in the originating population, seed dispersal patterns, reproductive phenology, natural selection, genetic drift, etc. Small, patchy highly related groups of trees are possible in naturally regenerated forests and successive generations may become inbred or extremely narrow in their genetic base. Effective population size, coancestry levels, and heterozygosity levels are all valid measures of genetic diversity, but each must be used in the proper context. As we attempt to discuss genetic diversity we must consider "what we want", "what we mean", and how we are going to measure it.

Keywords: Pinus taeda, effective size

INTRODUCTION

Increasing interest in the basic ecology of our forests has led to concerns about their ability to adapt to changes in the environment, their response to pestilence and other disasters, and the general population structure. Maintenance or enhancement of genetic diversity has become a driving force in many land management decisions and will continue to impact the forestry profession for many years. Genetic diversity has been used to describe the number and frequency of plant species that occupy a given area. It has also been used to describe the variability within a given species within a given area (El-Kassaby, 1992; Ledig and Conkle, 1983). The term means different things to different people. A commonly held belief among the general population is that natural systems promote diversity and artificial systems retard it. This belief stems from common selection and breeding practices whereby a sample of a population serves as the parents of the next generation. Agronomic crops such as corn and wheat demonstrate the potential of breeding programs to narrow a population's gene pool. Forest tree breeding is often viewed as synonymous with agronomic crop breeding and a rapid and perhaps permanent loss of the natural population diversity is cautioned against. Determining the change in genetic diversity in a forested system as a result of forestry activity can be a simple task or a difficult if not impossible endeavor. Simply noting the changes in the frequency distribution of species after a particular forestry activity is a fairly simple task on a relatively small area. Stands that are converted from mixed pine hardwood to pine plantation show obvious changes in species diversity. However, documenting the number of genotypes for a given species that occur in a section forest is a formidable task.

In natural pine stands that are being harvested and replanted with improved nursery stock, a reduction in genetic diversity within the given species might be assumed but might not necessarily be correct (El-Kassaby, 1992). Quantifying the genetic diversity within a pure stand of a single species is much more

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difficult than merely enumerating the species that are present in a multi-species stand. Discussion of genetic diversity relative to forestry activities requires a base line that accurately describes the reference point. Given an accurate reference point it is also essential to know what level of diversity is optimum or desired for a given situation. In other words you must know where you are starting and where you are going in order to decide what mechanisms are proper and what mechanisms are detrimental.

WHAT DO WE MEAN?

Genetic diversity can refer to the number of different genotypes that are present in stand or the level of heterozygosity that is present or the level of coancestry among the trees. The number of genotypes in almost any conifer plantation, either naturally or artificially regenerated, is virtually equal to the number of trees. The exception being clonal or vegetatively produced seedlings which all share the same genotype. Replacing 1000 trees from a natural stand with 1000 trees from seed orchard stock would not reduce the diversity level because their would still be 1000 genotypes. Measuring diversity in terms of heterozygosity requires specification of the loci to be considered and then careful analytical work to determine the genotypes at those loci. Using this measure may produce some surprises. It is possible to replace a 1000 tree natural stand with seed orchard stock and to increase the heterozygosity level. Naturally reproducing stands often have family structure and perhaps even some genetic drift effects which reduce heterozygosity levels. Seed orchard stock from a fairly large number of non-related parents could easily have a greater degree of heterozygosity.

Coancestry is another measure of diversity. In other words, what is the average relatedness of the individuals in a given area. The contrast with natural stands will depend on the size of the stand. Small stands generated from a relatively small number of parents may be highly related and actually have a lower diversity than the seed orchard stock. As the size of the area is increased the average conacestry would be reduced as more and more families were introduced. At some point, the coancestry of the seed orchard stock would be less, because it remains fixed and the natural stand level is decreasing.

Effective population size may also be used as a measure of diversity. The effective population size will be dependent on the number of parents, the family structure of the parents and their reproductive phenology . As with coancestry levels, the effective population size of a small stand may be much lower than that of the seed orchard stock. One or two trees may be dominating the gamete pool due to their fecundity (El-Kassaby, et al, 1989), their phenology (Askew, 1986), or their method of seed dispersal (Schuster and Mitton, 1991). As the stand size is increased, more and more parents will be represented in the gamete pool and eventually the effective size will be greater than the fixed level of the orchard stock.

