

12 *Genetic Considerations in Reforestation*

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INTRODUCTION

Most of this book addresses how environments can be modified to improve survival and growth of trees in southwestern Oregon and northern California. In this chapter, we turn to the genetic resource of the forest and discuss its diversity and patterns within the region. Because plant development depends equally on genetic and environmental resources, the manipulation of forests during plantation establishment, thinning, or harvest can change the genetic resource by affecting its diversity or patterns. Alternatively, manipulation of the genetic resource can improve or degrade forest yield and health. We also, therefore, discuss the problems and opportunities afforded the forester by management of the gene resource.

For convenience in understanding, the rich genetic diversity of forest trees can be categorized at four levels: among species, among geographic locations within species (stands), among individuals in stands, and within individuals. Except at the species level, the patterns of diversity in a region are not obvious. They must be made visible by some experimental procedure. Because these procedures often measure different aspects of genetic diversity, they sometimes provide confusing or conflicting pictures of genetic variation at the different levels of diversity. We believe an understanding of the genetic resource requires some concept of how it is measured. We therefore devote the first section of this chapter to this point.

The genetic resources available to a forester are not homogeneous. They exist in patterns in much

the same way that categories of soil exist in an ordered distribution within a region. The patterns reflect a response to evolutionary forces operating within historical environments. Recently, the human influence has become a dominant component of the environment in which the evolutionary forces still function. Many of the decisions foresters make in harvesting, reforestation, and silviculture may influence the historical patterns of genetic variation by altering the relative magnitudes of evolutionary forces. In the second section of the chapter, we therefore briefly discuss the role of the forces responsible for genetic diversity within a species.

In the remaining sections of the chapter, we describe the patterns of natural genetic variation and discuss the consequences of these patterns for silviculture. The patterns are presented for three levels of diversity: among species, among locations within species, and among individuals within locations. The fourth level, diversity within individuals, is discussed along with the third level, because variation among individuals is closely associated with variation within individuals.

MEASUREMENT OF GENETIC VARIATION

Tree-to-tree variation at all levels of diversity is often expressed in a variety of traits, including, for example, growth rate and rhythm, resistance to pests and disease, tree form, wood density, chemical composition of foliage, or even the chemical

product of a single gene. For any single tree, the expression of these traits (i.e., the phenotype) results jointly from its genetic composition (genotype) and the operational environment in which it develops. Furthermore, the influence of these two factors is usually confounded so that genetic diversity can rarely be appraised by direct observation of trees in the forest.

Patterns of variation at all levels, therefore, must be described by evaluating samples of genotypes from different sources in an experiment. For example, patterns of variation among geographical locations within a region may be studied by collecting seeds from several to many randomly sampled parent trees in a large number of locations sampled systematically across the region. The bulked seed from each location represents the genotypes at the location, and, thus, genetic differences among locations can be evaluated. The seedlot of any single tree, however, is representative of the genotype of that tree, so if seedlots of individual trees are separately analyzed, geographical variation can further be partitioned into genetic variation among parent trees within as well as between locations.

Estimates of patterns of genetic variation are influenced by the sample of parent trees and also by how genotypes are estimated. Because the genotype of each individual includes many thousands of genes that cannot be completely categorized either collectively or individually, genes within genotypes must also be sampled. In forest trees, genes in genotypes are commonly sampled by one of two methods: by determining the presence or absence of the chemical signatures of several to many discrete genes of unknown function, or by measuring one or more quantitative (measurement) traits, each expressing an unknown set of genes. The chemical signatures (markers) are relatively insensitive to environmental variation and can be assessed by laboratory analysis of either seeds or vegetative tissues sampled from parent trees (Adams 1983). Examples of quantitative traits are seedling height, date to bud burst or bud set, volume growth to 20 years, germination rate, etc. Although quantitative traits are of more practical significance to foresters than markers are, genetic analysis of them is complicated because these traits are usually controlled by many genes acting simultaneously. In addition, because quantitative traits usually have a large

environmental component, genetic differences among trees must be assessed by growing their progeny under uniform "common garden" conditions. The common garden may be a nursery bed or greenhouse when seedling traits are of interest, or uniform field sites, such as progeny-test plantations, for longer-term studies (Adams and Campbell 1982).

Regardless of the system for sampling genes, the genotype of a tree is never entirely characterized. Estimates of patterns of genetic variation consequently depend partly on the markers or quantitative traits chosen to sample the genotype. The perceived patterns of variation can differ markedly depending on the sampling procedure. For example, analyses of chemical markers have revealed little geographical variation in Douglas-fir of southwestern Oregon (Merkle and Adams 1987, Merkle et al. 1988, Moran and Adams 1988). In contrast, several common garden studies with seedlings have revealed large amounts of geographical variation for quantitative traits in the same region (Hermann and Lavender 1968, Sorensen 1983, Campbell 1986, Loopstra and Adams 1989). Although geographic variation for chemical markers is often limited within regions, these markers are the only quick, inexpensive means for examining diversity among genes within individuals.

FACTORS RESPONSIBLE FOR PATTERNS OF GENETIC VARIATION

Geneticists refer to the factors that alter the genetic composition of populations from one generation to the next as "evolutionary forces." The relative magnitudes of these forces when acting simultaneously determine the patterns of genetic variation between and within populations. The forces are also the vehicles by which foresters can influence either intentionally or unintentionally the genetic composition of forests and, coincidentally, their health and productivity. Five major evolutionary forces can be described: mutation, mating system, gene flow, selection, and genetic drift (Zobel and Talbert 1984, Hartl and Clark 1989). Mutation is the ultimate source of genetic variation

in species. It is a heritable change in the genetic code of an organism. Because mutations of any single gene generally occur at very low rates ($1/10,000$ to $1/100,000$ per generation), mutation alone produces only very slow changes in the genetic composition of populations. Thus, in the short term, mutations have little influence on the evolution of populations, but in the long term, they are essential to evolutionary change.

The mating system determines the pairwise combinations involved in mating, and involves any number of schemes including random pairing of individuals in populations (random mating) and mating together of individuals more closely related than individuals mating at random (inbreeding). Mating, in turn, is the process by which genes are distributed from parent to offspring. Every individual has many thousands of kinds of genes. Each kind is represented by a gene pair, one gene coming from each parent. Within each of the thousands of gene pairs, the two genes can be identical or different in expression. Variation among genes within individuals, the basic level of genetic diversity, derives primarily from gene pairs with two variant expressions. For some kinds of genes, several alternative gene variants exist in populations, ranging from extremely rare to common. The genetic diversity within individuals depends on the relative frequencies of the gene variants and the mating system.

In forest trees it is often assumed that mating occurs at random, or nearly so, such that any individual in a population has an equal chance of mating with any other member of the opposite sex, regardless of genotype. Random mating, however, may be the exception rather than the rule (Brown 1989). Trees in stands usually vary in flowering times and years, and those flowering in similar years tend to intermate (Erickson and Adams 1990). In most forest tree species there is a tendency for at least some inbreeding to occur (Muona 1989, Adams and Birkes 1991). Inbreeding results in decreased genetic diversity within individuals. Close inbreeding, such as selfing or brother-sister mating, has particularly serious implications in most forest trees because it leads to inbreeding depression, which is manifested in high embryo abortion (i.e., low seed set) and poor growth of surviving inbred progeny (Sorensen and Miles 1982, Woods and Heaman 1989).

The remaining evolutionary forces, gene flow, selection, and genetic drift, act by affecting the probability that a tree will have a gene of a certain variant type. The probability depends on the frequency with which the gene type is represented among trees in the parent stand. If, for example, many trees carry genes coding for high wood density, seedlings from that stand also are likely to have such genes. In other stands, genes for high density may be present at lower frequencies. Differences in gene frequencies among stands represent differences in their genetic compositions, and these differences will be reflected in the average values of quantitative traits such as wood density.

Gene flow is the migration of genes from one population into another in which they may be absent or present at different frequencies. In unmanaged forests, gene flow most often occurs through the movement of pollen or seeds. Gene flow can be an important source of new genetic variation in populations. In addition, because immigration of genes from one population into another decreases differences in gene frequency between them, it counteracts the diversifying influences of other evolutionary forces, such as selection.

Selection occurs when genetic differences among individuals influence their ability to reproduce, so that genotypes that enhance the reproductive potential of their carriers increase in populations while less favorable genotypes decrease. When populations develop in different environments, selection will lead to genetic divergence of the populations as each becomes adapted to the local environmental conditions.

