Impact of Alternative Regeneration Methods on Genetic Diversity in Coastal Douglas-Fir

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ABSTRACT. Genetic implications of natural and artificial regeneration following three regeneration methods (group selection, shelterwood, and clearcut) were investigated in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) using genetic markers (17 allozyme loci). In general, harvesting followed by either natural or artificial regeneration resulted in offspring populations little altered from those in the previous generation. Cutting the smallest trees to form shelterwoods, however, resulted in the removal of rare, presumably deleterious, alleles, such that slightly fewer alleles per locus were observed among residual trees (2.76) and natural regeneration (2.75) than found in uncut (control) stands (2.86). Thus, although the shelterwood regime appears quite compatible with gene conservation, it would be best to leave parent trees of a range of sizes in shelterwoods designated as gene conservation reserves, in order to maximize the number of alleles (regardless of current adaptive value) in naturally regenerated offspring. Seedling stocks used for artificial regeneration in clearcut, shelterwood, and group selection stands (7 total) had significantly greater levels of genetic diversity, on average, than found in natural regeneration. This is probably because the seeds used in artificial seedling stocks came from many wild stands and thus, sampled more diversity than found in single populations. FOR. SCI. 44(3): 390–396.
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AN ISSUE OF PARTICULAR CONCERN today in the practice of forestry is the extent to which management alters levels of biodiversity in forests. One important component of biodiversity is genetic variation within tree species at the population or stand level. Loss of genetic variation within populations leads to increased vulnerability to pest attack and climatic extremes, and reduces the ability of species to evolve in response to changing environments (Ledig 1986, Millar and Libby 1991). Variation within populations is also the primary source of genetic diversity employed by breeders in tree improvement programs (Adams et al. 1992a, El-Kassaby 1992). Despite the importance of genetic variation within populations, little data is available to assess the potential implications of alternative management practices on levels of diversity (Savolainen and Kärkkäinen 1992).

A study established by the College of Forestry at Oregon State University in 1989 provided an excellent opportunity to address impacts of forest management on biodiversity in a well controlled and replicated experiment. Plant and animal communities under alternative silvicultural regimes are being compared, over time, to those in uncut, mature stands, in each of three replicated blocks. The investigation reported in this paper added genetic composition of the dominant tree species to the higher levels of biodiversity already being addressed. The overall objective was to assess the impact of

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three regeneration methods (group selection, shelterwood, and clearcut) on the genetic composition of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) stands when followed by either natural or artificial regeneration. In particular, we used isozyme genetic markers (allozymes) to address three questions: (1) To what degree does partial harvesting affect genetic diversity of overstory trees? (2) To what extent does natural regeneration reflect genetic diversity in stands prior to harvesting? (3) To what extent does genetic diversity in artificial regeneration compare to that in stands prior to harvesting and to natural regeneration? Changes in genetic composition under silviculture regimes employing natural regeneration are of particular interest because if little or no change occurs, such regimes could be used in stands designated as *in situ* gene conservation reserves (Ledig 1986, Wilson 1990).

Because allozymes are relatively inexpensive to assay, are readily interpretable, and provide genetic information at the level of individual genes, they have had wide application in genetic studies of forest trees (Adams et al. 1992b). A major disadvantage of allozymes, however, is that they are weakly associated, at best, with variation in quantitative traits, many of which (e.g., stem growth, bud phenology) have important adaptive significance (El-Kassaby 1982, Lewontin 1984, Bush and Smouse 1992). Allozyme variants (alleles) that are rare in populations may have deleterious effects on the growth of individuals carrying these alleles (Bongarten et al. 1985, Strauss and Libby 1987, Bush and Smouse 1992). Occasionally allele-frequencies at individual allozyme loci (chromosome positions) are associated with patterns of environmental variation suggesting adaptive significance of alleles at these, or at closely linked, loci (Grant and Mitton 1977, Bergmann 1978). In most cases, however, allozyme frequencies are unassociated with environment, appearing neutral to the effects of selection (Muona 1990, Millar and Libby 1991, Savolainen and Kärkkäinen 1992). Thus, allozymes are most useful for assessing changes in genetic composition of populations due to evolutionary forces other than selection, such as changes due to reduction in population size (bottlenecks), migration of genes from other populations, and mating between relatives (inbreeding).

