

Structure of Genetic Variation and Implications for the Management of Seed and Planting Stock

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Abstract: This paper reviews what is known about genetic structure of forest trees, and how that knowledge is used to determine safe limits to the movement of plant material. Geographic genetic variation in adaptive traits is of greatest importance to concerns of seed movement. Genetic structure in adaptive traits may be ascertained through long-term provenance and progeny tests, or short-term common garden studies in a nursery or nursery-like environment. These studies have shown that variation patterns are not consistent among species, among regions within a species, or among traits. The first seed zones were developed based on differences in climate and vegetation, and did not account for differences among species. Seed zones were recently revised in Oregon and Washington to reflect current knowledge of geographic genetic variation for individual species. Seed zones are an administrative convenience that directs managers how to bulk seeds from different stands. The use of seed transfer guidelines, on the other hand, allows greater flexibility and better knowledge of the risks of seed movement. Transfer guidelines, however, require keeping track of many small seed lots, which involves more time and expense.

Keywords: genetic structure, seed zones, breeding zones, seed transfer guidelines, genecology

Introduction

Genetic structure here refers to the organization of genetic variability among individuals within populations and among populations. Genetic structure determines, in part, the degree to which populations are adapted to the range of environments that they might face. Consequently, genetic structure is important in determining how far individuals from a population may be moved from their source environment and still ensure that a large proportion of them survive and thrive.

A seed zone is a region within which seeds or plants from native stands may be moved with minimal risk of maladaptation. Seed zones are delineated on maps with distinct geographic and elevational boundaries. Genetic variation in forest trees, however, changes gradually in most cases, and, thus, does not have distinct boundaries. For this reason, seed transfer guidelines are more appropriate. Seed transfer guidelines, also referred to as continuous seed zones, are procedures or rules for directing the most appropriate transfer of plant material from a point of origin to a planting site—in other words, for evaluating a number of potential transfers on the basis of relative risk of maladaptation.

A breeding zone is a region from which parents in a tree improvement program come, and to which the progeny from those parents are operationally planted with minimal risk of maladaptation. Thus, seed zones generally refer to plant material from presumably native stands, and breeding zones generally refer to plant material from tree improvement programs. The parents in a tree improvement program do not necessarily come from the same area that will be planted with the operational planting stock. For example, some second-generation parents in the Northwest Tree Improvement Cooperative (NWTIC) breeding program come from much further north or south of the area for which they are being tested and expect to be planted. To better distinguish the two, the collection of parents in a tree improvement program may be referred to as the breeding population, and the region to which the progeny are to be planted may be referred to as the deployment zone.

This paper reviews what is known about the genetic structure of forest trees and how that knowledge is used to determine safe limits to the movement of plant material, focusing primarily on the Pacific Northwest. We review reasons for seed/breeding zones and seed transfer guidelines, the methodology used to examine genetic structure, some generalizations about the genetic structure of forest trees, and the development of seed zones or transfer guidelines.

Reasons for Seed and Breeding Zones

Interest in planting in the Pacific Northwest arose around the beginning of the twentieth century following numerous, large fires. The Wind River nursery, one of the first Forest Service nurseries, was established in 1909, largely to help in reforestation efforts after the extensive Yacolt fire in southwest Washington. In the first few decades, little attention was given to the origin of seeds. Seeds were primarily collected from downed trees in recently logged areas, most often from lower elevations. Two things happened, however, to begin to raise concern about seed origins. First, silviculturists on the National Forests began to notice plantation failures. These failures often occurred many years after seemingly successful establishment, and often after infrequent, climatic insect or disease events. Adjacent, naturally regenerated stands did not fail. Second, trees from many of the seed sources in one of the early seed source studies, the 1912 Douglas-fir Heredity Study, were damaged and began to die after a particularly severe freeze in November of 1955. Concern over the loss of formerly productive stands gave rise to the first seed zones in Oregon and Washington with a map published in 1966.

