

Genetic Considerations in Propagating Diverse Tree Species¹

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Nursery managers are growing a wider diversity of plant species for ecological purposes. These activities may affect the adaptation, diversity, and performance of lots. Managers can exercise control by selecting and working with lots at different genetic levels: species, seed zone, seed stand, parent phenotype, and even individual tree genotype. Judicious mixing of genetic sources is a powerful tool to enhance the genetic diversity and evolutionary potential of plantations. Selection for specific juvenile traits in the uniform nursery environment can be very effective. The genetics of non-commercial tree species can be developed to a working level quickly using biochemical markers, common gardens, and knowledge from the major conifers. In general, the other species have more complex genetic structures and are more specialized in their site and cultural requirements.

INTRODUCTION

The primary focus of forest managers is conservation of the basic natural resources: soil, water, air, and the rich, natural biota. This list includes genetic resources, because genetic variation among and within species is the basis for all biological diversity, including its composition, structure, and function. Biodiversity issues have by nature a very strong genetic component. Thus, genetics will have an enlarged role in ecosystem management, extending from major tree species to all plant and animal species and from stand level consideration to the landscape level.

Propagating forest trees has broad and lofty importance, because these dominant species have a "keystone" role in sustaining the overall health and productivity of forest ecosystems. This paper will address forest tree species only. Since little is known about the genetics and propagation of hardwoods and non-commercial conifers, I will draw upon the knowledge of the major west coast conifers to provide insight for propagation of other trees.

What genetic factors should be considered in propagating trees? This question relates to: why trees are planted, what is known about the genetic systems of trees, and how management practices affect genetic diversity and desirable characteristics of trees.

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WHY PLANT TREES?

Trees are planted when natural regeneration is likely to fail to meet land-use objectives. Planting bypasses two major problems of natural forests. First, the most vulnerable seedling stage is passed in the nursery where conditions highly favor survival and growth. Second, mature trees do not have to produce sprouts or flowers and seed in place for stand renewal. Thus, planted trees do not have to possess all of the same characteristics as wild seedlings or wild mature trees. Nature selects for reproductive success, but planting avoids the need for reproduction in the wild. Furthermore, planting allows control over several genetic levels: species, seed zone, seed stand, parent phenotype, and tree genotype.

Based on land-use objectives, forests may be grouped into four types: natural reserves, multiple-use, production, and research. Genetic considerations and the appropriate level of control will vary accordingly.

Natural reserves are set-asides that are nearly always regenerated by natural seeding and sprouting. An exception would be when an unnatural disturbance such as an introduced disease threatens the natural ecology of the area. For example, if Port-orford-cedar root disease or white pine blister rust posed a major threat, native parents could be screened artificially to find resistant progeny to plant. In this case, the level of control might extend down to the genotypic level (via genetic testing). Otherwise, control would normally reside at the seed zone or at the seed stand level to achieve the primary goal of species adaptation.

Multiple-use forests are a mixture of natural and planted stands. Emphasis is on species adaptation and diversity. Species and seed zone control would most often be used. The PSW Region's Base Level seed collections would be well-suited to most applications.

Production forests are primarily plantations that are dedicated to commercial production of wood for construction, furniture, paper, fuel, chemicals, and other useful products. These forests may produce three or more times as much wood per acre as multiple-use forests, because intensive selection and breeding programs provide the planting stock and cultural practices improve environmental conditions.

"Research" forests are special plantations that support production forestry and provide gene conservation banks for natural forests. Examples are: gene banks, grafted clone banks, genetic test plantations, and seed orchards. These are carefully designed and managed to track the genetic identity and performance of every tree.

The impact of plantations on local gene pools depends on the relative amounts and distribution of planted trees and the genetic differences between planted and natural stands. Also, the integration of these small, artificial populations across the natural landscape should be viewed in a broad context to consider their breeding linkages with local gene pools (stands).

GENETIC SYSTEMS

Nature of the Hereditary Material

The hereditary material (DNA) "programs" how plants function and respond to their environment and what they look like. DNA is capable of self-replication, and it is passed on from parent to offspring. Genes are not lost or "used up" when the parents die as long as they leave offspring. This transfer provides continuity or constance of genetic material representing a historical "library" of information across generations and from cell to cell in the same individual. The genetic material of tree species is highly organized in both structure (e.g. nucleotide, gene, chromosome, ploidy level) and process (e.g. meiosis, mitosis). Also, it is highly diverse all the way from the smallest functional unit, the gene, through the individual and population, to the species levels.