Bottlenecks lead to reduced levels of genetic diversity, but the losses in any one generation will be small and probably not meaningful, unless population size is drastically reduced (say to less than 20 or so interbreeding individuals; Falconer and Mackay 1996). Thus, harvesting, per se, is likely to have little effect on levels of allozyme diversity among residual adults in group selection or shelterwood methods. Poor flowering or seed production, however, could greatly limit the effective number of parents contributing to the next generation, resulting in significantly reduced genetic diversity in offspring, both in natural regeneration and in seed stocks collected for artificial reforestation. Reproduction in poor flowering years could also result in increased inbreeding, particularly self-fertilization, because the distance between flowering individuals is increased (Adams and Birkes 1991, Mitton 1992). On the other hand, gene dispersal by pollen and seeds is great in forest trees, such that individuals may mate and disperse seed over wide distances, keeping population sizes effectively large (Adams 1992, Ellstrand 1992). Previous reports on genetic effects of alternative silvicultural systems in Douglas-fir (Neale 1985) and other conifers (Savolainen and Kärkkäinen 1992) led us to expect that we would observe few, if any, negative impacts (e.g., reduced genetic diversity, increased inbreeding) in this study. Nevertheless, given the paucity of actual data, and concerns expressed in the professional literature regarding potential negative genetic impacts of forest management (e.g., Society of American Foresters 1991), we felt that a further test of this expectation was necessary.

Materials and Methods

Study Sites

The study was carried out on the College of Forestry Research Forests located in the Willamette Valley near Corvallis, Oregon. Distances between the three replicates (blocks) ranged from 3.6 to 6.5 km. Each block was subdivided into stands of at least 8 ha which were subjected to one of the treatments: clearcutting, group selection and shelterwood methods, or left uncut (control). The controls and all stands prior to harvesting were dominated by Douglas-fir (100–200 trees/ha) with overstory trees approximately 130+ yr in age and 30–60 m tall. Harvesting was done over three winters, from 1989–1990 to 1991–1992. In the group selection method, all trees were removed in 0.20 ha clearcut patches scattered throughout the stand, with about one-third of the total stand harvested. In the shelterwood method, 15–30 of the largest trees per hectare were left, distributed relatively evenly over the entire area. Leave trees were chosen to be wind-firm; about one-half were rough with large limbs suitable for nest sites and other wildlife use; the remainder were particularly valuable for timber productivity. With the exception of the few scattered individuals left (and later topped) for wildlife habitat, all trees were removed in the clearcut treatment. The harvested areas were replanted (usually the winter and spring immediately following harvest) with a total of seven Douglas-fir seedling stocks allocated haphazardly to treatments and blocks. The seven stocks originated from two seed zones overlapping the boundaries of the forest, including wild-stand (commercial) seed collections in two elevation bands (0–152 m, 152–305 m) of seed zone 262 and one elevational band (0–152 m) of zone 252 (Western Tree Seed Council 1966), and were raised in a total of three different bare root nurseries.

Sampling

One stand of each treatment type (control, group selection, shelterwood, and clearcut) was chosen for sampling in each replicate block. In all stands, a rectangular sampling plot averaging 6.5 ha (range 5.2–9.3 ha) was laid out, and in all plots with overstory trees (i.e., all except clearcuts), twigs containing dormant buds were collected in winter 1992–1993 from 120 mature trees located systematically on a grid covering the entire plot. In total, 1080 (3 treatments × 3 replicates × 120 trees) overstory trees were sampled. Dormant buds were also collected the same winter from 120

