

Maintaining Biodiversity in

# *Forest Ecosystems*

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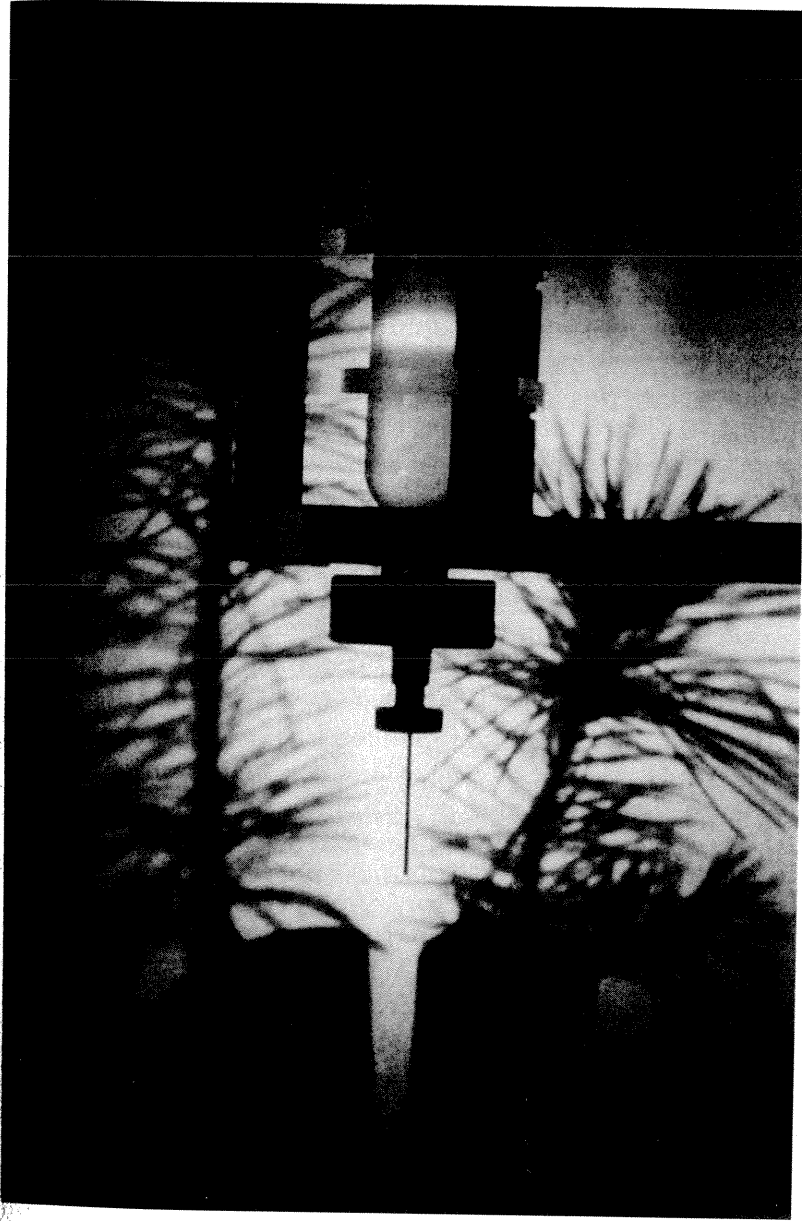
CONSTANCE I. MILLAR

Genetic diversity rarely makes headline news. Whereas species extinctions, loss of old-growth forests, and catastrophic forest fires are readily grasped public issues, genetic diversity is often perceived as arcane and academic. Yet genes are the fundamental unit of biodiversity, the raw material for evolution, and the ultimate source of all variation among plants and animals on earth (Dobzhansky 1970, Soulé and Wilcox 1980). Why then have they escaped central attention in conservation? Although genes are pervasive, controlling individual fates and determining offspring destinies, they are minuscule molecules, unyielding to meaningful direct observation even through a microscope: their direct structures and functions are essentially invisible. Over the decades we have learned about their existence and significance indirectly by studying the effects that genes have on individuals, populations, and species. Because genes are passed among generations in mathematically predictable ways, we have developed a towering theoretical understanding of the way genes ought to work in nature (Wright 1978). Increasingly we are able to penetrate the nature of genes directly, through biochemical and molecular analysis (Figure 14.1; Nei 1987, Neale and Harry 1994). We are beginning, dimly, to perceive empirical connections between changes in gene pool diversity and species declines, changes in forest health, and loss of ecosystem productivity. This cumulative knowledge teaches us that attention to genetic diversity will pay off in achieving the goals of forest conservation.

With an emphasis on North American conifers, this chapter presents general approaches to conserving forest gene pools and provides examples illustrating how genetic management can be integrated within other conservation efforts.