In addition to the mechanism of hereditary constance, genetic changes occur through natural evolutionary processes. Evolutionary forces cause changes in gene frequencies of populations. These genetic changes provide diversity and flexibility which allows species to adapt to changing environments. Genetic diversity arises from mutation, is distributed by gene flow (via pollen and seed dispersal), is reorganized by recombination, and is shaped

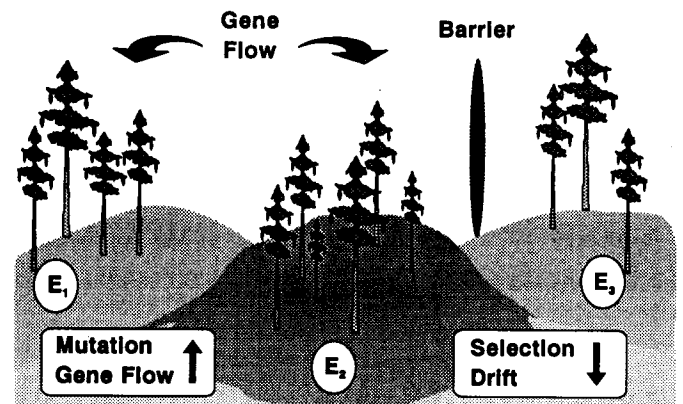


Figure 1.--Effect of evolutionary forces on genetic diversity.

and reduced by natural selection and genetic drift. The simultaneous action of these forces plus the mating pattern (degree of outcrossing and assortive mating) of the species results in the distribution of genetic diversity across the range of a species (fig. 1).

Natural Forces of Genetic Change

Individual trees along with their pollen and seeds are "containers" that carry the gene pool of a species. The target of natural selection is the individual phenotype. Natural selection prevents "poorly-adapted" phenotypes from reproducing. Consequently, they will not pass their genes on, while "favored" phenotypes will pass their genes on to their offspring. Thus, selection causes populations to adapt to their local environment. Trees growing in different environments are subject to different selection factors. Such tree populations will become genetically distinct as long as selection is strong relative to the counteracting forces: mutation, gene flow, and random genetic drift.

Mutations accumulate at very slow rates, are mostly recessive and deleterious, occur at random, and are the ultimate source of genetic variation. Genetic drift occurs in relatively small (< 100 interbreeding trees) and isolated populations as a result of random fluctuations in gene frequency due to sampling from few parents. Such populations undergo inbreeding depression and lose genetic variation. Genetic drift is most likely in areas with regular stand-replacing fires or other catastrophic events.

Gene flow is the migration of genes (via pollen and seeds) from one population into another causing a change in gene frequency in the receiving population. It is the major cohesive force that "connects" subpopulations of a species. Gene flow counteracts the diversifying effects of selection and drift. If a reproductive barrier exists between environment (E3) and environments (E1,E2) as depicted in figure 1, E3 will become

genetically distinct from E1 and E2.

Mating patterns affect how genes are distributed among and within individuals in a population. Trees in the same stands that are flowering at the same time are most likely to intermate. Inbreeding occurs at low levels in continuous natural stands. It will occur at higher levels in small, isolated stands. Inbreeding occurs in stands composed of sexually-mature relatives or trees with both male and female strobili (monoecious). Inbreeding reduces the genetic diversity within individuals (heterozygosity), while out-crossing increases it.

The breeding systems of major conifers are characterized by high out-crossing rates, wind-pollination, monoecious flowers, and inbreeding depression. This, along with wide seed dispersal, long-lived, and large size promotes great genetic mobility and high genetic diversity within individuals and within populations.

In contrast, angiosperms often have mixed mating systems, animal-pollination, sprout after disturbance, and are shorter-lived. This promotes limited gene dispersal, more inbreeding, and less diversity within individuals and within populations and more diversity among populations than gymnosperms.

These genetic mechanisms operate in each species to produce a pattern of genetic variation. Knowledge of how much variation occurs within individuals, among individuals in the same population (stand), and among populations (stands) is an important first step to managing forest ecosystems.