Genetic drift refers to change that occurs by chance in the genetic composition of populations. It is a consequence of sampling; genes passed to the next generation are a sample of the genes present in the parents. As long as a large number of parents (say in the 100s or more) contribute to the next generation, gene frequencies in the offspring should largely reflect gene frequencies in the parents, unless the frequencies are altered by selection or gene flow. On the other hand, if only a few parents (say in the 10s or less) out of a large population contribute to the next generation, changes in gene frequencies can occur because of chance sampling alone (i.e., genetic drift), regardless of

selection or gene flow. These changes will be random in direction and will result in reduced variation and a shift, perhaps, from the average genetic composition of parents.

Both selection and genetic drift can lead to differences in gene frequency among populations, but for different reasons and with different results. If populations are growing in a range of operational environments sufficiently dissimilar for strong selection to act, the populations are expected to be differentiated in a fashion associated with the environmental differences. If environments change gradually along an environmental gradient, for example, adapted traits will also probably change gradually along the gradient (clinal variation). If population divergence is due to genetic drift, however, patterns of genetic variation will be unrelated to environmental gradients. Gene flow between populations counteracts differential effects of both drift and selection. Only limited gene flow is necessary to prevent divergence resulting from genetic drift, but if selection is relatively strong, population divergence will occur despite strong gene flow (Slatkin 1987).

Forest operations affect the relative magnitudes of the evolutionary forces. Choice of species, seed transfer, and tree improvement, for example, act as strong selection, because some genotypes are greatly favored over others. Seed transfer and tree improvement contribute to gene flow, introducing genes into areas where they previously occurred at different frequencies. When harvest practices, wildfire, or epidemic pests result in greatly reduced population size, genetic drift may occur. Tree improvement programs include stringent controls of mating systems. In the following sections of this chapter, we discuss in more detail the effects of manipulating the genetic resource by common forest practices and tree improvement.

DIVERSITY AT THE SPECIES LEVEL

Variability among tree species reflects a high level of genetic diversity that foresters can easily recognize and use. Most tree species are readily identifiable and have predictable patterns of growth and reproduction. The large number of

species to select from plus the wide differences among them offer foresters many options for regenerating forests in southwestern Oregon and northern California. Understanding the natural occurrence of species over the landscape, including how they are adapted to their operational environments, should help improve regeneration success. In this section we discuss the diversity of tree species in the region, variation among species in mechanisms of adaptation, and considerations in choosing species to plant.

The Klamath Mountain Geological Province is floristically and environmentally diverse. Many plant species are indigenous only to this region, and several are at the edge of their natural range. Complex vegetation patterns have evolved because of the highly varied climate, geology, and topography in this transverse mountain range (Whittaker 1960). More than 30 species of forest trees are present (Franklin and Dyrness 1973). The diversity of species and their distribution on the landscape is not only a function of adaptation to the current environmental conditions in the region, but is also due to a long evolutionary history involving extreme climatic cycles that have preadapted these species to diverse environments.

Evolutionary History

Paleobotanical studies indicate that West Coast forests lost species diversity starting in the late Miocene [10 million years before present (B.P.)] and continuing into the Quaternary. Many taxa, especially deciduous hardwoods, disappeared from the West Coast while remnants became more narrowly distributed as a result of gradual development of long, warm, dry summers, which began in the mid-late Miocene. The rich mixed conifer and subalpine forests in the Siskiyou Mountains have retained relatively more species diversity because they have a somewhat milder temperature, a longer wet season, more summer rain, and less drought stress than those in the Cascades or the Sierra Nevada (Axelrod 1977). Most woody taxa represented in the Miocene and Pliocene floras are structurally indistinguishable from modern species. It appears that structural adaptations of forest trees were already established 15 million years ago, and adaptation to long, warm, dry summers was chiefly physiological (Axelrod 1977).

Extinction of much of the deciduous hardwood forest occurred with the onset of the Mediterranean climate in the region. Then, as even colder climates developed in the late Pliocene and during the glacial ages, many broad-leaved sclerophyllous taxa (Pacific madrone, tanoak, valley oaks, chinkapin) segregated out of the mixed conifer forest to lower elevations and coastward. This shift seems related to their susceptibility to cold winters and breakage of tops by heavy snowfall.

The Pleistocene Epoch was the most drastic and stressful climatic episode for woody taxa. Radical changes in climate between glacial and interglacial cycles resulted in range expansion and contraction of species. During the onset of a glacial cycle, species underwent a shifting, contracting, and fragmenting of geographic range. This was followed by a long period of geographic isolation and possibly genetic differentiation among refugia (widely separated) populations during glaciation. After the last glaciation, a shifting and expansion of the range and reestablishment of genetic contact with other populations occurred (Critchfield 1984).

The present occurrences of Jeffrey pine and other high-altitude species such as red fir, western white pine, and lodgepole pine at low altitudes on diverse ultrabasic rocks appear to be relicts from the Wisconsin glaciation. These species migrated downward and escaped competition from other conifers during cold climates, and were stranded as hardy relicts when warm climates returned (Axelrod 1977).

Significant forest evolution occurred about 6000 B.P. during the Xerothermic with the appearance of domination by single-species stands. These included pure Douglas-fir in some moist coastal and northern Oregon Cascade areas where mixed forests dominated earlier, and pure ponderosa pine at the lower edges of mixed conifer forests (Axelrod 1977). Ponderosa pine apparently had a very restricted range during the last glaciation (Spaulding et al. 1983), and it greatly expanded during the Xerothermic, indicating that it had become adapted to a warm, arid climate. Sugar pine, incense-cedar, and white fir moved northward and also increased in abundance in this region during the Xerothermic. The present broad ecological amplitude but small geographic

range of Port-Orford-cedar reflects a previously much larger geographic range (Edwards 1983).

Forest tree species, especially conifers, have among the highest levels of genetic variation found in plants (Hamrick and Godt 1989). The amounts of genetic diversity within individuals and populations, however, vary greatly among species, and evolutionary history may explain much of the differences observed. For example, a comparison of five southwestern Oregon conifers for variation in chemical gene markers reveals wide differences among them. Generally, genetic diversity within populations is greatest in western white pine (Steinhoff et al. 1983, El-Kassaby et al. 1987) and Douglas-fir (Neale 1985, Moran and Adams 1988), less in incense-cedar (Harry 1984) and Jeffrey pine (Furnier 1984), and almost lacking in western redcedar (Copes 1981, Yeh 1988). The exceptionally low diversity in western redcedar is likely the result of one or more ancestral bottlenecks in population size as a result of glacial advance or other factors, and there presumably has not been enough time for mutation to replenish genetic variation (Copes 1981, Yeh 1988). An ancestral bottleneck is also a likely explanation for why the disjunct populations of Jeffrey pine in the Klamath Mountains contain 25 percent less genetic variation than is found in Sierra Nevada populations to the south (Furnier and Adams 1986a).

Species Adaptations

In addition to evolutionary history, current species distributions in the region are primarily a function of adaptation. The present locations of species reflect genetic responses to the operational environments associated with variable seasonal temperature and precipitation cycles, soil properties, topography, competing vegetation, diseases, and pests. Adaptations have evolved over millenia, and the result is an integrated physiological expression of genotypes working appropriately with the operational environment. It therefore behooves foresters to consider carefully the physiological limitations of species when choosing species for reforestation.

The primary physiological adaptation of West Coast conifers to long, dry summers has been to shift germination and growth earlier into the growing season (Axelrod 1977), when moisture is more

favorable. Species vary in their timing of growth initiation and cessation. Some conifers are genetically programmed to grow earlier in the season when available soil moisture is high, while others grow later when soil moisture is relatively low (Fowells 1941). A second physiological adaptation to decreasing soil moisture during the summer is transpirational control by stomatal resistance. As soil moisture decreases, pines begin closing stomata earlier than Douglas-fir or grand fir. As soil drying continues, pines also control water loss more completely than firs (Lopushinsky and Klock 1974). The abundance of pines on relatively warmer and drier sites than those that support firs may be partly explained by the earlier growth initiation and height growth cessation of pines, as well as the capability of pines to control and reduce their rate of water loss better than firs when moisture becomes limiting in late summer.

Species often differ in total content and concentration of nutrients in plant organs. Some species require a higher concentration of nutrients than others to achieve adequate growth. Differences in nutrient content among species may result from differences in rooting habit, growth rate and period, distribution of biomass components, absorption efficiency, and cellular requirements (Epstein 1972). Among conifers, pines are considered to be less demanding of macronutrients than are firs (Powers 1983). Mature ponderosa pine assimilates a lower proportion of total site N (soil plus biomass) into biomass than incense-cedar (intermediate) or Douglas-fir (Zinke 1969). Incense-cedar, however, is more tolerant of low Ca than Douglas-fir (Waring and Major 1964).