Seed and breeding zones serve another function beyond the maintenance of adapted and productive forest stands. By restricting the environmental distance that plants may be moved from their native source, seed and breeding zones contribute to the conservation of genetic diversity and the maintenance of a species' geographic genetic structure. Localized seed collections serve an important role in gene conservation and ecological restoration. For example, a disjunct population of Douglas-fir on the Fremont National Forest was nearly completely consumed by the Silver Fire in 2002 (Stubbs 2003). Fortunately, recognizing the uniqueness of this population, seeds were collected some years earlier and may now be used to restore the population.

Methods to Explore Genetic Variation Structure in Forest Trees

Genetic variation may be found at the level of differences in: 1) DNA sequences; 2) simply inherited traits that are direct products of the expression of a single gene; or 3) quantitatively inherited traits that are controlled by several genes. Of greatest interest to the delineation of seed/breeding zones and seed transfer guidelines are traits related to adaptation, which are primarily quantitatively inherited traits. Genetic variation in these traits is revealed when trees from different families of different populations are grown together in the same environment, called

common garden studies. Differences observed between populations are then most likely due to differences in genetics. Common garden studies may be long-term, including provenance and progeny tests, or they may be short-term, such as studies conducted in nursery beds or farm-field plots.

Long-term provenance studies test various seed sources at a range of planting locations. Because they are long term, provenance tests should provide the most reliable information on the health and productivity over the life of a stand. The long-time interval exposes the provenances to fluctuating climates, particularly to extreme climatic events. Provenance tests are also valuable for exposing provenances to biotic stresses to detect source-related variation in tolerance or resistance to pests (for example, Ying and Hunt 1987; Ying 1991; Ying and Liang 1994; Wu and Ying 1996). Provenance tests have proved particularly valuable as a general screen of source-related variation when introducing exotic species to new countries. The few provenance tests established in the Pacific Northwest have included too few and widely scattered sources (for example, Munger and Morris 1937; Squillace and Silen 1962; White and Ching 1985); although adaptive differences among provenances are evident, interpolation between sources is difficult. Provenance tests are expensive to establish, and finding sufficiently large test sites is difficult. The advantage of provenance tests—their long-term nature—is also a disadvantage; one must wait a long time to be confident in findings. Nevertheless, results from older provenance tests have demonstrated 2 key points: 1) the consequences of maladaptation often do not show up until many years into the life of the stand; and 2) it is the rare, extreme climatic events that are important in determining long-term survival. For example, in the Douglas-fir Heredity Study (Munger and Morris 1937), all seed sources performed relatively well for 4 decades. In November of 1955, the area had an unusual and prolonged cold spell (Duffield 1956), killing or severely damaging many of the offsite seed sources in the study, while the adjacent naturally regenerated stand suffered less damage and continued to grow well (Silen 2003).

Progeny tests also may serve the purpose of looking at geographic genetic variation. Progeny tests evaluate the parents of tree improvement programs for purposes of selection to rogue seed orchards or proceed to the next generation. The Pacific Northwest has hundreds of progeny tests of several conifer species, but most are Douglas-fir (Lipow and others 2002; Lipow and others 2003). The parents in these tests are usually well distributed, and information about the location of the parents is readily available. But parents in most first-generation breeding zones came from a limited geographic and elevational range; thus, extrapolation beyond the limited set of environments is difficult. Nevertheless, information from some of these tests has demonstrated clinal variation patterns in growth, phenology, and cold hardiness (Silen and Mandel 1983; Balduman and others 1999). Second-generation progeny tests of the NWTIC should allow a better evaluation of the potential for deploying improved genotypes over a wider area, since the parents tested for a given deployment zone come from a wider area than those in the first generation.