PATTERNS OF NATURAL GENETIC VARIATION AND SEED ZONES

How do these genetic mechanisms relate to our work with forest trees? In the major conifers, the genetic composition of natural populations change along environmental gradients. Commonly, trees adapt to temperature and moisture gradients which are associated with geographic variables such as elevation, latitude, or distance from the ocean. Trees become generally adapted to local environments. They are not perfectly adapted because the environment is constantly changing and other forces of gene flow, recombination, and genetic drift may counteract the effects of selection.

General adaptation of trees along major geographic gradients is the primary reason for seed zoning. Seed zones are a management tool for protecting these natural adaptation patterns by controlling seed (gene) transfers. The purpose of seed zones is to partition the region into adaptively-similar zones within which native trees can be freely moved without problems of maladaptation.

The genetic gradients commonly follow paths from milder and more productive sites to harsher and less productive environments. Parent trees from the mild, productive sites produce offspring that: are faster growing, grow for a longer period of time during the year, and in some situations may be less resistant to drought and cold stress than those from the harsher environments (Adams and others 1992). This gradient within a seed zone presents a challenge. Managers must decide what seed trees to select and whether to keep seed separate or mix seeds from mild and harsh sites together, and if so, in what proportions.

Trees adapted to harsh sites may allocate proportionally more of their limited energy to defense and reproduction, and less energy to vegetative growth. Even so, improvement in productivity is possible even while maintaining adaptation by selecting the more productive genotypes out of each local population. This is exactly how selection is done in most tree improvement programs.

Genetic Diversity Levels

Common gardens and isozyme chemical markers are used to measure genetic variation in trees. Isozyme analysis provides direct comparisons of genetic diversity for certain gene loci among many different taxonomic groups of plants and animals. Although isozyme analysis underestimates the actual diversity, it does provide a relative comparison. Plants are much more variable than animals, and trees are more variable than other plants. Gymnosperms are more diverse than angiosperms.

Heterozygosity is the most common measure of genetic diversity. Heterozygosity is the presence of two different forms (copies) of the same gene within an individual. The average heterozygosity for all plant species is 15 percent for isozyme loci (Hamrick and Godt, 1989). Values for several conifers in California (M.T. Conkle, pers. comm. 1992 USDA Forest Service, PSW Station, Albany, CA) are listed below:

Douglas-fir	= 28 %
Jeffrey pine	= 25 %
White fir	= 24 %
Sugar pine	= 22 %
Ponderosa pine	= 21 %
Incense-cedar	= 21 %
Monterey cypress	= 18%
Monterey pine	= 16 %
Bishop pine	= 15 %
Knobcone pine	= 14 %
Digger pine	= 14 %
Coulter pine	= 13 %
Torrey pine	= 0 %

The top six major conifers above have highest total genetic diversity, and about 90 percent of it occurs within-stands (average for plant species is 78 percent). Hardwood species

have diversity levels similar to the non-commercial conifers listed above, and they have more genetic differences among-populations than the major conifers, perhaps twice as much. Stand and seed zone levels are more important with these other species because of their well-defined population (stand) structure.

Millar and Libby (1991) provide genetic architecture of some rare and widespread conifer species: 1) little or no genetic variation within species: red pine,

western redcedar;

2) no variation within-populations, little variation among-populations: Torrey pine;

3) little variation within- and among-populations: Santa Lucia fir;

4) high variation within-populations, little variation among-populations: western white pine, incense-cedar; 5)

high variation within- and among-populations:

ponderosa pine, white fir, Douglas-fir.

EFFECTS OF MANAGEMENT

Management can affect three major attributes of genetic resources: diversity, adaptation, and productivity. Diversity is necessary for adaptation to occur, and trees must be adapted to their environment in order to be productive. Our job as forest managers is to maintain or enhance genetic diversity and its adaptations, concurrently with providing useful forest products and values. It is important that managers know when they are making genetic decisions and what the implications of those decisions are. For example, a genetic decision is made when a tree is cut, and again when a tree is planted. When genes are added or lost from a population, gene frequencies change and so does diversity.

As genetic principles are used in ecosystem management, special attention must be given to the reproductive phase, because genes get distributed and recombined. Natural processes cause genes to be "moved around" and discriminated for or against. Similarly, when foresters collect and use seed for regeneration, species and parent trees are selected for reproduction, genes are sampled from a population, and then genes are moved around by planting. These cultural activities have implications relative to selection, gene flow, and drift. The method of sampling the genes, g collecting seeds or cuttings, affects the diversity of the seedlot. Sampling from a few parents or stands could impose a "bottleneck", and could lead to genetic drift. The planting location affects health and productivity of the plantation. Planting may contribute to gene flow if the planted trees have different gene frequencies than the natives. This incorporation of new genetic diversity may be advantageous to the tree population if the environment is changing rapidly. If the environment is relatively stable, the new genes may contribute little to improving adaptation of the population.