So the question "What do we mean?" is important. Any discussion of genetic diversity requires a specified measure and a common understanding of that measure. It may be possible to equate two stands using one measure and to find them vastly different using another. Both measures would be correct and both would have valid interpretations when used in the proper context.

WHAT DO WE WANT?

Commercial forestry concerns need a steady, reliable supply of wood. Pulpwood and sawtimber demands keep rising as the available land resource continues to shrink. Growing more wood on less land requires continued improvements in both the growing stock and the cultural techniques. Improvement in the growing stock necessarily involves some form of selection and perhaps some form of breeding. Selecting the fastest growing trees and the trees with the best characteristics such as form, specific gravity, disease resistance, etc. may require a breeding population that has only a fraction of the base population represented. **The number of potential parents involved in any one breeding program is affected by the breeding strategy, the available area for breeding and**

testing, and the breeding technique. Open-pollinated orchards generally can utilize a higher number of parents than breeding programs that rely on controlled crossings. Breeding programs that seek to perfect a given trait may be extremely limited in their breeding size due to cost of screening, effectiveness of screening, or the proportion of trees with the desirable trait. Improvement of a population mean necessarily requires a shift away from the less desirable trees to the more desirable trees. Will the shift eliminate too much of the genetic variability? If the program is completely successful it will eliminate virtually all of the genetic variability in the trait to be improved, but what about the non-selected traits?

Forest geneticists and the public in general are concerned about the maintenance of a broad genetic pool in all species in order to provide the adaptability that will be necessary to meet the changing environment (Millar et al, 1990). Where possible, natural systems are being preserved and even recreated by reintroduction of species that have been eliminated. As forest genetics work progresses will the genetic variability that we seek to maintain be reduced to an unacceptable level? What level is unacceptable? How will we know when we get there? What is the most rational approach to maintaining the gene pool in the species that we exploit for commercial gain: Seed banks, clone banks, DNA banks? What should we be doing about the species that are displaced or constricted when commercial species are favored? Do we need to conserve the gene pools of all species?

HOW DO WE MEASURE IT?

For the most part, answers to the questions "What do we mean?" and "What do we want?" are dependent on our method of measure. Genetic diversity is usually discussed in terms of species richness, species frequency distributions, number of species etc. Genetic diversity can be discussed in quantitative terms such as coancestry, inbreeding coefficients, effective population size, and heterozygosity levels. But it can also be discussed in terms of sustainability. That is, how well can the population be expected to maintain itself through time. If there is no interference with the population can you expect it to reproduce itself? Will the population become fragmented and less diverse due to drift? Will other populations migrate into it or will it emigrate into other populations?

It is reasonable to consider whether or not quantitative measures such as heterozygosity levels are correlated with performance levels. Does increased heterozygosity imply increased stability (Ledig and Conkle, 1983; Strauss, 1987). Will a population that has an equal distribution of 3 alleles for a given isozyme be measurably different in any morphological, physiological, or empirical traits from a population that is homozygous for any one of the alleles? These questions are important because we do not strive to maintain a number that is meaningless in practical terms of population dynamics. The idea that more is better may be true for genetic diversity but there needs to be some evidence that it denotes a healthier more adaptive population. Linkages and gene effects need to be documented. The adaptive ability of conifers relative to their measured heterozygosity using enzyme markers or DNA analysis is not well established. The amount of the gene pool that is lost by selection practices is impossible to determine. Inbreeding effects can be surmised using basic theory to estimate the loss in heterozygosity, but selection practices most often do not directly result in inbreeding and the degree of inbreeding in a given population is rarely known.