### Genes as the foundation of biodiversity

Genetic diversity may be mostly hidden to the naked eye, but when illuminated through genetic study, its variation and structure are complex.



**Fig. 14.1.** DNA, the basic molecule of inheritance, extracted from sugar pine (*Pinus lambertiana*) and visible with ethidium-bromide staining. (From Conkle 1986.) (P. Hodgskiss photo)

Genetic differences exist at many levels. Most obvious are the myriad differences that exist among individuals. Because of the way groups of individuals tend to become isolated and interbreed, genetic differences evolve that distinguish groups of individuals at many scales: for instance, among populations, among ecotypes or local strains, among geographic races or subspecies, and among species, genera, taxonomic families, and so on. Whereas mutation and recombination (primarily events occurring at cell division and in sexual reproduction) are the main sources of new genetic diversity among individuals, ecological effects, such as natural selection, gene flow, and genetic drift are the major architects of genetic patterns among groups. These forces are described in more detail below.

Although genetic differences distinguish species and higher taxonomic levels, genetic diversity usually refers to the genetic variation that exists within species (the *gene pool*). From the conservation standpoint, efforts to maintain biodiversity ideally blend seamlessly from the gene to the species to community levels. In practice, these are often separated and too often uncoordinated. In this chapter, I focus on genetic diversity within species, yet try to show the connection of genetic conservation to other biodiversity management levels. Natural diversity of genes within and among populations, ecotypes, and subspecies, movements of genes between them, and changes in gene pool compositions over time are the focus of forest genetic conservation efforts.

#### INFLUENCES ON GENETIC DIVERSITY

Many forces influence the dynamics of composition and structure in gene pools. When these are natural forces and natural changes, we call the process evolution. Mutations, or mistakes in DNA replications, occur as changes to the structure of DNA. Mutations occur with low but consistent frequency, from about 1 in 1000 to 1 in 1 000 000 cell divisions. Ultimately mutations are the source of all new genetic variation in nature, both detrimental and beneficial. Once new alleles arise by mutation, they are assorted and distributed among individuals by recombination, which leads to the remarkable diversity among individuals that exists even within families.

How individuals mate strongly influences the fate of genetic variation, both within and among populations. For instance, regular inbreeding (which some species do) or mating among individuals within a local population, leads to individuals within populations being genetically similar, but isolated groups becoming different. By contrast, regularly outbreed-

ing species, especially those that have high variability in their genes (genes).

Natural selection acts on individuals that survive or die, pass on or not, survive and function or not, whose suite of genes is passed on, such as surviving and reproducing (Hartl, 1988). The reason for this is 'average' rather than 'selective' called genetic composition during sexual reproduction. Some populations are much more likely to survive (rare species) than others. Chance events as well as natural selection, however, that result in adaptations of individuals and groups. When gene flow is high (being geographical distance), natural selection, geographical races, and so on (Daly and Hartl, 1971), both the widest set of genes as the continuing process in environments.

Human actions and evolution (Stearns, 1991, Hedrick and Hartl, 1992) show novel effects on background genetic diversity.

In general, activities that change the direction of evolution. Some affect the rate of change, others are likely to have significant effects.

ing species, especially those like conifers whose genes travel far and wide, have high variation within populations, but the populations remain rather similar due to the mixing effects of gene flow (long-distance dispersal of genes).

Natural selection is, of course, the grand architect. Individuals either survive or die, pass on many offspring or few, based on their ability to survive and function in their particular local habitats. Those individuals whose suite of genetic characteristics provides them with advantages, such as surviving extreme weather, attracting mates, or avoiding predation, produce more offspring on average than those more unlucky (Hartl 1988). The reason that these genetically endowed individuals only win 'on average' rather than always is because of chance. Many chance events, collectively called genetic drift, occur within natural populations and affect genetic compositions, from the roll-of-the-dice probabilities of recombination during sexual reproduction to events such as wildfires randomly burning some populations and not others (Patton and Feder 1981). These are much more likely to have large effects in small populations (including rare species) than where population sizes are large (Hudson 1991). Chance events aside, the advantages accumulating over generations, however, that result from natural selection translate into tremendous adaptations of individuals to local environments. They also result in adaptations of groups of populations to regionally distinct environments. When gene flow among groups is diminished, for example by groups being geographically isolated (e.g., by mountain ranges, or just enough distance), natural selection over time leads to the evolution of ecotypes, geographic races, and subspecies (e.g., Clausen *et al.* 1940, Antonovics *et al.* 1971, Daly and Patton 1990). Genetic conservation seeks to maintain both the widest set of adaptations that have evolved within species as well as the continuing potential of populations to adapt to ever-changing new environments.