Choosing the Best Species to Plant

Selecting the best species to plant on a forest site is a major decision. Species must be both ecologically appropriate for the site's operational environment and best suited to the management objectives. Klinka and Feller (1984) advocate three steps for this selection: (1) determine which species, individually or in mixtures, are ecologically viable on a given site; (2) evaluate and rank the species options for each management criterion, e.g., crop productivity, crop reliability, and silvicultural feasibility; and (3) select the most suitable species.

Basic information is needed about the operational environment of the site, the ecological characteristics of the species, and how management will affect the environment and species response. Each species has an ecological amplitude or range of sites in which it can survive. Within these limits, the competitive ability and growth rate of a species will vary on different sites, being highest near the center of the range and lowest at the edge.

Knowledge of the relative frequency of naturally occurring species on a site is a valuable clue to ecological suitability, as is knowledge of the plant association native to the site. These tools can be used to generate a list of potentially successful species for the site. The potential species may then be evaluated and ranked for each silvicultural alternative and for survival and productivity.

Methods of site preparation, planting, and release may influence choice of species. For instance, tractor piling and burning may result in losses of surface soil and organic matter, soil compaction, and nitrogen reduction on some sites. If the underlying operational environment is appropriate, ponderosa pine would have a much greater chance for success than white fir or sugar pine on these less fertile and highly disturbed sites. The use of herbicides to release conifers from competing vegetation may directly affect a species' performance. Sugar pine and incense-cedar, for example, are extremely sensitive to herbicide injury from Velpar LTM (Ballew 1988).

Susceptibility to pests affects crop reliability. Both the kinds of pests and their specificity must be considered. For example, annosus root rot is known to have two species, both of which occur in this region, and which are believed to have host specificity. One species infects pines but not true firs. The other infects true firs but not pines (Otrosina et al. 1988). If the history of the previous stand showed infected pines and uninfected firs, it would be prudent to replace the stand by planting firs. Similarly, black-stain root disease (*Leptographium wageneri*) has two host-specific varieties in the region, one which attacks Douglas-fir only (var. *pseudotsugae*) and another which attacks most hard pines (var. *ponderosum*) (Harrington and Cobb 1984). True firs are not susceptible. An existing stand of infected Douglas-fir might best be replaced with pines or true firs. Another example is dwarf-mistletoe, which has

varieties specific to ponderosa and Jeffrey pines, Douglas-fir, white and grand firs, and red and noble firs. Nevertheless, in the search for pest-resistant species, care must be taken not to choose a species otherwise poorly adapted to the site.

Availability of genetically improved stock and the quality of nursery stock may also affect choice of species. The natural resistance of sugar pine to white pine blister rust is so low, and the incidence of rust and its devastation are so high, that planting resistant sugar pine is essential to maintaining genetic integrity of the species. If rust-resistant stock were unavailable, the reliability of sugar pine as a crop species would be extremely low, because sugar pine would be unlikely to survive to maturity. Quality of nursery stock will also affect survival after outplanting. For example, sugar pine stock infected with *Fusarium* spp. in the nursery will have reduced root growth capacity and may incur high mortality under stress conditions. The solution may require planting at a higher density or not planting the infected stock at all.

Silviculturists must choose between using a single species or a mixture of species to reforest a site. The choice depends on the characteristics of the site, compatibility of the species, and management objectives. Most forest sites in the region support a rich mixture of conifer and hardwood species and thus provide a broad range of choices to the silviculturist. Sites that are extremely wet, dry, infertile, or highly disturbed may require a single species, e.g., lodgepole pine in wet meadows, Jeffrey pine on xeric serpentine soils, ponderosa pine on dry, exposed slopes at low elevation, and Douglas-fir on mild, moderately moist sites.

A combination of planting and natural seeding is often used to achieve species diversity. Genetically improved stock of shade-intolerant species, e.g., Douglas-fir and ponderosa pine, is often planted. Concurrently, more tolerant species, e.g., white fir and sugar pine, are often encouraged to seed naturally. Some species of true fir are difficult to regenerate artificially, but being strong colonizers, they often are easy to regenerate naturally from desirable seed trees.

Selecting the proper mix of species involves evaluating compatibility of species in terms of shade tolerance, space requirements of crown and roots, growth rate, and nutritional effects on site. A major advantage of using mixed stands is the

buffering effect against pests and environmental hazards. Stands with mixed composition and structure similar to that found naturally in the area are more resistant and resilient to the natural hazards of the area (Klinka and Feller 1984).

Each species-site option requires a different series of silvicultural treatments during a rotation. Cost of producing the timber crop may be the decisive criterion for species selection. Species requiring minimum outlay for treatment may be more desirable. Management of even-aged, pure stands is simpler and less expensive than management of mixed stands. Higher crop yields or greater reliability may be necessary to compensate for the greater expense and difficulty of obtaining the desired mix of species. Often, however, natural regeneration combined with planting a single species will produce the desired mixture and achieve full site occupancy.

GEOGRAPHICAL VARIATION WITHIN SPECIES

In this section, we turn from the subject of choosing species for reforestation to the choice of seed lots from the many possibilities existing within a species. Because populations in a species vary genetically, seed lots vary in genetic potential; thus, the forester is confronted with risk of loss or opportunity for gain, depending on his or her choice of seed source. Both risk and opportunity stem from the likelihood that, in large part, genetic variation among populations results from natural selection. Local populations may be slow-growing but well adapted to the local environment; non-indigenous populations may be fast-growing but less well adapted. Correct decisions in choosing seed lots depend on using available information to balance risk and opportunity. In this section, we briefly discuss natural patterns of geographical variation revealed by common garden studies, present a selection model relevant to predicting risk of seed transfer, discuss seed-transfer guidelines recently developed for sugar pine and Douglas-fir in southwestern Oregon, and examine opportunities for using genetic resources to enhance site productivity while minimizing risk of poor adaptation.

Natural Patterns of Geographical Variation

From the results of common garden studies, two general observations can be made about geographical patterns of genetic variation in forest trees. The first is that when geographical sources are from wide-ranging environments, geographical patterns often occur as linear or curvilinear trends (clines) associated with one or more geographic features. That is, when families of parent trees along a geographic gradient are grown in a common environment, the family average height, for example, often varies according to where the parent trees grew along the gradient. This change represents a change in genotypes systematically associated with geography. Geography, in turn, often indexes gradient trends in environmental factors; for example, average temperature and precipitation often depend on latitude, elevation, and distance from the ocean.

The major gradients of geographical variation commonly follow paths from milder (warm moist) to harsher (warm dry, cool dry, cool moist) environments, especially if traits of growth vigor or growth rhythm are used to estimate genotypes (Rehfeldt 1989). Genotypes of trees from the harsher end of the gradient usually produce trees with slower growth and shorter vegetative periods. In mountainous regions, if moisture is not limiting, trees with such genotypes are clustered on mountaintops and upper slopes. Surrounding these populations, at lower elevation, are populations with genotypes for faster growth and longer growing season. This fact alone suggests a response of populations to environments—that natural selection has produced populations adapted to local environments.

The second general observation from common garden studies of forest trees is that, although extensive genetic divergence is often found among populations along geographical gradients, considerable proportions of the total genetic variation in a region can be attributed to differences among individuals within populations. The amount of total genetic variation in a region as a result of geographical differentiation (versus that resulting from variation among individuals within populations) varies according to the size of the area sam-

pled and the species. The amount of geographical variation is usually assumed to reflect the amount of environmental diversity within the region. Variation, however, may reflect geographical area as much as it does environmental diversity, because diversity cannot be disassociated from the size of the region sampled. In a southwestern Oregon study covering an area of 18,200 km², differentiation among populations of Douglas-fir on the basis of seedling quantitative traits accounted for 65 percent of the variation among genotypes (35 percent was due to differences among genotypes within populations) (Campbell 1986). As expected, the proportion of total genetic variation resulting from population differentiation was much smaller, 40-50 percent, in two similar studies of Douglas-fir over smaller geographical areas, i.e., 61 km² in central Oregon (Campbell 1979) and 260 km² in northern Idaho (Rehfeldt 1974).