seedlings of each of the seven stocks used in planting the harvested areas. Our intent was to sample buds from seedlings resulting from natural regeneration in all harvested plots. Natural regeneration, however, was poor in all group selection plots and in all but one of the clearcuts (Ketchum 1995). Thus, dormant buds were collected from natural seedlings (120/plot) in only the three shelterwood replicates and in one clearcut, which was immediately north of one of the shelterwoods. The adjacent shelterwood was probably the primary source of seed for this clearcut. Collections were done over two winters (1995–1996), again using a grid system so that seedlings were sampled throughout the plots. Great care was taken to ensure that the natural seedlings sampled were from seed crops in years after harvesting. Allozyme analyses were performed on the bud tissues according to procedures described by Adams et al. (1990). In total, 12 enzyme systems (ACO, PGM, PGI, SDH, GDH, GOT, G-6PD, F-EST, 6-PGD, IDH, DIA and MDH) and 17 loci were assayed.

Data Analyses

Most of the calculations were done using the BIOSYS-1 computer program (Swofford and Selander 1989). To test the significance of allele-frequency differences between population samples (e.g., between controls and overstory of partially harvested stands, controls and artificial regeneration), contingency χ^2 statistics were calculated. Because contingency χ^2 tests are sensitive to very small allele-frequency differences, we chose a probability level of 0.01 for testing the null hypothesis of no difference between populations. The degree of allele-frequency differentiation between pairs of populations was quantified by estimating Nei's (1987) genetic distance, d (unbiased for small sample size).

Gene diversity within each population was described by estimating three parameters: number of alleles per locus (A), the percentage of polymorphic loci (P) (i.e., loci with two or more alleles), and expected heterozygosity (H_e). H_e measures the probability that two alleles sampled at random from two individuals in the same population are different, and is estimated as

$$1 - \sum p_i^2,$$

where p_i is the frequency of the ith allele at a locus. A and H_e were calculated for each locus separately and then averaged over all 17 loci. To evaluate the extent to which inbreeding may have occurred in each population, we estimated the fixation index (F_{is}). When there is no inbreeding, $F_{is} = 0$ in offspring, but with inbreeding, $0 < F_{is} \leq 1$. Because estimates of F_{is} are very sensitive to error when a single allele predominates in a population (Brown 1979), we estimated F_{is} only for loci where the most common allele had a frequency less than 0.95. Population estimates were then calculated by averaging over individual loci. Differences between treatments in gene diversity and F_{is} estimates were evaluated using t-tests (Steele and Torrie 1960). For all comparisons of overstory populations, the tests were based on paired observations within replications. When comparing overstory (adult) versus offspring populations, or natural versus artificial seedlings, t-tests were calculated from unpaired observations of each population type. Because of the relatively low precision of detecting differences in gene diversity and F_{is}, we used a 0.10 significance level for t-tests.

Results and Discussion

Genetic Composition of Control Stands

Consistent with earlier reports for coastal Douglas-fir (Shaw and Allard 1982, Neale 1985, Moran and Adams 1989), the untreated stands in this study showed considerable variation at allozyme loci. All but one locus (*Gdh*) was polymorphic, with up to four alleles detected over the three control populations (mean 3.18 alleles/locus). Allele frequencies at five loci were significantly ($P < 0.01$) heterogeneous among control stands, but the largest allele-frequency difference between any two populations at polymorphic loci averaged only 0.05 (range 0.008–0.164). Furthermore, estimated genetic distances between populations were very small (mean $d = 0.0033$, Table 1), on par with observed differences between similarly distanced natural stands of Douglas-fir in southwest Oregon (Moran and Adams 1989). Genetic diversity within individual control populations was consistently high across the three replicates, with mean estimated P = 90.2%, A = 2.86 and H_e = 0.197 (Figure 1). In addition, estimated fixation indices were consistently small (Figure 1), and a t-test showed that the mean F_{is} = 0.007 was not significantly ($P < 0.10$) different from zero. Thus, overstory trees contained few, if any, inbreds.