Human actions almost always have some consequence on gene pools and evolution (Stern and Roche 1974, Schonewald-Cox *et al.* 1983, Ledig 1991, Hedrick and Miller 1992, Baradat *et al.* 1995). They may mimic natural influences, exceed them in rate of change or strength of selection, or show novel effects. Some consequences are minor compared with background genetic changes; some far overwhelm the path of evolution.

In general, activities of greatest concern to management are those that change the direction and rate of natural selection and gene flow significantly. Some affect gene pools directly, others indirectly. Some activities are likely to have significant genetic effects. These include activities that:

- add or remove a significant number of individuals from natural populations (e.g., tree, grass, or forb planting, fish stocking, timber harvest, fishing and hunting);
- significantly change population sizes (especially decrease) of native species (e.g., livestock grazing, land clearing and habitat type conversions, biological control);
- eliminate populations, especially systematically from portions of a species range (e.g., by urban development, dam construction);
- move individuals among ecologically distinct locations (e.g., ecological restoration, fish stocking);
- significantly alter sex ratios, number of breeding individuals, reproductive capacity, fecundity, viability of individuals, or survival and mortality of certain age classes (e.g., grazing, timber harvest, fire suppression);
- introduce disease vectors or insect pests, especially those that are non-native (made worse by roads, trails and other access points into native populations);
- significantly increase the potential for hybridization over what would occur naturally (e.g., tree planting or introducing non-local germ-plasm);
- fragment populations such that gene flow is drastically reduced; conversely, alter population structure such that formerly isolated populations regularly interbreed (e.g., road and dam construction);
- disrupt or significantly alter meta-population structure and other geographic patterns and related processes (timber harvest, fish stocking, dam construction).

By and large we lack data on actual genetic effects of these activities and our predictions about their significance come from population-genetic theory (Ledig 1988, 1991, Hedrick and Miller 1992). In the few cases where we have data, we find that the actual genetic consequences depend on how each activity is conducted. With timber harvest, for example, the type of cutting and intensity, the phenotype and ages of trees cut and the season of harvest, may have different genetic effects. Where ecologically appropriate silvicultural procedures have been applied, no significant changes in genetic frequencies have been found (Savolainen and Karkkainen 1991). Similarly, studies have shown no significant changes in gene frequencies have occurred due to normal nursery and outplanting practices for forest trees (Campbell and Sorenson 1984, Kitzmiller 1990). In the case of air pollution's effect on genetic diversity, however, there is some evidence that human-caused atmospheric effects cause changes in allelic proportions within populations, although the ecological or evolutionary significance of these changes has not been easily interpreted (Hertel and Ewald 1995).

## Genetic conservation

Forest genetic diversity is a key component of the future condition of the forest and the health and vitality of the ecosystem. Although genetic diversity and restoration are other equally important goals advocated in conservation (Soulé 1981, 1970), maintaining genetic diversity for agriculture (O'Brien 1984). Key early work on breeding and population genetics. In these cases, many of these programs and provided early genetic-adaptation, inbreeding, and conservation that developed important foundations for genetic conservation.

## GOALS FOR BIODIVERSITY

Environmental conservation of species in many forms, disturbance, and changes such as impacts. In forest diversity and evolution, species retention. There is no significant variation, because of the forested lands. Species diversity with local appropriate actions for genetic conservation.

### Genetic conservation

Forest genetic conservation focuses on managing the current and future condition of genes in forest species for the purpose of influencing the health and adaptability of individuals, populations, and species. Although genetic conservation is usually associated with maintaining biodiversity and restoring ecosystems (the context of this book), there are other equally important goals. Maintenance of genetic diversity has been advocated in contexts of crop breeding and animal husbandry (Frankel and Soule 1981), experimental research (e.g., *Drosophila*, Dobzhansky 1970), maintaining indigenous cultivars and wild relatives of crop plants for agriculture (Oldfield 1984), and for medicinal (e.g., Pacific yew, *Taxus brevifolia*, for cancer drugs; Wheeler 1996) and horticultural uses (Oldfield 1984). Key early work in wildland genetic conservation was done to benefit breeding and production programs for commercial forest trees and fish. In these cases, maintenance of genetic diversity was paramount to success of these programs (e.g., for trees, Zobel 1977, Libby, 1973, Ledig 1988), and provided early insights into the importance of local origins and genetic-adaptation zones, maintenance of diversity, potential problems of inbreeding, and contamination from poorly adapted stocks. The information that developed in these breeding and production contexts provided an important foundation of knowledge, which has proved valuable for developing genetic conservation goals within biodiversity protection contexts.