Proportions of variation resulting from geographical differentiation can vary among species coexisting within the same region. As we have already seen, some species such as western redcedar and red pine apparently lack appreciable amounts of genetic variation of any type (Yeh 1988, Fowler and Morris 1977). Others, such as Douglas-fir, exhibit high proportions of geographical variation for quantitative traits, as well as large amounts of genetic variation within populations. In still others, individuals vary genetically, but a relatively small proportion of the variation is due to geographical differentiation. Western white pine is of this latter type (Steinhoff et al. 1983, Rehfeldt et al. 1984, Campbell and Sugano 1989). Sugar pine in southwestern Oregon performs as an intermediate between species such as Douglas-fir and western white pine. For example, a common garden study with seedlings indicated that, in an area of 22,550 km², only 50 percent of the estimated variation among sugar pine genotypes was associated with geography (Campbell and Sugano 1987). As seen above, in an area 80 percent as large, the comparable figure for Douglas-fir was 65 percent (Campbell 1986).

Selection Model

Gradient trends in genetic variation of seedling quantitative traits associated with geography could conceivably derive from any one of several origins:

maternal effects (seed preconditioning), limited gene flow between populations after divergence resulting from genetic drift, or natural selection favoring genotypes best adapted to each environment along geographical gradients. Only maternal effects and natural selection can reasonably explain the consistencies found in macrogeographic patterns of genetic variation. The influence of seed weight, a major contributor to maternal effects, can probably be discounted in many western conifer species. The correlation between seed weight and growth traits often is either lacking (Campbell 1979, Sorensen 1983) or is opposite to any expected effect of preconditioning (Sorensen and Miles 1978; F. Sorensen, personal communication). Rowe (1964) proposed other preconditioning effects, but none are likely to be large enough to cause the trends observed in geographical variation. Natural selection, therefore, is the most likely basis for gradient trends.

Natural selection's power is suggested by the variation among indigenous populations of Douglas-fir in mountainous regions. Very steep gradients of geographic variation occur in regions with steep environmental gradients (Sorensen 1979). Natural selection apparently has molded populations to fit environmental changes along the gradient. Since natural selection operates by eliminating unfit individuals, we might also expect it to eliminate poorly adapted individuals after artificial regeneration. Because of its possible effect on survival and productivity, natural selection is a factor to consider during reforestation.

Many models exist for explaining natural selection of populations. Most have the object of describing how adaptation comes about. The following explanation is based on a practical model (Campbell 1987) developed to point out potential consequences of some forestry practices on population adaptation. The model assumes that the stand of trees remaining after natural selection (the local population) comprises the biologically adapted population. Local populations strictly speaking do not have boundaries; they grade into one another. A practical definition of a local population might be: a group of trees occupying an environment that does not vary appreciably in space, as indicated by homogeneity in major geographical or local factors such as elevation, slope, aspect, soil classification, topshade, etc. As seen above,

the local population is not uniform genetically, but is a heterogeneous mixture of genotypes. This heterogeneity arises from several mechanisms that will be discussed later in this chapter, but one important mechanism, selection of individuals by elements in the environmental mosaic, will be discussed here in order to help in understanding risk of seed transfer.

A natural stand occupies a complex environmental mosaic whose elements differ in operational factors. Shade, soil color, soil organic matter, surface roughness, micro- and macro-topography, and many other conditions affect energy factors. Soil parent material, organic matter, debris, species composition, topography, and geography affect resources. These variable elements provide a matrix of variable microhabitats. If a tree is to survive and reproduce, it must, by chance, encounter a microhabitat within which it can survive. In addition, the genotypes of trees in neighboring microhabitats are, in themselves, a factor in natural selection. Whether these neighboring trees are strong or weak competitors affects the microhabitat and, therefore, the environmental mosaic.

Operational factors of environment usually change along gradients. In southwestern Oregon and northern California, for example, water availability changes with precipitation and temperature, which, in turn, change with elevation. Precipitation decreases, temperature increases, and moisture usually becomes less available at lower elevations (Froehlich et al. 1982). At any particular spot on the gradient, however, microhabitats still vary, because moisture availability (among other factors) is affected by many things other than precipitation and temperature.

Thus, according to the selection model, adaptation to changes in operational environments along gradients results in gradient changes in the average genotype, and within local populations along the gradient, adaptation to varying microhabitats results in mixtures of genotypes. Trees in an adapted population can produce offspring capable of reproducing themselves under natural conditions, and, according to the model, these trees consist of a mixture of genotypes in which the types are proportional to the types of microhabitats present. As microhabitats change in their proportions along an environmental gradient, the mixture of genotypes in the adapted population also changes.

Within any species, however, the ability of genotypes to process environmental factors is limited. If, for example, moisture decreases along a gradient, moisture becomes limiting to some genotypes at some point along the gradient. In addition, microhabitats occur that cannot be colonized by any member of the adapted population. If the gradient continues, fewer and fewer of the microhabitats provide enough moisture for genotypes that can be produced by the local population. Eventually, a point may be reached where microhabitats cannot support any member of the species—its biogeographical distribution limits have been reached (Campbell 1987). In northern California and southwestern Oregon, many tree species either approach or reach distribution limits at low or at high elevations.

Opportunities in the Choice of Genetic Resources

On some forest sites, natural regeneration may be the preferred option for regenerating all future generations. On other sites, it may not be an option in any future generation; that is, the sites may be dedicated in perpetuity to tree crops planted anew each rotation, as is done in agriculture and horticulture. The distinction is important, and must be decided administratively. If natural regeneration is the option, the biologically adapted population should be able to regenerate itself under any suitable system of natural regeneration, although the adaptability of local populations might be seriously compromised in the future if rapid climatic changes occur as a result of global warming (Harrington 1987). If natural regeneration is not an option, the ability of trees to naturally regenerate an area is no longer a criterion of adaptation. The planted stand need only produce a marketable product as efficiently as would the local seed source. Theoretically, populations can survive without harm or growth loss in environments that would prohibit natural regeneration, and may even produce more product than local populations of the same species (Namkoong 1969). This theory, however, requires long-term and expensive trials to validate. The prudent path is to maintain some semblance of the biologically adapted population on all sites.

Some options remain for improving productivity even while maintaining biological adaptation. One is to favor the more productive genotypes in the genetic mixture of the local population. Fertilization or irrigation directly changes operational factors of the environment, and operational factors can be indirectly changed by modifying inter- and intraspecific competition by weed control and the regulation of stand density. Adding to environmental resources, either directly or indirectly, tends to favor genotypes expressing longer vegetative growing seasons and faster growth. Another option is to use a seedling lot that includes a higher proportion of productive genotypes than is found in the native population—higher productivity is balanced with higher risk of poor adaptation. Increased productivity is achieved by using seed from a non-local source or an improved strain.

Risk in Seed Transfer

Although gains in productivity theoretically can be obtained from seed transfer (i.e., from planting a non-local seed source), every transfer entails some risk that all or part of the resulting stand will be poorly adapted. The potential risk from poor adaptation ranges from minor loss in productivity or quality to loss of the entire stand. If loss does occur, it can happen during regeneration or much later. The least well-adapted trees might die early, the better adapted later, and the nearly adapted might live but yield less product or product of poorer quality. The appropriate choice of seed lot hinges on (1) the proportion of non-local genotypes in the transferred seed lot, (2) the regeneration prescription, including probable regeneration success (Campbell 1987), (3) the direction of seed transfer along major environmental gradients, and (4) the degree of site modification during logging, site preparation, and early phases of regeneration.

The safest course in seed transfer is to choose a seed source with at least some genotypes in common with the local population. With the appropriate information, the proportion of seed of local type in any potential seed source can be estimated. The genetic composition of natural populations usually changes along environmental gradients. The genotypes of local type consequently make up a smaller and smaller proportion of the seed lot as the regeneration seed is chosen from farther and far-