A common concern and misconception is that conifer plantations, even when composed of a mixture of species, are genetically uniform and therefore more susceptible to ill health. The genetic systems of commercial conifers generate enormous genetic diversity through recombination. For example, if only two parents are mated, and if these parents are heterozygous at only 10 gene loci, they can produce 59,049 different genotypes (3^{10}) at those 10 loci, and over 98 percent of these progeny are heterozygous at one or more loci. For 20 loci, over 3.5 billion different genotypes (3^{20}) are possible (Adams and others 1992). If this amount of diversity arises from only two parents and 20 loci, how much arises from a seed orchard of 50 parents and several thousand loci? Also, since each tree is highly heterozygous and is from a different stand, all but rare alleles will be represented. Would plantations from seed orchards represent a genetic monoculture? Obviously not, however, many people including some biological science professionals are not aware of these genetic principles.

Seed Collection

Certain basic information is essential for all plant materials collected and used in artificial regeneration. This knowledge includes: origin (seed zone and local area), genetic base (sampling design, numbers of stands, parents, etc.), phenotypic characteristics of parent trees (selection criteria), and the appropriate adaptive zones of use. Other information may be appropriate for certain species and uses. For example, collection for gene bank preservation of threatened, endangered, or sensitive (TES) species may also require data on demographics and other ecological data.

The USFS PSW Region uses their Base Level Tree Improvement Program to guide tree seed collections (Kitzmilller 1976, 1990) as a practical approach to integrating gene conservation with reforestation. It was designed to maintain or enhance adaptation, genetic diversity, health, and productivity of managed plantations. Key elements are:

- 1) use native species and local (zone of origin) seed;
- 2) sample several (preferably 20 or more) stands and trees
- 3) select mildly for desirable stand and tree characteristics;
- 4) convert the resulting plantations to seed production areas.

It is important to view seed collection in part as a gene sampling process, because the genetic diversity in planted stock is confined by the level of diversity in the seed collected. Once seed is collected, the maximum potential diversity is fixed for that seedlot. Each seed is genetically-different. Subsequent nursery and reforestation activities are likely to reduce genetic diversity due to: 1) random mortality which eliminates some genotypes, and 2) selection factors that cause non-random mortality of genotypes which changes gene frequencies of the seedlot. Therefore, selection in the nursery should be closely scrutinized. Managing for high seedlot diversity will allow natural selection a chance to

operate more effectively at the outplanting sites (Campbell and Sorenson 1984, Kitzmiller 1990).

Nursery and Reforestation Practices

Nursery managers should consider the genetic effects from each practice in the sequence of nursery activities. For example, what affect will immature seed or short- or longperiods of seed stratification have on the genetic diversity of the lot? What effect will they have on adaptation and performance at the planting site? Evaluating each nursery and reforestation practice for expected effects on diversity, adaptation, and desired performance traits could lead to substantial improvement in some practices. Also, genetic diversity should be evaluated at two levels: among- and within-individuals.

Any nursery practice that tends to produce seedlings that cannot survive after outplanting reduces genotypic (among individuals) diversity. Improper sowing- and lifting-dates are good examples. Sowing too late often results in seedlings that are small and susceptible to cold and drought. Lifting too late results in reduced root growth capacity of seedlings. The nursery environment also influences the growth rhythm of seedlings. If the nursery environment is greatly different from the outplanting environment, selection factors in the nursery may result in seedlings that are poorly-adapted to the outplanting site (Campbell and Sorenson, 1984).