Effects of Partial Harvesting on Genetic Composition of Overstory Trees

Residual overstory trees in the group and shelterwood treatments differed significantly in allele frequencies from the control stands in the same replicates at an average of only two loci (range 0-4). In addition, genetic distances between residual overstories and controls were very small, with no tendency for shelterwood stands to be more differentiated than group stands (Table 1). Genetic distances between treated and control stands were no greater than between control replicates, indicating differences between treated and controls are more a reflection of minor allele-frequency differentiation between locations, than the effects of harvesting, per se.

There is no evidence that genetic diversity in the overstory of group stands was less than in the controls, but harvesting the smaller trees in shelterwood stands resulted in slightly, but significantly, fewer alleles per locus (2.76 in shelterwoods versus 2.86 in controls, Figure 1). Alleles not found in the shelterwood stands were rare in controls (mean frequency = 0.015, range 0.004–0.04). If rare alleles have deleterious effects on the growth of their carriers, culling smaller trees may remove some of these deleterious alleles from the population. Estimates of P and H_e were also smaller in shelterwood stands than in controls, but these differences were not significant (Figure 1).

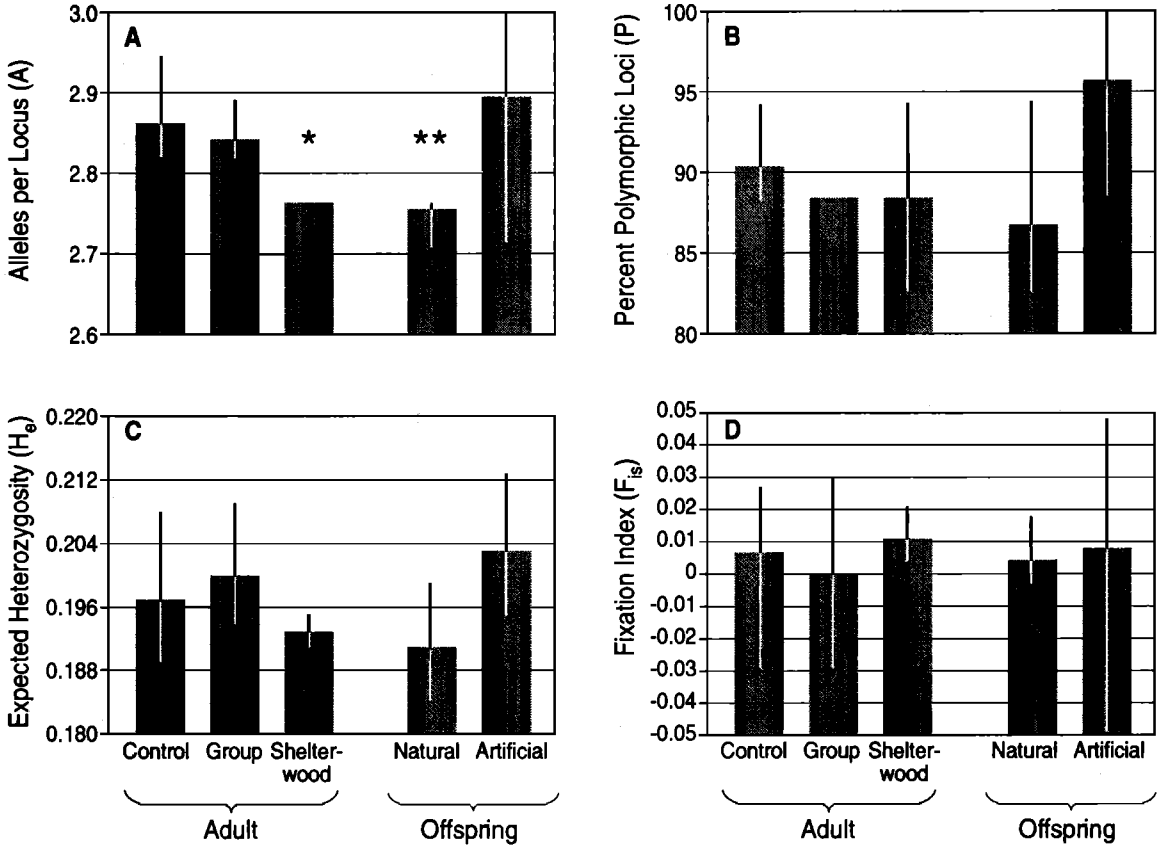

Figure 1. Mean estimates of gene diversity parameters and fixation index for three adult (Control, Group selection, Shelterwood) and two offspring (Natural and Artificial) population types of coastal Douglas-fir growing in the same vicinity. Brackets with each bar give the range over replicates (3 for each adult population type, 4 for natural offspring, and 7 for artificial offspring). Based on 17 allozyme loci for gene diversity statistics and 9–11 loci for fixation index (n = 120 for each population replicate). * and ** mean significantly different from Control at $P < 0.10$ and $P < 0.05$, respectively.

Genetic Composition of Natural Regeneration

Allele frequencies in each of the four naturally regenerated seedling populations were compared to the control stand in the same block. Differences were significant at an average of 3.25 loci (range 2-5), but mean d (0.0028; Table 1) was less than observed among control replicates, suggesting again that the differences were due more to stand location than the effects of natural regeneration after harvesting. This hypothesis is supported by comparing each naturally regenerated population with its immediate shelterwood overstory (or adjacent shelterwood in the case of the clearcut) (Table 1). In these comparisons, only one locus, on average, showed significant allele-frequency differentiation (range 0–2), and mean d was 0.0005.