Short-term common garden studies in nurseries or farm-field tests are an alternative to longer term provenance and progeny tests. They have the advantage that many families and provenances may be grown in a relatively small area, usually at a location that is convenient for measuring a wide variety of traits. The environment within a test is usually very uniform, allowing less replication and better expression of genetic differences. The short-term nature and convenience of nursery common garden studies reduces the costs relative to long-term trials. The disadvantage of short-term tests is that they do not sample the range of climatic and biotic environments over the life of a stand, particularly extremes in climate. However, traits important for adaptation to climatic extremes (for example, growth, bud phenology, cold hardiness, drought hardiness) may be easily measured. Strong correlations of these traits to the physiographic and climatic variables of the seed-source locations is strong evidence that the traits have responded to selective pressures and are of adaptive importance. The inclusion of many well-distributed seed sources allows adaptive genetic variation to be mapped across physiographic space (Campbell 1986). The study of the relation between geographic genetic variation and environmental variation at a seed source has been termed "genecology" (Turesson 1923; Campbell 1979). The development of genecological studies using short-term common garden tests owes much to the pioneering work of Campbell in the Pacific Northwest (Campbell 1974b, 1979, 1986; Campbell and Sorensen 1978) and Rehfeldt in the Interior Western United States (Rehfeldt 1978, 1982, 1989).

Molecular markers consider genetic variation at the level of DNA, either as differences in the sequence of base pairs in DNA itself (for example, microsatellites, restriction fragment length polymorphisms, single-nucleotide polymorphisms), or as differences in gene products (for example, isozymes, terpenes). Molecular markers are generally considered to be neutral with respect to natural selection, that is, differences among markers are not indicative of adaptive differences among individuals or populations. For this reason, molecular markers are less valuable for delineating seed/breeding zones or seed transfer guidelines than quantitatively inherited adaptive traits. Differentiation among populations is generally much less for molecular markers compared to quantitative traits (Karhu and others 1996; Merilä and Crnokrak 2001; McKay and Latta 2002). Some studies have shown geographic patterns in marker variation, but they generally involve samples distributed over a very large range (for example, Li and Adams 1989; Lagercrantz and Ryman 1990) or markers that are associated with maternally inherited organelles that show limited dispersal (for example, Aagaard and others 1995; Latta and Mitton 1999). Neutral markers are most useful for distinguishing variation arising from nonselective evolutionary forces—migration (random movement of alleles among locations), genetic drift (random loss or fixation of alleles), or mutation (random change in the form of an allele). Future studies, however, hold promise for identifying genes that are controlling adaptive traits, and for exploring relations between variation in such genes and variation in quantitative traits identified in genecological studies.

Generalizations About Genetic Structure of Forest Trees

Temperate forest trees are predominately outcrossing with large amounts of gene flow due to widely distributed pollen and mostly continuous distributions. As a result, common garden studies have shown predominately clinal patterns of variation in which trait means change gradually in association with environmental variation (Figure 1). The patterns of variation, steepness of clines, and the strength of the association with the environment, however, differ greatly among species. Rehfeldt (1994) determined the environmental distances (differences in elevation and frost-free days) that were needed to detect differences among seed sources for several conifers in the Northern Rockies (Table 1). Species like Douglas-fir and lodgepole pine may be termed specialists. These species have populations that inhabit a relatively narrow niche; populations separated by only 200 to 220 m (660 to 720 ft) in elevation and 18 to 20 frost-free days may be considered genetically different. In contrast, populations of western redcedar and western white pine inhabit broad niches and show very little differences among populations over large environmental distances. These species may be termed generalists. Other species are intermediate between these extremes.

Patterns of genetic variation may differ among regions within a species' range. Western white pine shows very little geographic differentiation in the Northern Rockies, but a greater degree of differentiation along the Cascade Range in western Oregon and Washington (Rehfeldt 1979; Rehfeldt and others 1984; Campbell and Sugano 1989). In Douglas-fir, elevational clines in seedling size were much steeper in the Cascades than in the coastal mountains (Campbell and Sorensen 1978). In ponderosa pine, seedling size was more closely associated with differences in elevation east than west of the southern Oregon Cascades (Sorensen and others 2001), with an abrupt transition zone found at the Cascades crest (Figure 2). An abrupt change in a cline is referred to as a stepped cline, and is usually associated with secondary contact after historical separation between 2 differentiated races or taxa (Sorensen and others 2001).