#### GOALS FOR GENETIC CONSERVATION WITHIN A BIODIVERSITY CONTEXT

Environmental challenge comes to individuals and groups of native species in many forms. These range from 'expected' events, such as predation, disturbance, and succession (fire, disease), to chance events or long-term changes such as volcanic eruptions, climate change, or human impacts. In forest genetic conservation we attempt to maintain genetic diversity and evolutionary processes so that individuals and populations of native species retain their resiliences to changes in the short- and long-term. There is no single approach or one right way to practice genetic conservation, because there are so many different management objectives of forested lands. Specific applications require that genetic goals be integrated with local and regional management objectives to determine appropriate actions (Ingram 1996).

Genetic conservation optimally involves a combination of *ex situ* and *in*

situ practices. In *ex situ* conservation, germplasm (seeds, pollen, whole plants and animals, sperm, and other genetic propagules) is removed from native habitats and preserved in storage, such as refrigeration, dehydration, cryopreservation, or as whole plants in nursery plantations (Oldfield 1984, National Resource Council 1991, Millar 1993). Although these tissues prove useful for genetic analysis, the main purpose is to store genes in a safe environment and make them available as needed for reintroduction or augmentation of natural populations. For example, in the late 1980s, the rare Torrey pine (*Pinus torreyana*) was threatened by a bark beetle epidemic, which caused many drought-weakened trees to die. Germplasm was needed to restore the greatly diminished population. Seeds collected years earlier from a large number of healthy trees in the same population were used for restoration (Ledig 1991). Approaches to gene sampling and maintenance of genes *ex situ* have been designed to meet such conservation goals (Bonner 1990, Brown and Briggs 1991, Center for Plant Conservation 1991, Eriksson 1995).

A drawback to *ex situ* methods is that genes are preserved in a static condition with no opportunity for continuing adaptation to dynamic environments (Soule and Wilcox 1980, Oldfield 1984). The environments for reintroduction change (due to climate, pathogen or insect, or anthropogenic pressures) while the germplasm is in storage, causing samples to 'slip behind' evolutionarily. Further, potential losses to germplasm while in storage, such as seed or sperm death, reduce the value of the collections for restoration. Practical concerns that collections might be lost accidentally due to fire or technological breakdown cannot be underestimated. For instance, fires burned the seed storage facility not once but twice at the Centro de Genetica Forestal in Chapingo, Mexico, devastating irreplaceable germplasm collections and burning research labs and storage buildings. Despite the limitations and risks, however, storage of germplasm in various ways is a critical element in integrated gene conservation programs (Falk and Holsinger 1991).

Genetic conservation for maintenance of biodiversity is usually practiced through many *in situ* approaches, that is, where natural populations are managed to achieve genetic conservation goals (Ledig 1988, Holsinger and Gottlieb 1991, Adams et al. 1992, Baradat et al. 1995). This can range from establishing single-purpose genetic conservation areas to developing genetic management prescriptions for lands that are actively managed for other purposes, such as production forestry or recreation. *In situ* gene conservation comes into consideration in designing nature reserves (e.g., biosphere reserves, natural areas), protecting populations of rare or

endangered species, restoring or mitigating activities and animals (e.g., harvesting regulations after natural disturbances) follow emphasize *in situ* conservation.

#### MEASURING GENETIC DIVERSITY

Any decision to develop management plans implies there is a concern for genetic diversity, gene pools, and a desire to manage genetic effects. Because species vary in susceptibility to management actions such as fire, tree harvest, ecological changes, knowledge about the genetic diversity available or can be measured is important.

By and large, genetic variation is measured by an observer, and is effectively a summary of methods (see review by Baradat et al. 1995, Hunt 1995). The frequency of individuals in a population with different biological variants (e.g., specific alleles) represents genetic variation. If a population, however, the range of genetic and environmental influences on environmental variation will be large.

To detect heritable variation requires much more work. 'Controlled' experiments must be done subject to randomization, with treatments which they are raised kept uniform. Common-garden studies to compare plants are relatively straightforward in some cases to yield useful information, but takes many years, requiring controlled breeding. Further, although information about genetic variation about gene or genotype frequency is available.

Genetic diversity can also be measured at the population level, which involves determining

endangered species, restoring species, habitats, and communities, planning or mitigating activities that manipulate native populations of plants and animals (e.g., harvesting, grazing, fish stocking), or in restoring populations after natural disturbances such as flood and fire. Discussions that follow emphasize *in situ* conservation.

#### MEASURING GENETIC DIVERSITY

Any decision to develop genetic conservation or genetic management plans implies there is a known or suspected concern for impacts to gene pools, and a desire to protect species from assumed detrimental genetic effects. Because species vary widely in their genetic attributes and in susceptibility to management actions and situations (e.g., prescribed fire, tree harvest, ecological restoration), this decision presupposes that knowledge about the genetic structure of species and its potential vulnerability is available or can be measured or inferred.