All gene diversity statistics for natural regeneration were smaller than in the controls, but of similar magnitude to the overstory trees in the shelterwood stands (Figure 1). Thus, the net loss of rare alleles caused by harvesting in the shelterwoods was not replenished by migration of pollen or seeds from nearby stands. Immigration of rare alleles,

Table 1. Estimated mean genetic distances (unbiased, Nei 1987) between A. adult populations, and B. adult and offspring (seedling) populations.[a]

				B[c]	Adults	
A[b]	Control	Group	Shelterwood	Offspring	Control	Shelterwood
Control	**0.0033**	**0.0020**	**0.0020**	Natural	**0.0028**	**0.0005**
	(0.002–0.004)	(0.001–0.004)	(0.000–0.004)		(0.001–0.005)	(0.000–0.002)
Group		**0.0013**	**0.0010**	Artificial	**0.0020**	—
		(0.001–0.002)	(0.001–0.001)		(0.000–0.004)	
Shelterwood			**0.0023**			
			(0.001–0.003)			

[a] Ranges over pairwise combinations are in parentheses.
[b] On the diagonal, genetic distances are between replications of the same population type (three comparisons of each). On the off-diagonal, genetic distances are between different population types within each replication (three comparisons of each).
[c] Offspring populations resulting from natural regeneration (4 total) are compared to the Control and Shelterwood adult populations in the same replication. Each of the 7 artificial regeneration populations are compared to each of the 3 adult Controls (21 total comparisons).

however, would be difficult to detect if the proportion of migrants was not high.

Estimated fixation indices were low (Figure 1) and not significantly different from zero in natural regeneration. Assuming that the proportion of viable seeds produced by selfing is roughly equivalent to that estimated for Douglas-fir shelterwoods in southwest Oregon (0.05; Neale and Adams 1985), the fixation index at the seed stage is expected to be around 0.025 (Shaw and Allard 1982), which is six times greater than the average observed in naturally regenerated seedlings. Thus, either the proportion of seed due to selfing (or other close inbreeding) was very low in our shelterwoods or most inbreds were lost prior to our sampling because of poor germination and survival of inbred individuals (Sorensen and Miles 1982).

Impacts of Artificial Regeneration on Genetic Composition

Despite the wide variation in seed sources and nursery locations, the average genetic distance between pairs of seedling populations used for artificial reforestation (21 total comparisons) was only 0.0006, and never exceeded 0.002. The variation in gene diversity statistics among seedling lots was somewhat greater than observed among replicates in the other population types (Figure 1), but this is expected given that there was more than twice the number of replicates than in any other group. On average, pairwise comparisons of allele frequencies between artificial seedling lots and control stands (21 total) were significant at only 2 loci (range 0–5). The mean genetic distance was 0.002, which is no greater than observed between control stands and natural regeneration (Table 1).