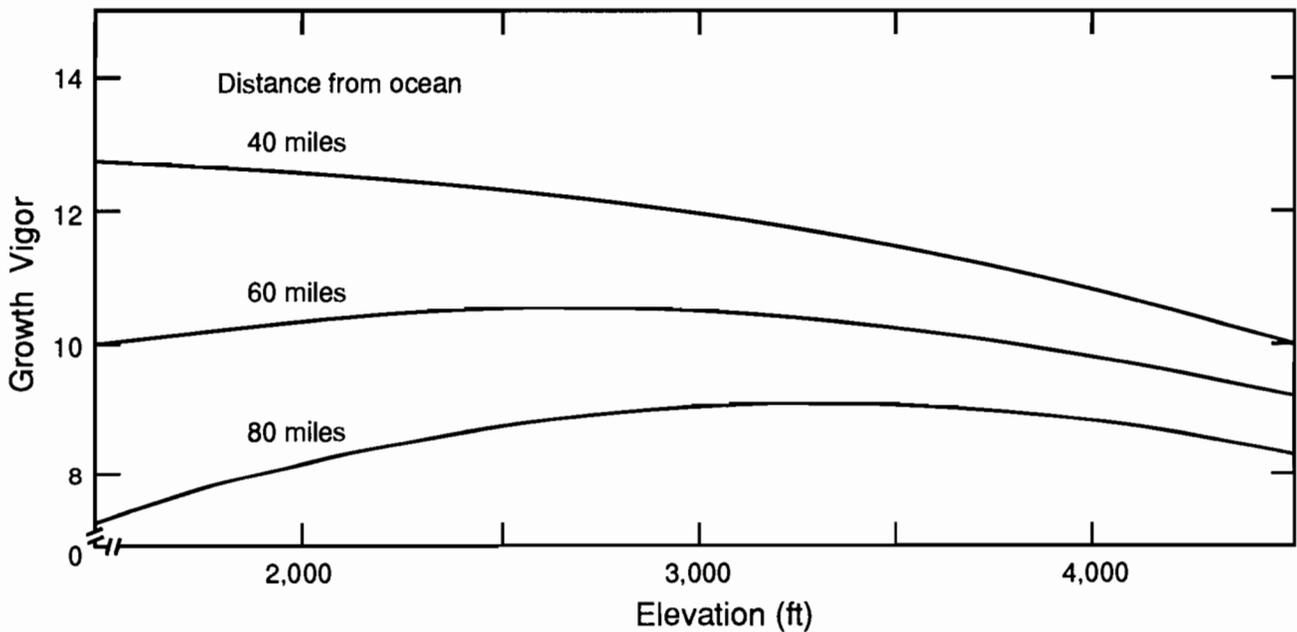


Figure 12-1. Genetic gradients in growth vigor (factor scores of the first principal component) with elevation and distance from the ocean for Douglas-fir in southwestern Oregon. Growth vigor is a composite (multivariate) trait derived from principal component analysis of seedlings in a common garden study; larger numbers indicate greater growth potential. Adapted from Campbell (1986).

ther away along these gradients. Genetic changes occurring over geographical or topographical gradients often reflect the underlying environmental changes (e.g., winter temperature, summer moisture, frost-free days), with the steeper genetic gradients associated with more rapid environmental differentiation over the same physical distance. As genetic gradients associated with geographical or topographical distances steepen, the risk of seed transfer over a given linear distance increases.

Knowledge of genetic gradients and the genetic variation within populations, then, is the basis for estimating proportions of local genotypes in a transferred seed lot. Several researchers report on direction and steepness of Douglas-fir gradients in northern California and southwestern Oregon. A strong west-east (coast-inland) gradient exists in the region (Griffin 1978, Sorensen 1983, Campbell 1986), in accordance with trends of annual and seasonal precipitation. This gradient is steeper at lower than at higher elevations (Figure 12-1). Other studies, not designed specifically to investigate gradients, indicate a fundamental difference in the annual pattern of height growth in seedlings of coastal and inland populations of Douglas-fir in

southwestern Oregon (Loopstra and Adams 1989, Kaya et al. 1989). Even this difference hints at a coast-inland gradient. Some genotypes of the inland pattern are found in coastal populations and vice versa (Kaya et al. 1989). Another major gradient in northern California and southwestern Oregon follows elevation (Hermann and Lavender 1968, White et al. 1981, Mangold 1987). This gradient is influenced by distance from the ocean, latitude, and other variables (Griffin 1978, Campbell 1986) (Figure 12-1). Among other factors influencing genetic gradients in the region are latitude, slope aspect and percent, and sun exposure (Campbell 1986, Hermann and Lavender 1968). In northwestern California breeding zones, up to 80 percent of the genetic variation in height growth is associated with geographical gradients (Kitzmilller 1990a). Thus, a number of genetic gradients could influence the choice of seed lots in any seed transfer.

Seed transfer in southwestern Oregon and northern California has been guided for two decades by seed zone maps prepared by the Western Tree Seed Council (1966) and the California Chapter of the Society of American Foresters (Buck et al. 1970).

These maps ostensibly partition the region into zones within which native trees can be freely moved without problems of maladaptation. Data from long-term tests to validate the zones are not available. Although evidence from common garden studies with seedlings suggests that the Oregon zones may not be of optimum configuration, the evidence is conflicting. Loopstra and Adams (1989) found little adaptive differentiation among populations along latitudinal, longitudinal, and elevational gradients within breeding zones in southwestern Oregon. Campbell (1991), on the other hand, found that 16 to 23 percent (depending on the trait) of the genetic variation among locations occurs along environmental gradients within 1,000-ft bands within seed zones. This finding suggests that the present zones might be improved by reconfiguration but that the present sizes of zones are not drastically wrong. In com-

parison, present seed zones are probably much too small for sugar pine in southwestern Oregon (Campbell and Sugano 1987).

Common garden studies with seedlings have supplied information about genetic gradients from which the proportion of non-local genotypes in transferred seed can be estimated; these proportions can be used as guidelines for seed transfer in southwestern Oregon (Campbell 1986, Campbell and Sugano 1987). Figure 12-2 displays patterns of geographical variation in Douglas-fir for two composite (multivariate) traits, one for growth vigor and the other for growth rhythm. Seed lots from populations in the northwestern part of the region include a higher proportion of seeds with high growth potential than do lots from the southeastern section. The change in average growth potential on the isolines reflects this change in mixtures. The pattern of genetic variation for growth rhythm is somewhat different; here the greatest changes are oriented east-west, with seed sources closer to the coast producing seedlings with later bud burst and bud set. The isolines for both traits are separated by distances that represent fixed amounts of relative risk in seed transfer. Moving seed from any origin on a major (solid) line, for example, to a plantation site on a minor (dashed) line represents a relative risk of 0.30 in respect to the part of the genotype affecting the trait of interest. Thus, 30 percent of seedlings would be poorly preadapted with regard to that trait in the new site. A move of seed between the nearest adjacent major lines increases the risk to 0.56. Therefore, east-west movement of seed in this example entails a greater risk in terms of growth vigor than growth rhythm, because the distance between isolines is least with growth vigor. A recently devised mismatch index combines the relative risks associated with growth vigor and growth rhythm into one estimate, the proportion of seedlings that might be poorly preadapted for growth, for growth rhythm, or both (Campbell 1987). The amount of mismatch can then be used to guide direction and distance of seed transfer, and to estimate proximity of the plantation or seed source to the biogeographical limits of Douglas-fir. Knowledge of mismatch can also help in delimiting seed zones.

Before the mismatch index can be intelligently used, a decision must be made about appropriate limits of transfer—what is the maximum propor-

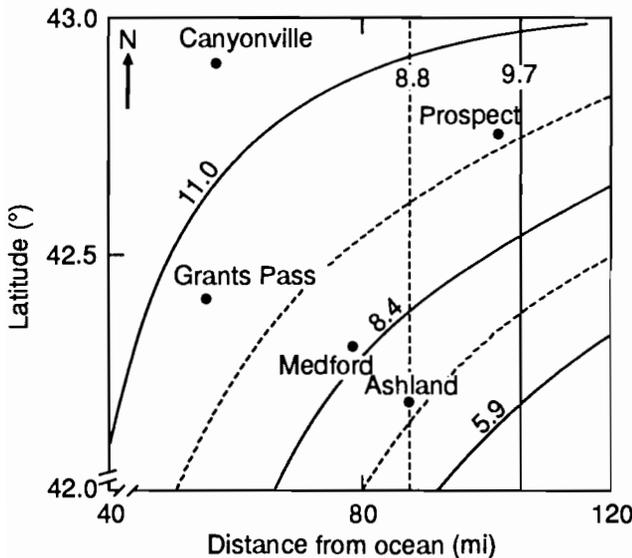


Figure 12-2. Genetic variation of Douglas-fir from low elevations (<2,000 ft) and mild slopes (0-10 percent) in southwestern Oregon. Curved isolines connect locations where growth vigor is predicted to be the same; larger numbers indicate greater growth potential. Vertical lines connect locations where growth rhythm is predicted to be the same; larger numbers indicate earlier bud burst and bud set. Both growth vigor and growth rhythm are composite (multivariate) traits derived from principal component analysis of seedlings in a common garden study. Adapted from Campbell (1986).

tion of non-local genotypes permissible in a seed transfer? One model suggests the limit can be based on the probability of obtaining a local genotype as a crop tree (Campbell and Sugano 1987). In this model, local genotypes serve as a safety reserve that would be available as crop trees should potentially more productive non-local types falter before rotation age. The model suggests that several factors will influence the proportion of local genotypes among crop trees at rotation (Campbell 1987). Obviously, the fewer the seedlings planted per crop tree, the smaller the chance that at least one will be of local type, unless all are of local type. Mortality during regeneration or in early precommercial thinning also lowers the probability; early regeneration failures and removals of local or non-local types in early thinning are likely to be more or less at random. Therefore, in situations where few seedlings are planted per crop tree, losses in regeneration are likely to be substantial, or early thinning is planned, seed transfers should be carefully controlled so that few non-local types are planted. In the average situation, ensuring that at least 50 percent of the genotypes within the transferred lot are of local type seems to be reasonable (Campbell and Sugano 1987). If the plantation site is near the biogeographical distribution limits of the species, using strictly local seed is recommended (Campbell 1987).