Differences in genetic structure also exist among traits. In lodgepole pine in central Oregon, a set of traits associated with seedling size and vigor differed primarily with elevation, presumably in response to temperature, whereas a set of traits associated with seed and root size differed primarily with latitude and longitude, presumably in response to moisture availability (Sorensen 1992). In ponderosa pine in the Upper Colorado Basin, geographic clines in growth potential were northwest to southeast (at a constant elevation), whereas geographic clines in growth initiation varied more in an east-west direction (Rehfeldt 1990). Growth appeared to be related to temperature differences associated with latitude, whereas growth initiation appeared to be related to geographic patterns of spring and summer precipitation. Differences in geographic patterns among traits is expected, since different traits may be responding to different environmental factors, and the strength of selection may vary relative to the nonselective factors of migration and genetic drift.

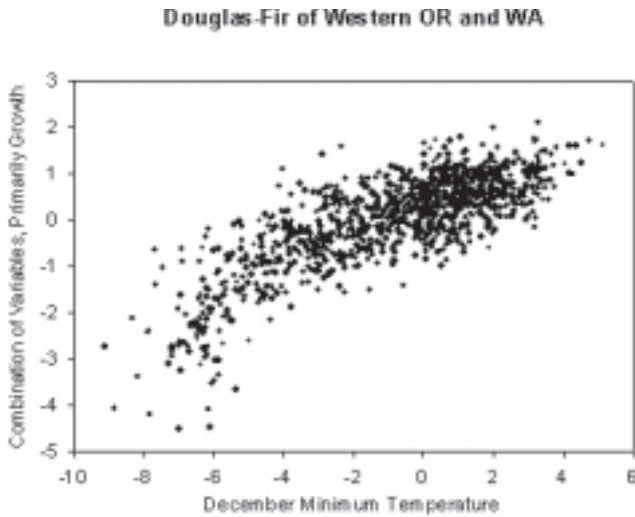


Figure 1—Graph of a composite trait representing growth vigor as related to December minimum temperature (°C) for Douglas-fir seed sources from western Oregon and Washington.

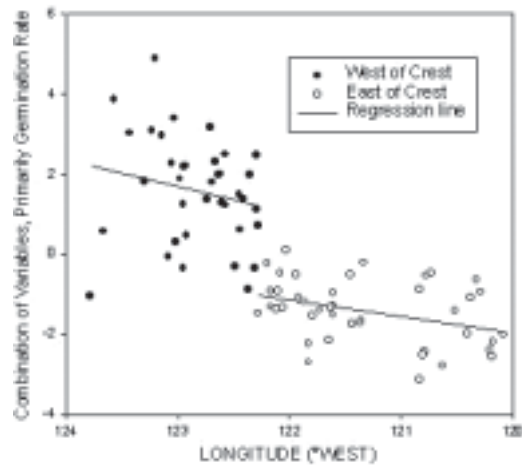


Figure 2—A stepped cline as illustrated in a graph of a composite trait, representing primarily germination rate, as related to longitude in a transect of ponderosa pine seed sources across the Cascades crest in southern Oregon.

Developing Seed and Breeding Zones or Transfer Guidelines

The first seed zones were developed in 1966 based primarily on differences in climate and vegetation. A slightly revised version was published a few years later (Tree Seed Zone Map 1973). The maps assumed that geographic differences in adaptive genetic variation were largely in response to past climates as reflected by the current climate and vegetation. These seed zones were fairly restrictive, both geographically and elevationally (Figure 3). Elevational transfers were restricted to zones of approximately 150 m (500 ft). The seed zones were the same for all species; it was not recognized at the time that species have different patterns of genetic variation.