By and large, genetic variation is hidden to the eye of the general observer, and is effectively revealed only through expensive and time-consuming methods (see reviews in Adams *et al.* 1992, Boyle and Boontawee 1995, Baradat *et al.* 1995, Hunter 1996). It is tempting to consider counting the frequency of individuals in a sample having readily observed morphological variants (e.g., specific flower or fur color) and assume this represents genetic variation. If counts are made on individuals in wild populations, however, the resulting frequencies combine both genetic and environmental influences, and only those few traits unaffected by environmental variation will yield genetic information.

To detect heritable variation in these traits (i.e., genetic diversity) requires much more work. 'Common garden' tests or captive rearing projects must be done subject to experimental controls (such as replication and randomization), with the age of individuals and the environment in which they are raised kept uniform among all individuals (Figure 14.2). Common-garden studies to determine genetically based variation in plants are relatively straight-forward but take many years (decades, in some cases) to yield useful information. Pedigree analysis in animals also takes many years, requiring several generations in captivity with controlled breeding. Further, although these tests reveal general and indirect information about genetic variance, they do not yield direct information about gene or genotype frequencies.

Genetic diversity can also be measured at the molecular and biochemical levels, which involves detecting variants in, for instance, DNA, RNA,



**Fig. 14.2.** Variation in height among equal-aged white fir (*Abies concolor*) plants growing in a common plantation in California, USA. Seedlings collected from throughout white fir's range in western North America were planted together, and over the years the differences that were observed reflect genetic differences both among individuals and among groups of individuals adapted to different parts of the species range. Seedlings from two populations shown here come from populations at 2380 m (left) and 975 m (right) in the Sierra Nevada (Libby et al. 1980). (C. I. Millar photo)

isoenzymes, terpenes, and flavonoids (Clegg 1990, Neale and Harry 1994). Some of these are under strong genetic control, allowing genetic diversity to be directly measured. For example, DNA and isozymes do not appear to be modified by the environment in which organisms are living, and samples from an organism of any age and any site can be taken directly from the field and reliably yield a genetic interpretation (i.e., a common-garden test or captive rearing is unnecessary) (Figure 14.3). Although they require sophisticated laboratory equipment and experienced geneticists for interpretation, these methods do give genetic information about specific genes, are relatively rapid, and can often be consistently applied across taxa.

Unfortunately the relationships among the various kinds of genetic data (morphological, biochemical, and molecular) are difficult to interpret (Asins and Carbonell 1987, Adams et al. 1992, Baradat et al. 1995). Different genetic traits (and different approaches to measuring them) regularly yield different patterns of genetic architecture. This is likely due to differing evolutionary and ecological influences on different genes. For

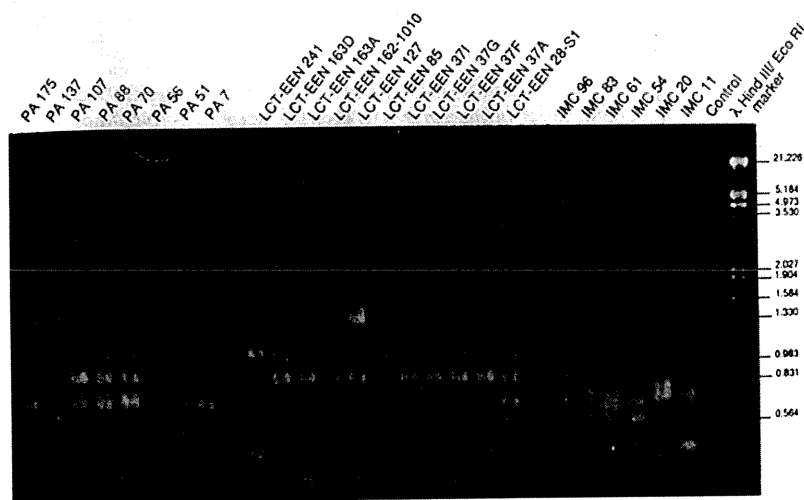


Fig. 14.3. Molecular (DNA) variation among 25 accessions of *Theobroma cacao* as determined by polymerase chain reaction (PCR) techniques, whereby differences in low-copy genes can be assessed. (From Russell et al. 1995.)

genetic conservation, genes actually or potentially affecting survival and fitness are most important. Some morphological or physiological traits (e.g., body or foliar weight, drought or frost resistance) seem to reflect adaptive variation, and thus reveal important information for conservation.