Any transfer of seed calls for a decision about direction of transfer. Genetic gradients almost always follow lines between places where stands are more productive to places where they are less productive. Trees in productive stands generally are faster growing, have longer non-dormant seasons, and are less resistant to drought or cold stress. Trees in less productive stands are slower growing but more resistant. Therefore, if the planting site is somewhere between the least and most productive ends of a genetic gradient, as is usual, a silviculturist with alternative sources of seed has a choice. Seed can be moved from the more productive or the less productive direction on the gradient. If the seed is taken from the more productive side, the non-local genotypes in the seed lot will, on the average, be more productive than local types, yet more susceptible to potential damage from environmental stress. If seed is taken from the less productive side, the non-local types will be more hardy than the local types, but also slower grow-

ing. Thus, either productivity or survival can be emphasized in many transfers of seed.

To some extent, the direction of transfer may depend on whether the plantation site has been improved or degraded during logging or site preparation. A site may be made colder, or hotter and dryer, for example, by some cutting practices. If either happens, the local population may be poorly adapted to the new conditions, at least in early years; regeneration may be extremely difficult. When this is the case, early survival, and even volume per hectare at later ages, may be improved using seed sources from environments colder or drier than the local environment (Eriksson et al. 1980). Similar considerations will need to be addressed if local climates change because of global warming (Ledig and Kitzmiller 1991). In this event, however, choosing adapted seed sources is likely to be complicated, because the changes in environment are likely to be complex (Harrington 1987).

Situations where using non-local seed sources could be advantageous usually occur because operational environments of the plantation site have been altered from the natural condition. But many changes that accompany site preparation and other forestry practices are likely to have only a temporary effect on operational factors. In particular, silvicultural practices seldom permanently influence heat energy rhythms. Heat energy drives the growing season, and adaptation to growing season depends on synchronizing vegetative period with it. Consequently, trees adapted to the local rhythm may still be more productive than introduced ones in the long run, regardless of other indications from early growth performance. In the absence of information from long-term tests, any transferred source should therefore include a substantial proportion of genotypes of local type. Such inclusion is ensured by restricting seed choices to those from within an appropriate zone or to those with acceptable mismatch indexes.

GENETIC VARIATION WITHIN GEOGRAPHICAL LOCATIONS

The magnitude of genetic variation in local populations is often considerable, as is the diversity

of genes within individuals. In this section we discuss the sources of diversity, its patterns within local populations, and the implications of diversity for forest management.

Sources of Genetic Diversity

Analysis of chemical gene markers in forest trees indicates that 15 percent or more of the gene pairs in individuals often include two gene variants (Steinhoff et al. 1983, Furnier 1984, Harry 1984, Neale 1985). Actual proportions of pairs with two variants, however, may be as high as 60-80 percent, because the use of the chemical-marker method detects as little as one-quarter of the potential variants (Lewontin 1974). With high diversity within trees, considerable variation among individuals can be generated in offspring from only a few parents. For example, if two individuals with two gene variants in each of 10 gene pairs are mated, more than 59,000 different genotypes could be produced in their progeny. With 20 variable gene pairs, the number of different offspring increases to nearly 3.5 billion! Because genetically variable tree species may have hundreds or thousands of variable gene pairs, it is likely that every seed produced by trees in these species has a different genotype.

In the section on geographical variation within species it was argued that much of the genetic diversity within local populations is a selection response to the extensive environmental heterogeneity, both in space and time, found within forest stands. Additional properties of forest trees contributing to within-population genetic diversity are large population size, longevity, high levels of outcrossing and gene dispersal within populations, and gene flow between populations (Hamrick et al. 1979, Mitton 1983, Loveless and Hamrick 1984, Ledig 1986a).

Population genetics theory indicates that selection of genotypes by spatially heterogeneous environments, in particular, can play a significant role in maintaining genetic diversity within populations (Hedrick et al. 1976, Powell and Taylor 1979). More direct evidence for the adaptive significance of genetic variability is the increased susceptibility of crop plants and forest trees to pests and climatic extremes when genetically uniform varieties have been planted (Kleinschmit 1979, Ledig 1986b). The

presence of genetic diversity in populations increases the likelihood that at least some individuals will be resistant to pest infestation or damage from climatic extremes, which otherwise might completely destroy a population with only one or a few genotypes. Genetic diversity, however, may not be essential for survival; red pine and western redcedar both have extensive ranges, yet both, especially red pine, are extremely limited in genetic variation, even within locations and individuals.

Many forest tree species occur in large stands and have more or less continuous distributions over broad areas. Large populations and longevity of trees are two factors reducing susceptibility to genetic drift. Long generation intervals mean trees are less frequently subjected to potential bottlenecks (reduced numbers) during reproduction than are species with short life cycles. In addition, multi-aged stands contain cohorts (a group of individuals of like age or character) that have been established at different times. Older cohorts may differ genetically from younger cohorts because environments differed during their respective establishments. Among sources of genetic diversity, another related to longevity is mutation (Ledig 1986a). Because of their large size and longevity, trees are expected to accumulate more mutations per generation than short-lived plants. That the majority of accumulated mutations are expected to be deleterious may explain the low self-fertility typically observed in forest trees (Sorensen 1971, Ledig 1986a).

High effective outcrossing (the mating of unrelated individuals) and gene dispersal are particularly important in maintaining genetic diversity within individuals. Evidence based on genetic markers indicates that the proportions of offspring resulting from outcrossing (versus selfing) are very high in trees, frequently exceeding 90 percent (Muona 1989, Adams and Birkes 1991). The low proportion of offspring resulting from selfing is due more to high levels of embryo abortion after self-fertilization than to low occurrence of selfing *per se*. Because there are no absolute mechanical or temporal barriers to self-pollination in conifers, self-pollination may be as high as 50-60 percent in stands with abundant pollen production (Sorensen 1982). While the proportion of outcrossed progeny is generally high, it can vary considerably among individual mother trees. For

example, in a study of 19 Douglas-fir trees from western Oregon, Sorensen (1973) estimated outcrossing to range from 72.5 to 100 percent, and values as low as 50 percent have been observed in seed orchard trees (Erickson and Adams 1990). A major factor contributing to variation in outcrossing is differences among trees in self-fertility; that is, more selfs are expected to produce viable seeds when self-fertility is high than when it is low. In addition, any factors increasing the proportion of self rather than outcross pollen around a tree during female receptivity are likely to increase self-pollination and, subsequently, decrease outcrossing. Thus, trees that are isolated (widely spaced) or have particularly high production of male cones relative to other trees are prone to produce higher levels of selfed offspring (Farris and Mitton 1984, Shea 1987).

The expectation that near neighbors are genetically related suggests that close inbreeding other than selfing may be a frequent occurrence in forest stands. Evidence from genetic marker studies, however, indicates that this is not the case, and at most, matings among close relatives other than selfing account for only small percentages of offspring (Brown 1989). Thus, clustering of family members may not be as prevalent as previously thought, or pollen gene dispersal may be extensive within forest tree populations. The average dispersal distances effective in fertilizing viable offspring in two Douglas-fir shelterwood stands were estimated with gene markers to be 55 and 81 m, respectively—values three times the average distance between trees in each shelterwood (Adams 1992).

Gene flow from surrounding stands is an important source of new variants within populations. When strong, it can counteract genetic differentiation among populations, especially for traits that are neutral to selection or are weakly selected (Slatkin 1987). Observations that pollen can be dispersed, *en masse*, over large distances suggest that gene flow may be extensive in forest trees (Silen 1962). Supporting evidence for strong gene flow, at least between neighboring stands, comes from studies on pollen contamination in conifer seed orchards. These studies revealed that pollen from surrounding stands can account for as much as 40-50 percent of viable orchard seed when protection against contamination is limited to the

establishment of narrow isolation zones around orchards (Adams and Birkes 1991).