Seed zones were recently revised for western Oregon and Washington to reflect current knowledge of geographic genetic variation based on geneecological studies (Randall 1996; Randall and Berrang 2002). In most cases, seed zones were

enlarged, particularly in a north-south direction (Figure 4). Species differences in geographic patterns of genetic variation were recognized in the new seed zones. Specialist species like Douglas-fir retained many seed zones with narrow elevational bands (Figure 4). Generalist species like western redcedar were given few seed zones with none to few wide elevational bands. Western redcedar may be moved large distances without concern for maladaptation, whereas Douglas-fir seed zones, although enlarged, are still relatively restricted. In a similar manner, Douglas-fir breeding zones used in NWTIC programs were enlarged between the first and second generation (Figure 5).

Seed zones are an administrative convenience for directing managers on how to bulk seeds from different stands for seed inventory purposes. But, as has been pointed out, genetic variation is continuous and predominately without discrete boundaries. Furthermore, similar genotypes may recur in similar environments in other seed zones, particularly as you move towards seed zone edges. For these reasons, seed transfer guidelines are more appropriate biologically. Campbell

Table 1—Environmental differences associated with genetic differentiation among populations of conifers in the Interior Western United States (from Rehfeldt 1994).

Species	Elevation difference to find genetic difference	Frost-free days to find genetic difference	Evolutionary mode
Douglas-fir	200	18	Specialist
Lodgepole pine	220	20	Specialist
Engelmann spruce	370	33	Intermediate
Ponderosa pine	420	38	Intermediate
Western larch	450	40	Intermediate
Western redcedar	600	54	Generalist
Western white pine	none	90	Generalist

^a1 m = 3.3 ft.



Figure 3—Original Washington tree seed zones.



Figure 4—Revised tree seed zones for western Oregon and Washington for (A) Douglas-fir and (B) western redcedar.

(1974a,b) laid the groundwork for the use of continuous models to estimate the effects of seed transfer. He later developed a method to quantify the relative risk of maladaptation from seed movement based on the amount of overlap between populations at 2 different environments (Campbell 1986). The amount of overlap is dependent upon the predicted means for a trait in the 2 environments as determined by

regression models and the amounts of within population variation. Figure 6 presents a hypothetical example for transfers along an elevational gradient. Movement of a population from 500 to 600 m (1,640 to 1,970 ft) involves little risk as indicated by the considerable proportion of the populations in common at each location. Movement from 250 to 600 m (820 to 1,970 ft), however, could lead to considerable maladaptation (greater risk) as indicated by the small amount of overlap between populations. Campbell's method provides a quantifiable estimate of risk of maladaptation for seed movements from a source environment to a planting environment. It is a relative risk and does not give an absolute proportion of a population that may not be expected to survive.

Monserud (1990) developed a rule-based expert system to guide seed transfer movement. This system is currently being used to guide seed movement of Douglas-fir, ponderosa pine, and western larch in the Northern Rockies (Mahalovich 2003). It uses models developed by Rehfeldt (for example, Rehfeldt 1990) to determine compatible seed sources for a given planting site.

Parker (1992) used geographic information systems software (GIS) to create a map of genetic variation in 2 sets of traits representing vigor and survival for jack pine in Ontario. Using GIS, he then mapped areas that were similar to what might be expected for a trait at a given point on the map. The mapped area, called a "focal point seed zone," indicates areas



Figure 5—Douglas-fir first- and second-generation Northwest Tree Improvement Cooperative breeding zones.

that may be reforested with seeds from the given point with minimal risk of maladaptation, or, alternatively, areas where seeds from the given point may be used for reforestation. As an example, we show the focal point seed zone for a site in the central Oregon Cascades based on the results for geographic genetic variation in seedling vigor in a recent, unpublished genecological study of Douglas-fir (Figure 7).