An example of nursery selection is heavy grading of seed and seedlings to produce very large stock. This not only eliminates homozygous inbreds, but may also eliminate whole families from mixed lots, and thereby reduce genotypic diversity (Silen and Osterhaus 1979). However, if heterozygotes are superior in size, selection may actually increase the average heterozygosity (gene diversity within individuals), even though the genotypic mixture is reduced through removal of homozygotes. For example, if the large seed and seedlings are primarily large because they are more heterozygous, then saving only the large seeds would remove many of the homozygous seeds and thus increase diversity for those genes that affect seed size. Since there is evidence for heterozygotes having some size advantage in Scots pine seed (Szmidt 1987), and since small seed and seedlings may die anyway, a moderate culling level may be appropriate to eliminate inbreds and other more homozygous and inferior stock. Also, some nursery stresses may actually favor heterozygotes because of their greater range of tolerance. If this were the norm, selection in the nursery would result in seedlings that could tolerate a wide range of outplanting environments.

A potentially dysgenic nursery practice is saving the smallest, least vigorous portion of a normal seedlot for transplanting or holding-over another year. These "runts" are likely inbreds and genetically inferior with a low initial

genetic base and an even lower final base. In contrast, if the entire seedlot is small due to environmental rather than genetic problems in the nursery, then transplanting or holding-over may be justified.

Nursery practices that maximize tree percent (percentage of seeds sown that develop into plantable seedlings) and seedling survival will preserve the maximum potential genetic diversity (Campbell and Sorenson 1984). Nurseries and species with large nursery factors (high mortality) undergo greatest genetic change. Certain species like red fir and small seeds of giant sequoia, cedars, and cypresses have high losses in bareroot nurseries. Sugar pine and white fir have disease problems that may have genetic consequences (Kitzmiller 1990). As new species are incorporated into nursery production, entirely new cultural practices may have to be adopted for the new species and seed sources.

Site preparation and planting practices should similarly be evaluated. Seedling storage and handling factors combined with site conditions can cause losses when seedling requirements are not met. In addition, low survival rates for true firs due to drought and gophers and the devastation of sugar pine by blister rust and Port-orford-cedar by *Phytophthora* root disease necessitates special effort towards broadening diversity of seedlots of these species.

Mixing: Species, Seedlots, and Genotypes

Nursery managers have the option of keeping seedlots separate by clone, family, or stand at different stages in the nursery to tailor the activities to best meet plant requirements and maximize seedling percent. Then, at some desired stage in the process, reforestation managers can synthesize the desired mixture of species, seedlots, and genotypes for outplanting. This powerful tool of mixing and "building" different kinds of genetic stock has many applications.

A common practice at the USFS Placerville Nursery seed bank is to mix seedlots collected in different years from the same zone, providing the seed has similar germination values or other performance qualities known from past experience with the individual seedlots. This practice widens the parental base in the combined lot.

A more radical approach is to mix lots from different zones. This may be desirable if the environment at the planting site has been greatly changed. For example, to reforest a severely burned, hot, south-facing slope, one strategy might involve mixing a local zone seedlot with a lot from the next lower elevation band or from the adjacent zone to the south. As a general rule, a local lot should comprise at least 50 percent of the mixture (Campbell and Sugano 1987).

Rapid global climate change is a potential threat to biodiversity. Rapid climate change could trigger a series of events leading to major reductions in the natural range of

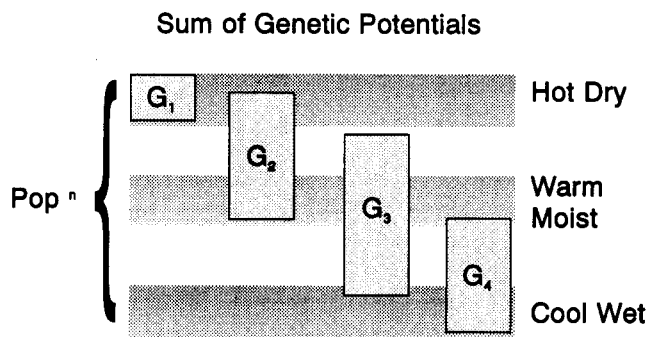


Figure 2.--Adaptive potentials for hypothetical genotypes

many species. Increases in pest outbreaks, wildfires, drought, reduced seed production, and problems in natural regeneration are predicted. If these changes occur, planting and gene banks will assume great importance. If the adaptive ranges of species and seedlots is identified through testing over a wide range of sites, then appropriate mixtures could be developed for planting almost any site (fig. 2). In addition, deployment of nursery stock with greater diversity and planting at higher densities should help to maintain or restore species in trouble (Ledig and Kitzmiller 1992).