All three measures of gene diversity were significantly greater ($P < 0.05$) in artificial regeneration than in naturally regenerated seedlings (Figure 1). Gene diversity statistics in the artificial stocks were also greater than in the control stands, but only significantly so, for P (Figure 1). It is likely that the artificial stocks included seeds from multiple stands, and thus, more gene diversity was sampled in these collections than would be typically found in individual populations. There is no evidence that F_{is} is greater in artificial regeneration than in naturally regenerated seedlings (Figure 1). In addition, as in the other population types in this study, mean estimated F_{is} was not significantly different from zero.

Conclusions

Consistent with our expectations, harvesting followed by natural regeneration appears to have had little impact on the allozyme composition of Douglas-fir stands in this study. High individual-tree heterozygosity, high outcrossing, and strong pollen and seed dispersal within and between stands are all factors preventing the loss of genetic diversity when the number of parents within populations is reduced due to harvesting or other factors (Neale 1985, Neale and Adams 1985, Adams et al. 1992a, Hamrick et al. 1992). The observed loss of rare alleles after harvesting in the shelterwood regime is not consistent with findings in an earlier Douglas-fir study in southwest Oregon, where similar culling rates in two shelterwood stands did not reduce the number of alleles per locus (Neale 1985). The southwest Oregon stands, however, were much older (200+ yr), such that trees with deleterious alleles may already have been removed from the populations through natural competition.

Presumably, loss of deleterious alleles, either by natural or artificial selection, enhances the mean fitness of a population Nevertheless, the importance of currently deleterious alleles for adaptation to future environments is unknown. Therefore, although silviculture regimes involving partial harvesting and natural regeneration seem to be compatible with gene conservation, it is advisable to choose parents without regard to growth or stem form (i.e., apply no artificial selection) in areas designated as gene conservation reserves, in order to maximize the number of alleles in offspring. This practice results in no loss of harvest yields if all overstory trees are removed from the site after adequate regeneration has been achieved.

Even in the shelterwoods, enough trees were left in the study plots that 120 parent trees could be sampled for allozyme analysis. This is the same number of parents assayed in the control stands; thus, no changes in allele numbers due to sampling alone were expected. If the number of residual overstory trees was greatly reduced, however, the resulting bottleneck would be expected to result in fewer alleles, with rare alleles the most susceptible to loss. For example, if only 20 random parents are left on each plot (i.e., about three trees/ha, on average), only one-third of alleles occurring at a frequency of 0.01 before harvest are expected to be present among the residual trees, while 98% of alleles occurring at 0.10 before harvest would still be found. Nevertheless, if only a small proportion of the residual adults actually mate or produce seed, even alleles relatively frequent prior to harvest are in danger of being lost in the next generation.

Thus, the success of natural regeneration can greatly affect gene conservation. There was little natural regeneration in the group openings of this study because little mineral soil was exposed for a seed bed. Logs were skidded from the openings to adjoining skid trails, and there was little equipment traffic in the openings. In the shelterwood and clearcut methods, soil disturbance was more widespread because larger volumes of logs were removed and traffic was more widespread. Natural regeneration was plentiful in the shelterwoods and in the one clearcut adjacent to the shelterwood where seedfall was particularly abundant (Ketchum 1995). Regeneration, however, was poor in the remaining two clearcuts, despite mineral-soil seedbeds, probably because of the lack of seed. In gene conservation reserves where plentiful natural regeneration is a goal, it is important to plan harvests and/or subsequent site preparation to coincide with good seed years.