By contrast, the adaptive or ecological significance of many sequences of DNA or isoenzyme variants is unknown. For this reason, the latter are referred to as marker genes, meaning that, to a certain degree, they indicate (or mark) the nature of genes that may be of greater interest but are intractable to analysis. For many of these genes, although we may know the specific function of a gene we are measuring (e.g., an enzyme in the Krebs's Cycle), we have little idea of the physiological role played by the variants that we can measure. Variants in marker genes generally seem to have relatively neutral or minor adaptive values, and tend to reflect events in a species' evolutionary history, such as colonizing events, bottlenecks, and other chance effects rather than natural selection. Our ability to evaluate the condition and vulnerability of a gene pool is thus compromised by our inability to understand the specific physiological importance of the genetic variants we are most able to detect.

Because of these limitations, direct analyses have been undertaken for only a small number of taxa, especially those species of special interest,

such as commercial forest trees or rare and endangered species of high conservation visibility. Because measuring genetic diversity is expensive and time-consuming, indirect approaches have been sought as alternatives to direct analysis. In plants, such studies have indicated that weak but significant correlations exist between genetic architecture and some life-history traits. For instance, Hamrick and his associates (see Hamrick and Godt 1990, Hamrick 1983, Hamrick *et al.* 1979) reviewed statistical correlations in 400 plant species between isozyme diversity and features such as geographic range, longevity, seed-dispersal mechanisms, and mating system (Table 14.1). Although these correlations are useful at a general level, they provide little help when evaluating individual populations or species because of the many exceptions that exist (i.e., the weak regression among genetic diversity and life-history traits).

Clearly we are still learning about the relationships among the questions we ask, the genetic data we collect, and the adaptive, evolutionary, and conservation implications of these data. It is important for natural resource managers to be aware of the biases of different types of genetic variation, and the difficulties in interpreting their significance before assessing vulnerability or making management prescriptions. Significantly, information is lacking about current and historic genetic structure for most forest species (except a few of high significance), and will likely remain this way in the future. In regard to wildland taxa, we are in the position where genetic assessments, vulnerabilities, and priority setting must, for the time being, be based primarily on inferred consequences rather than on empirical measurements.

#### SETTING PRIORITIES FOR GENETIC CONSERVATION

Sometimes priorities are obvious. For instance, a species listed as endangered must be evaluated for genetic vulnerability prior to a project approval. Or, a set of species is targeted for ecological restoration, and genetic guidelines for these taxa at specific sites must be determined. In other cases, priorities are not targeted nor obvious. Rather, conservation planners are faced with the daunting challenge of how to address genetic conservation at a bioregional scale, where thousands of taxa (i.e., natural ecosystems filled with abundant native plants and animals, including invertebrates, fungi, etc.) must be considered. Allocating priorities among the conservation needs let alone genetic issues, and winnowing the list of many taxa and their genetic subunits (ecotypes, races, important populations) down to a manageable number, becomes an essential task.

Setting priorities for genetic management begins by identifying those

Table 14.1. Correlations of genetic variation with life history characteristics as an indirect approach to measuring genetic variation. Upper figure: within species; middle figure: among populations, and lower figure: within populations

| Correlates with genetic variation within plant species <sup>a</sup>                   |                               |                                |
|---------------------------------------------------------------------------------------|-------------------------------|--------------------------------|
| Trait <sup>b</sup>                                                                    | Highest level                 | Lowest level                   |
| Geographic range                                                                      | Widespread                    | Endemic                        |
| Life form                                                                             | Long-lived, woody perennials  | Short-lived perennials         |
| Breeding system                                                                       | Mixed mating, wind pollinated | Mixed maint, animal pollinated |
| Seed-dispersal mechanism                                                              | Attached                      | Explosive                      |
| Taxonomic status                                                                      | Gymnosperms                   | Dicots                         |
| Regional distribution                                                                 | Boreal-temperate              | Tropical or temperate          |
| Mode of reproduction                                                                  | Sexual                        | Sexual and asexual             |
| Successional status                                                                   | Late successional             | Mid successional               |
| Correlates with genetic variation among populations within plant species <sup>a</sup> |                               |                                |
| Trait <sup>b</sup>                                                                    | Highest level                 | Lowest level                   |
| Breeding system                                                                       | Self-pollinated               | Outcrossing, wind pollinated   |
| Life form                                                                             | Annuals                       | Long-lived, woody perennials   |
| Seed-dispersal mechanism                                                              | Gravity dispersed             | Gravity attached               |
| Successional status                                                                   | Early successional            | Late successional              |
| Taxonomic status                                                                      | Dicots                        | Gymnosperms                    |
| Regional distribution                                                                 | Temperate                     | Boreal-temperate               |
| Correlates with genetic variation within populations of plant species <sup>a</sup>    |                               |                                |
| Trait <sup>b</sup>                                                                    | Highest level                 | Lowest level                   |
| Breeding system                                                                       | Mixed mating, wind pollinated | Self-pollinated                |
| Geographic range                                                                      | Widespread                    | Endemic                        |
| Life form                                                                             | Long-lived, woody perennials  | All others                     |
| Taxonomic status                                                                      | Gymnosperms                   | Dicots                         |
| Seed-dispersal mechanisms                                                             | Attached                      | Explosive                      |
| Regional distribution                                                                 | Boreal-temperatures           | Temperate or tropical          |
| Successional status                                                                   | Late successional             | Early successional             |