In the Pacific Southwest Region, between 10 and 20 percent of the families tested in evaluation plantations have shown wide adaptability across environments at age 10 years for Douglas-fir and ponderosa and sugar pines (Kitzmiller and Stover 1992). A mixture of genotypes having these broad and different genetic potentials or tolerances would provide a wide range of adaptability and protection in case of rapid climate change. Illustrated in figure 2 are hypothetical genotypes with different adaptive ranges. G2 and G3 are broadly adapted and when mixed together extend the adaptive range even further.

SPECIAL CONSIDERATIONS FOR NON-COMMERCIAL SPECIES

In general, concerns about maintaining genetic diversity and adaptation will become more important, not less, as we work more with the "non-commercial" conifers and with hardwood species. The reason is these species have less total genetic diversity at the species and individual tree levels, and they apportion more of the diversity they have among-populations. They often occur in small populations, have more inbreeding, and more restricted recombination. These factors facilitate the evolution of locally-adapted gene complexes (Levin 1978). Therefore, these species are likely to be more specifically adapted to local environments, require smaller seed zones, and may have more specific

cultural requirements to maintain their diversity. If inbreeding is more frequent in these species, nursery culling levels and stand thinning regimes may have to be adjusted to eliminate undesirable inbreds without adversely affecting genetic diversity.

Greater use of the clonal option may be expected with these species, because many of them are capable of vegetative reproduction, have more specific site adaptations, and have less individual tree genetic diversity. Clonal propagation may be better-suited for species with unique genotypes having special adaptations to specific environments than propagation from seed. In such cases, recombination of genes through the sexual process may produce too many undesirable offspring. Examples might include: McNab cypress, a rare species, growing on serpentine soil, and certain Pacific yews with very high taxol concentrations, or black oaks having exceptionally high mast production.

SELECTION FOR SPECIFIC, DESIRABLE TRAITS

Nurseries provide a great opportunity to screen stock for desirable juvenile traits, because the environment is quite uniform and many factors can be controlled. Nursery stock can be subjected to different controlled environments to evaluate the response of species and learn about their growth requirements and ecological amplitude. Container nurseries are especially useful for genetic selection, because each seed can have the same volume and mixture of soil medium, uniform water, nutrients, light, photoperiod, etc. Traits such as timing and rate of growth, tree form, resistance to pests, and wood quality have several genes controlling their expression and they can be changed by selection.

Some juvenile traits can be improved in normal nursery operations by culling undesirable phenotypes during thinning, grading, or packing. For example, stem diameter, height, foliage color, branching habit, late season shoot activity, and number of dormant buds are traits related to health, vigor, and growth rhythm. Setting the appropriate culling level is very important, since it will affect the amount of improvement and the level of diversity in the stock. For example, if the culling level is set high to save only a few of the largest Douglas-firs, the mean size will increase relative to the unselected lot, and the variance will decrease. If the large size was achieved through growing longer into the fall, this selected stock could be uniformly less resistant to early frost. So, when selecting for one trait, it is important to know what other trait(s) are genetically correlated, and how they will change indirectly.

Each resource area (recreation, timber, watershed, wildlife, fishery) may emphasize different desirable traits. For example, trees planted for shelter and aesthetics in camp grounds may require large, vigorous, locally-adapted stock. Trees planted for erosion control may require large root

systems with high root growth capacity. Trees planted along streams for shade to improve fish habitat may require trees with vigorous wide-growing branches. Pacific yew has both tree- and shrub-form types that may have different wildlife values and this can be identified in the nursery.

Other heritable traits may require special genetic trials in the nursery to identify and propagate seedlots, families, or genotypes with desirable characteristics. Some examples are screening for: high root growth capacity and its timing, resistance to WPBR or Phytothera root rot, formation of desirable mycorrhizae, tolerance to herbicides, competitive capacity, and response to fertilization.

CONDUCTING PROPAGATION STUDIES

Managing new species for new objectives may necessitate conducting nursery studies to improve our understanding and methods of propagating each species and seedlot. Propagators can improve results by considering genetic factors in nursery studies.

Knowledge of the source and parentage of genetic stock (clones, half- and full-sib families, etc.) can be useful for controlling the amount of unexplained variability in experiments dealing with propagation methods and cultural treatments.

Knowledge of genetic variation patterns among and within seedlots should be considered when conducting studies of cultural practices. Where little is known about such patterns, creative managers will capture the opportunity to observe differences between seedlots of the same species and cultural treatment, when these are grown together.