Managers must decide at what level to bulk parents, whether they are using discrete seed zones or seed transfer guidelines. Ideally, one would bulk seeds from trees collected within a single stand at a specific location. Small geographic seed lots would allow greater flexibility for moving seeds to different planting environments and better knowledge of the risks involved. Keeping track of many

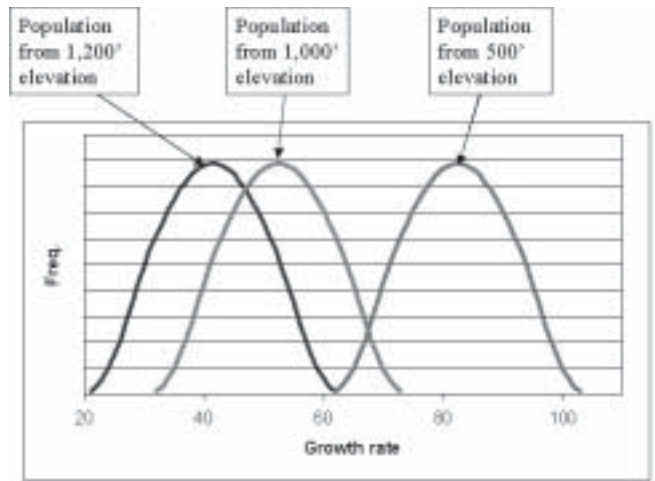


Figure 6—Hypothetical example illustrating seed transfer risks as the amount of overlap between populations from different elevations for a trait such as growth rate as evaluated in a common garden study (1 ft = 0.3 m).

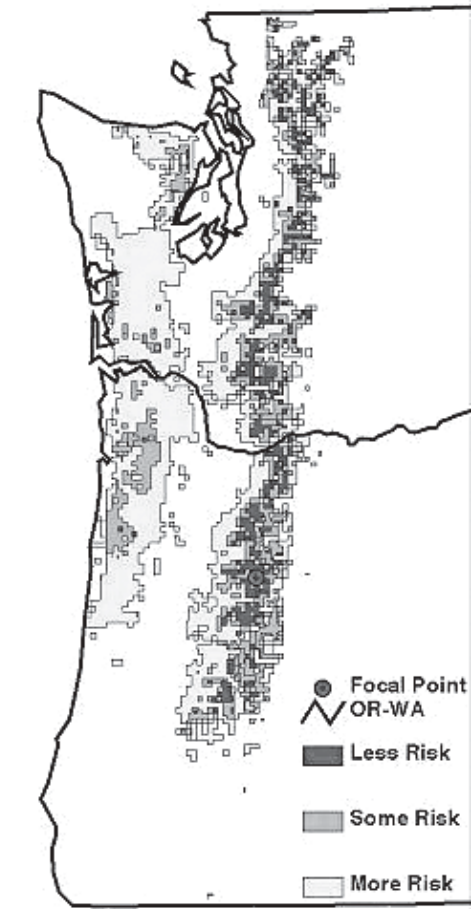


Figure 7—Focal point seed zone illustrating transfer risks for a focal point at mid-elevation in the Oregon Cascades.

small seed lots, however, is relatively expensive. For seed and seedling inventory purposes, bulking seeds at some higher spatial scale is desirable. Temperature appears to be a critical environmental factor for the adaptation of many tree species to their environments, and temperature is strongly affected by elevation, particularly within a seed zone. If parents are to be bulked at a finer scale than the elevation bands within seed zones, we recommend narrower elevation bands, and keeping track of those bands.

Summary

Moving plant materials has important consequences for the health, productivity, and diversity of forest ecosystems. Seed and breeding zones, and seed transfer guidelines, restrict the movement of plant material to minimize risks of maladaptation in plantations. Genetic structure determines the risk of maladaptation from seed movement; thus, knowledge of genetic structure is critical to delineating seed/breeding zones and developing seed transfer guidelines. Early seed zones assumed that genetic structure was largely reflected by geographic variation in climate and vegetation. They served their purpose well, but were rather conservative and did not consider species differences in genetic structure. Seed zones have been revised in the last decade to reflect current knowledge of genetic structure for each species. Revised seed zones are less restrictive, particularly for species with little geographic genetic variation. Managers face the issue of how large of an area to bulk parents into seed lots. They must evaluate the tradeoffs of the greater flexibility and better knowledge of risks of seed movement from using many small geographic seedlots versus the administrative ease and cost savings of using fewer large seedlots.

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