## Notes:

<sup>a</sup> Derived from Hamrick and Godt 1990; Hamrick et al. 1979.

<sup>b</sup> Traits are arranged in approximate order of their strength of correlation with genetic variation. Thus, breeding systems and geographic range are very strongly correlated with genetic variation within populations, but successional status is only mildly related.

taxa which, by virtue of inherent or evolutionary condition, specific social value, or conservation vulnerability, deserve special attention (Millar and Libby 1991). In the former category, taxa would be targeted for specific genetic conservation evaluation if there are:

- evolutionarily distinct taxa, such as the sole representative of a genus or family in an area, marginal populations, populations at extremes of distribution limits or outside the primary range, unusual ecotypes, or populations containing individuals with unusual attributes (distinct morphologies);
- ecologically distinct situations, such as species or populations outside the expected ecological conditions, unusually diverse communities, extremely rare taxa, unusual hybrid populations.

Species may also be considered separately for genetic conservation when they have unique value to humans, such as:

- species or populations of actual or potential medicinal, horticultural, agricultural, or agronomic importance, including wild relatives of domesticated species;
- taxa of value to indigenous cultures;
- taxa of value to production industries, such as commercial forest trees and sport fisheries;
- taxa of value to wildland reclamation, such as grasses and soil stabilizers.

Sometimes genetic risk comes to a species by management context rather than inherent in its evolutionary or ecological conditions. Candidates for special attention include those populations and species with urgent conservation liabilities, specifically those species or populations whose existence is threatened or endangered by some human activities. In addition, there are many management situations or activities which, because of their potential to detrimentally affect gene pools, act as a red flag signaling a need to evaluate genetic effects and plan mitigative management. In general, these include actions that could lead to significant:

- changes in genetic diversity (losses are likely most risky, but increases in diversity can also lead to loss of adaptability);
- changes in populations sizes;
- changes in mating structure (e.g., reductions in population sizes can lead to increased inbreeding, which for many species is detrimental);
- disruption of natural patterns of gene exchange among populations (fragmentation on one hand, merging formerly isolated populations on the other);
- systematic losses of populations in particular habitat zones (e.g., at low elevations, on distinct soils, at extremes of range distribution);
- at the landscape and regional levels losses of ecotypic, racial, or subspecies diversity;

Genetic diversity

- gene contamination, native, local
- intraspecific
- not occur naturally

Management plans include actions to remove individual exotic species; additions; move individuals; change number behavior, or natural timber harvest; land development; and forest tree plantation and dam construction.

None of these practices have genetic effects. While effect, although this management is poorly thought out for these activities.

#### GENERAL GUIDELINES

Given the goal of maintaining natural levels of genetic diversity, the term adaptability, the flow, natural selection at the species level. For species as high risk, specific conservation plans for the species and the context profile of the population about its genetic structure and ecological conditions and challenges, and unique circumstances. One approach is outlined. In situations where specific management has been developed to aid in

- gene contamination, that is, non-local genes being incorporated into native, local populations;
- intraspecific or interspecific hybridization and introgression that would not occur naturally.

Management practices or land uses that could lead to these effects include actions noted earlier that significantly add individuals to, or remove individuals of native species from, natural populations; introduce exotic species; add individuals of native species adjacent to natural populations; move individuals from place to place; and activities that significantly change number of breeding individuals, demography, reproductive behavior, or natural mortality. Specific examples of practices include:

timber harvest; tree, shrub, or grass breeding; wildlife habitat improvement; land development; fire suppression, prescribed fire, ecological restoration and reclamation; fish planting and other wildlife introductions; forest tree planting; livestock grazing; forest health control; road and dam construction.

None of these practices or methods in and of itself leads to detrimental genetic effects. When applied prudently, many may have no significant effect, although this depends on the species targeted. However, if management is poorly thought out, or if genetic effects are ignored during planning for these activities, undesired consequences are more likely.