The potential for inadvertently altering the genetic constitution of populations is greater when artificial regeneration is employed. Levels of genetic diversity in artificial stock are primarily a function of the number of trees from which seed is collected; when this number is very small, genetic diversity may be severely limited (Adams 1981, Kitzmiller 1990, Adams et al. 1992a). Differential germination, emergence,

and competition among different genotypes or families, and practices such as seed sizing and seedling culling, could further alter, and perhaps lower, genetic variation in seedling stocks (Campbell and Sorensen 1984, El-Kassaby 1992, El-Kassaby and Thomson 1996). In addition, the relatively benign environments in nursery beds or greenhouses may favor the survival of inbreds that otherwise would fare poorly in harsher natural forest conditions (Adams et al. 1992a, Muona et al. 1988). We stress that none of these potentially negative outcomes of artificial regeneration were observed in the seedling lots sampled in this study. In fact, allozyme variation was greater in artificial seedlings than in natural regeneration, and no evidence of inbreeding was found. Although the numbers of parents contributing seed to the artificial seedling stocks in this study are unknown, attempts are made by most forestry organizations in the Pacific Northwest to include large numbers (i.e., at least 15–20) of widely scattered trees in wild-stand seed collections (Kitzmiller 1990, Adams et al. 1992a). In addition, it is recommended that seed orchards contain at least 50 unrelated clones or families. By all appearances, such numbers are more than adequate to ensure high levels of genetic diversity in planting stock (Adams 1981, Kitzmiller 1990, El-Kassaby and Ritland 1996b).

We said in the introduction that allozymes generally provide little information on the effects of selection in altering genetic composition of populations, and that quantitative traits are much more useful for this purpose. The question remains, therefore, to what extent does selection of parent trees for growth or stem form alter genetic variation in these traits or in closely associated characteristics, especially those influencing adaptability? There is an opportunity to improve the mean value of selected traits in offspring when positive selection is employed in choosing parents, and gains are expected to be particularly promising in intensive tree improvement programs involving seed orchards and progeny testing (Zobel and Talbert 1984). Genetic gains in growth rate or stem form (and changes in associated characters) when positive selection is used in choosing individuals for natural regeneration or for collecting wild seed for artificial regeneration, however, are not likely to be very large, because of the weak inheritance of these traits and because pollen sources are not controlled (Zobel and Talbert 1984, Adams et al. 1992a). Furthermore, when quantitative traits are weakly inherited, selection has a very small effect on reducing genetic variation of these traits in any single generation (Chapter 11, Falconer and Mackay 1996). Thus, parent tree selection in wild stands followed by seed production in place is expected to have little or no impact on the adaptive potential of offspring. Of course, in cases where selection favors disease resistance or other strongly inherited adaptive characteristics, parent-tree selection could go a long way towards enhancing the adaptability of naturally regenerated offspring (Zobel and Talbert 1984).

Because allozyme differentiation between populations within geographic regions is typically small and poorly, if at all, associated with differentiation in adaptive traits (Merkle and Adams 1987, Moran and Adams 1989, El-Kassaby and Ritland 1996a), the small genetic distances observed in this study between artificial seedling stocks and control stands is not evidence that the seedling stocks are well adapted to the planting sites. Adaptation, however, should be reasonably assured as long as suitable seed transfer guidelines, such as seed zones (Randall 1996, Western Tree Seed Council 1966), or other seed movement rules (e.g., Campbell 1986), are used in matching seed sources to planting sites, as was done in this study. Broad genetic diversity further enhances the adaptability of seedling stocks by helping to ensure the presence of at least some genotypes in each plantation that are adapted even to extreme conditions that might be experienced in the life of a stand.

The overstory trees in the shelterwood stands of this study will not be removed as soon as regeneration is established, which is usually done in the shelterwood method. Instead, the overstory trees will be left to form an irregular shelterwood (Smith 1986), in order to provide nest sites and stand structure for future wildlife habitat. Similarly, groups of trees from the original cohort will be retained in the group selection treatment. Other studies in these stands have shown that both bird and small mammal diversity is enhanced by the older trees in both of these stand types (Chambers 1996). Thus, the silviculture regimes in these stands not only foster the maintenance of genetic diversity within the dominant tree species, but also species biodiversity.

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