Effective population size is a reasonable measure of the relative fitness of a population. However, many factors affect the measure. The number of unique genotypes is one factor, but the role of reproductive phenology and fecundity are very important in many instances and germination and seedling survival must also be considered. Also, knowledge of the geographic position of the trees is vital to understanding their interaction potential. Fecundity, phenology and germination percentage may change each year or work in some cyclical fashion and the effective population size will fluctuate as these factors change. Effective population size is measure that is not stable and is only a snapshot of the situation.

Any measure is only meaningful relative to some standard. A high level of genetic variation in one instance may be low in another. Small isolated naturally occurring stands of trees may have a severely restricted gene pool. Replacing them with seed orchard stock may provide a doubling of the variation. That same level of variance may be a step backward if the original stand is vast and not well structured (genetically). Increasing the number of parents may be an improvement by one definition but if the parents are not well suited for each other in terms of reproduction, the stand will not be stable and may quickly develop into small inbred, isolated stands with poor variation within the stands and perhaps great variation between them.

With all of the choices for measuring diversity, which one is ideal? All have their application and all could be considered ideal for a given situation. For the forest geneticist the question is usually "Will the breeding and selection program produce a population that is too restricted?". If the question pertains to the outplanted population that will be produced from the breeding material, the entire gamut of reproductive characteristics and pedigrees must be considered. Open-pollinated seed orchards produce seed that have genetic qualities imparted from the parents and weighted by the parental contributions. Measurements of reproductive phenology, fecundity, germination potential must be **included along with the parental pedigrees. In this case the effective population size is a reasonable estimate of the potential genetic diversity to be imparted by the breeding population to the outplanted population. If the breeding population alone is to be considered, pedigrees and coancestry coefficients may be sufficient.**

Regardless of the measure of diversity, a basis of comparison is still necessary. If we anticipate a 50% reduction in heterozygosity, is it too much? What is a proper balance between selection differential and diversity.

Is it reasonable to use a "natural" population as a basis for comparison? Are most natural populations structured without any influences from development or from logging, high-grading, or other land manipulation? Should each breeding program be expected to incorporate all of the base population's diversity into its selected parents? If it were to do so the selection differential would be 0. How should we proceed? Complete improvement completely eliminates diversity for the trait and complete diversity eliminates improvement. Moreover, how many traits must be considered when measuring diversity. By including a sufficient number, the diversity measure would be imperceptibly changed even when one or two traits were completely fixed or lost.

It is obvious that there are more questions than answers and sufficient ambiguity to allow for justification of any stance. In the mean time, breeding and selection must proceed and new methods of improvement i.e clonal forestry, gene technology, etc. will still further complicate the questions. It is in our own best interest to establish some working definitions and guidelines for conserving the gene pool in our forest species. We need measures of diversity that are both meaningful and calculable. Most importantly, we need to understand the implications of our breeding and improvement systems.

HOW DO WE ACHIEVE A BALANCE?

In order to determine the impacts of forestry activities and genetic improvement programs a solid scientific determination of the species' genetic diversity must be developed first. Major commercial species such as loblolly pine (Pinus taeda L.) need to be surveyed to document as much as possible about their range-wide diversity. Linkages between traits of interest for improvement and other more basic traits such as reproductive phenology should be determined so breeding system implications can be estimated.

Deployment strategies for orchard derived material or vegetatively propagated material can be designed to maximize use of the available genotypes

in the mix. The question "How many clones?" was asked several years ago (Libby, 1980) and is still a viable question. The answer must include the level of diversity that exists within the clones. Use of uneven age management systems may allow for a better mix of genotypes by planting smaller groups within a given management unit and then spreading the total unit replacement over a longer period of time. Multi-species management may also be viable alternative if the productivity level can be maintained and the cost does not become prohibitive. Diversity within a given species may be reduced by the breeding program but the species diversity may be greater than would be maintained with a single species approach.

Breeding populations must kept as broad as possible. As we continue to select for desirable traits we must make every effort to include as many genotypes in the mix as possible. Mating designs must be designed to prevent rapid narrowing of the population and coancestry levels must be considered in all schemes. Before we can formulate methods of maintaining or improving genetic diversity we must develop sound, meaningful, realistic measures of diversity that can be used to evaluate what already exists and to examine the implications of proposed management systems.

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