Patterns of Genetic Diversity

Genotypes within forest tree populations often appear to be more or less spatially clustered rather than randomly distributed (Mitton 1983, Muona 1989). Such clustering could be the result of limited seed dispersal (which promotes family groups), microhabitat heterogeneity favoring different genotypes in different areas, or chance association of genotypes (Epperson and Allard 1989). Evidence for spatial clustering of genotypes is primarily of two types. In the first, crosses between near neighbors in white spruce and tamarack stands produced greater frequencies of empty seeds than crosses between trees further away, suggesting that neighbors in these stands are closely related (Park and Fowler 1982, Park et al. 1984). The second type of evidence is the spatial clustering of genotypes within stands of several conifer species (Linhart et al. 1981, Knowles 1984, Furnier and Adams 1986b, Furnier et al. 1987). Other studies, however, have failed to find groupings of genotypes within stands, indicating that spatial clustering can also be weak or nonexistent in conifer populations (Roberds and Conkle 1984, Epperson and Allard 1989).

Management Implications of Genetic Diversity

The wide genetic diversity found within populations and individual trees provides both an opportunity and a challenge to the forester. The opportunity lies in exploiting variation among trees to genetically improve species through tree improvement programs. The challenge is to ensure that seed sources used in reforestation possess plenty of genetic variation so that populations will be adequately buffered to environmental extremes and pest attack.

Opportunities for tree improvement

Opportunities for tree improvement are available at all levels of management, including natural

regeneration (Zobel and Talbert 1984). If the best individuals are left in a shelterwood or seed tree cut, the genetic resource is not degraded and small improvements might be obtained in selected traits in the next generation. Possibilities for genetic improvement are especially favorable for selected traits under strong genetic control, such as bole straightness and disease resistance.

Genetic improvements can also be made in seed collected from wild stands if seed stands or individually designated seed trees are identified. These methods can serve as interim sources of seed until seed orchards come into production. They may even be the sole sources of improved seed in species whose value or land base does not justify intensive tree improvement programs. In the seed stand method, seeds are collected from stands having high proportions of good-quality (i.e., fast-growing, straight-stemmed, disease-free) trees. The genetic value of seed produced in these stands may be further improved by selectively thinning to remove poorer individuals. The most common approach for increasing genetic quality of seed from wild stands in southwestern Oregon and northern California is to select individual seed trees widely scattered along road systems (Kitzmilller 1976, Silen and Wheat 1979, Thiesen 1983). A principal advantage of this approach is that bulked seed lots from a large number of widely scattered seed trees within a seed zone will likely possess more genetic diversity than bulked seed from one or a few seed stands, although the costs associated with collecting seed from widely scattered trees will be greater. Genetic gains from selection for faster-growing trees are expected to be low under both the seed stand and seed tree methods because of the weak inheritance of growth traits and because pollen sources are not controlled (Zobel and Talbert 1984). Nevertheless, both methods ensure that seed will come from a known source and from at least average or better trees. Seed trees, however, often are an intermediary step in more intensive tree improvement programs where the progeny of seed trees are tested in evaluation plantations to provide information for establishing or roguing seed orchards and for advanced generation selections. Information from the evaluation plantations is used to limit seed harvesting to trees with progeny of proven performance. Under these conditions, modest genetic

improvements can be expected even in weakly inherited traits (Silen and Wheat 1979).

A detailed discussion of intensive tree improvement programs in southwestern Oregon and northern California is beyond the scope of this chapter (see Kitzmilller 1976, Silen and Wheat 1979, Thiesen 1983 for details). Nevertheless, a brief overview of current tree breeding will aid in understanding the impacts of tree improvement on forest management in the region. More than 20 tree species are under some form of genetic manipulation, with most programs emphasizing improvement in bole growth rate and quality, but with disease resistance receiving primary attention in special cases (e.g., resistance to blister rust in western white pine and sugar pine). By far the greatest effort is in coastal Douglas-fir, and our remaining comments will address this species only.

Because of the environmental heterogeneity in the region, the land base has been subdivided into many geographically and elevationally defined breeding zones, each zone presumably circumscribing locally adapted populations that differ between zones (Silen and Wheat 1979, Adams 1981). Southwestern Oregon, for example, has been subdivided into 13 geographical areas (breeding units), each further subdivided into two or more elevation bands 152-457 m wide, giving a total of 35 Douglas-fir breeding zones (Figure 12-3). Similarly, the USDA Forest Service has designated seven breeding zones for Douglas-fir in northern California (Kitzmilller 1976). Seed orchards providing seed for each zone are derived only from trees selected within each zone. In this manner, the risk of breeding new strains of trees not well adapted to local planting environments is minimized. Furthermore, within each zone a large number of parent trees (usually > 200) widely scattered among wild stands have been selected in order to ensure that breeding populations consist of a broad base of genetic diversity. Wind-pollinated offspring of these parent trees are subsequently planted in evaluation plantations chosen to sample the range of environments within the zone. Parent trees whose progeny combine improved economic value with broad adaptability are identified and selected for further breeding and seed orchard use. Summary statistics for the Northwest Tree Improvement Cooperative, which accounts for

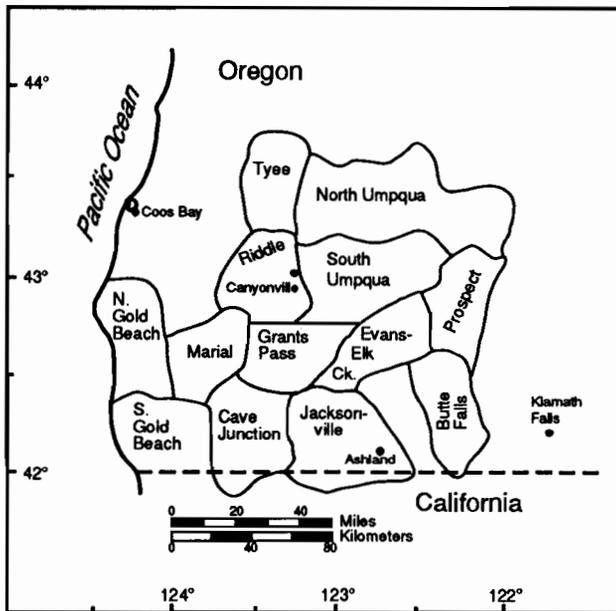


Figure 12-3. Douglas-fir breeding units in southwestern Oregon.

most, but not all, of the breeding activities in the 35 breeding zones in southwestern Oregon, are impressive: 1.06 million hectares under Douglas-fir tree improvement, 9,744 parent trees selected, and 331 test sites (Quam 1988). Because most of the intensive tree improvement programs in southwestern Oregon and northern California are less than 10 years old, their full impact in terms of availability of genetically improved seed is yet to be felt. Nevertheless, with anticipated genetic gains in bole-volume growth of 10-20 percent in the first generation (Silen and Wheat 1979), the bulk of planting in the near future will involve genetically improved stock.

Challenge to conserve genetic diversity

Foresters must avoid both drastic reductions in genetic diversity and increased inbreeding in reforestation stock, whether regeneration be by natural or artificial means. Although apparently not the case in Douglas-fir, large reductions in the parent tree population during shelterwood or seed tree regeneration may result in less genetic variation than in pre-harvest stands. In addition, the proportion of inbred progeny may increase because,

Table 12-1. Estimates of genetic diversity within individuals and proportions of outcrossed progeny (*t*) for two pairs of adjacent old-growth uncut and shelterwood Douglas-fir stands in southwestern Oregon. From Neale (1985), Neale and Adams (1985).

| Stand location and type | Trees/ha | Genetic Diversity | | |
|----------------------------|----------|-------------------|------------------------|----------|
| | | Adults | Offspring ¹ | <i>t</i> |
| Benshell | | | | |
| Uncut | 35 | 0.211 | — | 0.96 |
| Shelterwood | 100 | .244 | 0.213 | .96 |
| Cutmore | | | | |
| Uncut | 15 | .225 | — | 1.00 |
| Shelterwood | 100 | .220 | .214 | .94 |

¹ Sample of 3- to 5-year-old seedlings in understory of shelterwoods. Comparable samples were not taken in the uncut stands.

as stand density decreases, the frequency of self pollen around each tree is expected to increase (Farris and Mitton 1984). Genetic impacts of the shelterwood regeneration system in Douglas-fir were investigated in two pairs of adjacent uncut and shelterwood old-growth stands in southwestern Oregon (Neale 1985, Neale and Adams 1985). The average per-hectare density of leave trees in the shelterwoods was 35 and 15, while the uncut stands had a density of 100 trees/ha. No evidence for shelterwood regeneration having a significant impact on either genetic diversity or outcrossing was found (Table 12-1). Neither expected genetic diversity within trees nor outcrossing was consistently lower in the shelterwood leave trees than in the uncut stands. Furthermore, the shelterwoods had gene frequencies quite similar to those in the uncut stands (Neale 1985). The general lack of genetic changes as a result of shelterwood cutting can be attributed to the high genetic diversity within trees, the high effective outcrossing, and the strong gene dispersal in this species. It is interesting that there was evidence for some inbreeding other than selfing in the progeny of the uncut stands but not in that of the shelterwoods (Neale and Adams 1985). This could be explained by the family substructuring in the uncut stands that was eliminated in the shelterwood harvesting. Thus, overall inbreeding may actually have been less in

the shelterwoods than in the uncut stands. Furthermore, many shelterwoods in the region are underplanted. Because planted seedlings rarely originate from the shelterwood stand, they represent a potential gene flow into the site. The genetic diversity of the resulting seedling population, therefore, is likely to be greater than that under natural stands.