Since nursery environments are relatively uniform, several seedlots can be compared in the same environment (common garden), which reveals genetic differences. Adaptive traits such as growth rate and timing of growth initiation and cessation can be studied efficiently in the nursery. These observations can be made during the normal process of growing stock for outplanting, or during planned common garden studies.

Nurseries provide the opportunity to monitor the effects of management on genetic resources. For example, seed or tissue samples can be subjected to isozyme analysis to determine baseline genetic patterns. Sampling after treatments would then allow comparison of genetic diversity before and after treatment. Such efforts could rapidly advance our knowledge of non-traditional species.

CONCLUSIONS

Several decades of research in forest genetics and experience from tree improvement programs with

commercial conifers and hardwoods have provided a tremendous base from which to draw for propagating new, diverse species. The operational mechanism for handling these species is in place via established nursery, reforestation, and tree improvement programs. The special requirements for growing each species must be learned and applied. Genetic variation patterns can be determined rather quickly from common garden and isozyme studies. This knowledge will guide collection and use zones for nursery stock, and provide a baseline for sound gene conservation.

Management of genetic diversity in the nursery will be difficult with the non-commercial species until more is known about their cultural requirements, inbreeding depression levels, and genetic variability. Conservative "learn as you go" approaches seem appropriate. Nurseries provide an excellent environment for controlled studies as well as operational observations that will aid learning. Nursery managers can expect to work with smaller seed zones, numerous small lots, and diverse, special cultural methods. Clonal propagation will be employed to a greater extent to multiply unique genotypes and to facilitate reproduction of sprouting species.

REFERENCES

- Adams, W.T., R.K. Campbell, and J.H. Kitzmiller. 1991. Genetic considerations in reforestation. In Reforestation Practices in Southwest Oregon and Northern California. Ed. by S.D. Hobbs, S.D. Tesch, P.W. Owston, R.E. Stewart, J.C. Tappeiner II, and G.E. Wells. p. 284-309.
- Campbell, R.K., and F.C. Sorensen. 1984. Genetic implications of nursery practices. In Forest Nursery Manual: Production of Bareroot Seedlings. Ed. Duryea, M.L. and T.D. Landis. Martinus Nijhoff/Dr. W. Junk. Dordrecht. p. 183-191.
- Campbell, R.K., and A.I. Sugano. 1987. Seed zones and breeding zones for sugar pine in southwest Oregon. USDA Forest Service, Portland, OR. Research Paper PNW-RP-383. 18 p.
- Hamrick, J.L., and M.J.W. Godt. 1989. Allozyme diversity in plant species. In Plant Population Genetics. Breeding, and Genetic Resources. Ed. A.H.D. Brown, M.T. Clegg, A.L. Kahler, and B.S. Weir. Sinauer Associates, Sunderland, Mass. p. 43-63.
- Kitzmiller, J.H. 1976. Master plan for tree improvement in the California Region, USDA Forest Service, San Francisco, CA. 96 p.
- Kitzmiller, J.H. 1990. Managing for genetic diversity in a tree improvement program. *For. Ecol. Manage.*, 35:131-149.
- Kitzmiller, J.H., and P. Stover. In Press. Growth of sugar pine progenies in California plantations. In Symposium

Proceedings Sugar Pine: status, values, and roles in ecosystems. Mar.30-Apr.1, 1992. Univ. of California, Davis, CA. 24 p.

Ledig, F.T., and J.H. Kitzmiller.1992. Genetic strategies for reforestation in the face of global climate change. For. Ecol. Manage. 50:153-169.

Levin, D.A. 1978. Some genetic consequences of being a plant. In Ecological Genetics: The Interface. Ed. P. Brussard, p. 189-912. Springer-Verlag, New York.

Millar, C.I., and W.J. Libby. 1991. Strategies for conserving clinal, ecotypic, and disjunct population diversity in widespread species. In Genetics and Conservation of Rare Plants. Ed. D.A. Falk, and K.E. Holsinger. Oxford University Press, New York, Oxford. pp. 149-170.

Silen, R.R., and C. Osterhaus. 1979. Reduction of genetic base by sizing of bulked Douglas-fir seedlots. Tree Planters' Notes, 30(1): 24-30.

Szmidt, A.E. 1987. Genetic composition of seed orchard crops. For. Ecol. and Manage., 19: 227-232.