The above results suggest that the genetic composition of populations may be little altered with natural regeneration, but this hypothesis needs to be tested with more species and conditions. The insensitivity of outcrossing rate to stand density in this case is probably mostly a function of the low self-fertility in this species. Sorensen (1982) has shown that when self-fertility is low, as in Douglas-fir, differences in the frequency of self-fertilization must be great for differences in the proportion of outcrossed progeny to be detected. It must be remembered, however, that self-fertility varies substantially among species and among individuals within species; and as self-fertility increases, the relationship between the frequency of self-fertilization and proportion of selfed offspring grows stronger. An example of stand density's appearing to have had a substantial effect on outcrossing is reported by Farris and Mitton (1984) for ponderosa pine in Colorado. In this case, outcrossing was estimated to be 0.96 in a high-density stand (230 trees/ha) and only 0.81 in a low-density stand (13 trees/ha) nearby.

Increases in selfed progeny may have only limited impact under the relatively harsh environmental conditions present during natural regeneration, because most offspring resulting from selfing are eliminated fairly early in stand development because of their poor survival and growth (Muona 1989). Under artificial regeneration, however, seedlings are produced in mild nursery environments where inbreds have a much greater chance of survival. Outplanting these inbred seedlings could seriously decrease survival and growth of plantations (Sorensen 1973). For this reason, it is best to avoid isolated trees or extremely low-density stands in seed collections. In the seed tree method, seed trees are often cultured (e.g., fertilized, close neighbors removed) to encourage flower production. Because nearby trees are not cultured, it is possible that good flower crops will occur in seed trees in years when pollen pro-

duction in the surrounding trees is poor or absent. Under these conditions it would be unwise to harvest the resulting cone crop of the seed trees, because seed set is expected to be low and a large proportion of the viable seed will probably be the result of selfing.

The main factor determining levels of genetic diversity in seed lots produced under artificial regeneration is the number of parents contributing to the seed (Brown and Moran 1979). Thus, if plenty of genetic variation in regenerated stands is to be ensured, wild collections should include seed from a large number of mother trees, and seed orchards should consist of large numbers of unrelated clones or families. Regional norms for both wild-stand collections and seed orchards seem more than adequate to maintain high levels of genetic diversity in seed stocks. USDA Forest Service guidelines in California, for example, state that each wild-stand seed lot should consist of seed from one or more trees in a minimum of 20 widely separated stands in each seed zone, with each stand contributing no more than 10 percent of the seed lot (Kitzmilller 1990b). Data for ponderosa pine suggest that such a sampling scheme provides an adequate representation of the natural genetic diversity within the collection zone. A survey of three geneticists from federal agencies indicates that similar guidelines are operational in southwestern Oregon; under the seed tree method, bulked seed lots consist of a minimum of 10-15 mother trees, with 30 or more trees preferred. USDA Forest Service policy in southwestern Oregon and northern California is that at least 50 unrelated clones or families should be included in seed orchards (Thiesen 1983, Kitzmilller 1990b); most orchards well exceed this standard (Cress and Daniels 1990). Data from a number of conifers indicate that genetic diversity in seed orchard offspring is comparable to that observed for natural populations in the same region (Adams 1981, Knowles 1985, Szmidt and Muona 1985, Muona and Harju 1989).

As long as efforts continue to include large numbers of parent trees in seed collections from wild stands, seed orchards, and breeding populations, artificially regenerated populations of forest trees should be in little danger of having inadequate levels of genetic diversity (Adams 1981, Ledig 1986b). Nevertheless, broad-scale replacement of natural

populations with artificial stock is altering the gene pools of tree species. This alteration is expected to occur most rapidly in areas where forest production is greatest and where tree improvement is most intense. Because these alterations will eventually reduce the overall pool of genetic variation in species, it is critical to employ long-term conservation strategies that will ensure current levels of diversity in future generations. Preservation of genetic diversity is essential to the continued natural evolution of species and to the ability of future breeders to meet challenges presented by unforeseen pests, changing environments, or new products. The best approach to gene conservation is to establish *in situ* reserves that represent the geographical variation in a species (Ledig 1986b and 1988). Lands that are already protected, such as national or state parks, wilderness areas, and research natural areas, may fulfill much of that need. Unfortunately, areas undergoing the most intensive management, and thus in most immediate need of preservation, are usually not well represented by previously established reserves. One problem in deciding on the number and distribution of genetic reserves is the lack of adequate information on the distribution of genetic variation within species. A pragmatic approach in intensely managed areas is to set aside at least one large natural stand within each seed zone to be managed for gene conservation (Wilson 1990).

SUMMARY

In this chapter the rich genetic diversity of tree species in southwestern Oregon and northern California is categorized at four levels: among species, among geographical locations within species, among individuals within geographical locations, and within individuals. For each level, patterns of natural genetic variation are described and the consequences of these patterns for silviculture discussed.

The presence and distribution of tree species in the region are functions of both evolutionary history and adaptations to current environmental conditions. Recurring climatic extremes resulting from ice ages and intervening dry periods have not only limited the variety of tree species, but have preadapted the survivors to diverse environments.

Variation in amounts of genetic diversity found within different species may, in large part, be a function of the extent to which species have experienced bottlenecks in population size during recent climatic extremes. In addition to evolutionary history, current species distribution is primarily a function of adaptation to the operational environments associated with soils, seasonal cycles of temperature and precipitation, competition, and herbivory. When choosing species to plant, one needs information on the operational environment of the site, the adaptive characteristics of species, and the potential influence of management on the environment and species response. Planting mixtures of species, or encouraging mixed composition through combinations of planting and natural regeneration, may increase buffering of stands to pests and environmental hazards.

Patterns of natural genetic variation within wide-ranging tree species are often characterized by two general observations: (1) geographical variation among populations is closely associated with environmental gradients; and (2) a considerable proportion of the total genetic diversity in a region is due to differences among individuals within populations. The close association of geographical variation with environmental gradients suggests that genetic variation on a geographical scale is primarily the result of adaptation; thus, great care must be taken in moving seed used in artificial reforestation. Genetic variation within populations may largely be a reflection of adaptation to the extensive heterogeneity of microhabitats within forest stands. Although it is possible to improve stand productivity by planting fast-growing, non-local seed sources, there is the risk that such seed sources will be poorly adapted. The safest course is to choose a seed source with a large proportion of genotypes in common with those found in the local population. The proportion of local types in a transferred seed lot can be estimated from knowledge of genetic gradients derived from common garden studies with seedlings. As genetic gradients associated with geographical or topographical distances steepen, the proportion of like genotypes between any two locations on a gradient decreases, and the risk of seed transfer increases. Seed-transfer guidelines based on genetic gradients have recently been developed for Douglas-fir and sugar pine in southwestern Oregon.

In addition to microhabitat selection, many properties of forest trees contribute to the large amounts of genetic diversity observed within populations. Among these are large population size and longevity, high effective outcrossing and gene dispersal within populations, and gene flow between populations through long-distance dispersal of pollen and seed. The wide genetic variation within and between populations can be exploited by artificial selection to improve species through tree improvement programs. In southwestern Oregon, nearly 10,000 Douglas-fir parent trees have been selected in wild stands, and their progeny are currently being tested in more than 300 evaluation plantations. Because most seed orchards in the region are still young, the full impact of tree improvement in terms of providing genetically improved seed is yet to be felt. Foresters must take care to ensure that reforestation practices do not drastically reduce genetic variability or increase inbreeding in seed stocks, both of which increase susceptibility of regenerated stands to damage from pest attack and climatic extremes. Regional norms for numbers of parent trees represented in seed orchards and seed collections from wild stands seem more than adequate to maintain high levels of genetic variation in artificial seed stocks. Continued domestication of our tree species, however, is altering their gene pools and ultimately will reduce overall genetic diversity. It is critical that long-term strategies for gene conservation be implemented so that the current levels of diversity in tree species can be preserved for future generations.



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