#### GENERAL GENETIC CONSERVATION GUIDELINES

Given the goal of maintaining genetic diversity for short- and long-term adaptability, the primary objective for genetic conservation is to maintain natural levels of genetic diversity and genetic processes (gene flow, natural selection, etc.) at the individual, population, race, and species level. For species of concern or management situations identified as high risk, specific attention may be needed. Developing genetic conservation plans for these situations requires an approach tailored to the species and the context. The potential for risk depends on the genetic profile of the populations, including the amount of information known about its genetic structure and function, its general reproductive fitness and ecological conditions relative to other native taxa, nature of environmental challenges, and specific details of the proposed action. Because of unique circumstances in these cases, management takes different forms. One approach is outlined below for sugar pine (*Pinus lambertiana*).

In situations where otherwise non-vulnerable taxa are at risk due to specific management or land-use circumstances, general guidelines have been developed to aid management (Box 14.1). These focus on the goals of

**BOX 14.1 General management guidelines for maintaining genetic diversity in situations where it may be threatened or at risk.**

I. When introducing individuals into natural habitats: (e.g., tree or grass planting, species reintroductions, biological control):

- Use germplasm from local donor populations that are geographically close and ecologically similar to those of the introduction site. Determining what is local depends on the species and context, but is related to the size of genetic neighborhoods, selection gradients, and historic events.
- Collect donor germplasm from local populations that are large, viable, uncontaminated (by non-local genotypes of the same species or interspecific hybridizations).
- Do not use germplasm of unknown origin.
- Maintain natural sex ratios and demographically appropriate age-class structure.
- Maintain high effective population sizes when collecting and propagating germplasm for reintroduction. Maximize the number and diversity of distinct founding genotypes, and maintain equal contributions from each donor individual through to the outplanting or introduction phase.
- Introduce healthy founders; avoid introducing disease with founders.
- Favor rapid early population growth.
- Choose introduction sites that match the optimal habitat requirements of the species (both physical and ecological, e.g., metapopulation structure).
- Avoid sites near (i.e., within significant gene flow distance of) populations of non-local genotypes or races of the same species capable of contaminating the introduced populations.
- Choose sites that are geographically large enough to accommodate large effective population sizes, unless metapopulation structure suggests otherwise.
- Minimize inbreeding (in species that naturally outbreed) by maintaining large population sizes, minimizing relatedness in founders (avoid using clones), equalizing sex ratios, maintaining representative age-classes, and maximizing diversity (within above standards).
- Promote reproduction and dispersal by favoring natural pollinators, seed dispersers, connectivity, disturbance regimes, and habitat availability (safe sites) for sexually reproducing species.
- For asexually reproducing species, maintain high numbers of clones, as they will determine the amount and distribution of resident genetic diversity.

**BOX 14.1 (cont.)**

II. When removing individuals from natural habitats (e.g., harvest, hunting and fire):

- Avoid significant reductions in census contributions from fluctuating populations.
- Avoid unnatural clumps of retention.
- Avoid increases in disturbance regimes (e.g., changes in genetic structure, patterns and disturbance regimes).
- Maintain or restore natural insect, pollinator relationships.

maintaining local genetic diversity within the range of management actions in disturbed areas (e.g., v. Rice 1994), rare and endangered species (e.g., Falk et al. 1996), and such 'best genetic management' specific genetic prescriptions.

Principles of ecosystem management should be focused on a few individual taxa targeted by management ideally across species. Because of the expense and sophistication of genetic information approach is needed for species and habitat conservation. This is because of evolutionary processes) o

## BOX 14.1 (cont.)

## II. When removing individuals from natural populations (e.g., timber harvest, hunting and fishing):

- Avoid significant reductions in effective population size (e.g., significant reductions in census number of individuals, unequal sex ratios, unequal contributions from parents, unequal numbers of offspring, drastically fluctuating population sizes).
- Avoid unnatural changes in mating systems (e.g., isolated seed trees or clumps of retention trees may promote inbreeding).
- Avoid increases in undesired intraspecific or interspecific hybridizations (e.g., changes in gene-flow corridors, fragmentation).
- Mimic natural structural patterns (spatial distributions, age-class distributions, patterns and intervals of mortality) and processes, especially disturbance regimes.
- Maintain or restore natural selection regimes (e.g., native pathogens and insects, pollinator relationships, nature fire regimes).

maintaining local germplasm and promoting natural genetic processes in the range of management situations met in wildlands, from minimally disturbed areas (e.g., wilderness) to multiple-use or manipulative situations. Sometimes these guidelines specifically emphasize genetic conservation within ecological restoration (Millar and Libby 1990, Knapp and Rice 1994), rare and endangered species conservation (Falk and Holsinger 1991, Falk et al. 1996), or production forestry (Kitzmilller 1990) contexts. Such 'best genetic management practices' help guide development of specific genetic prescriptions, as the examples later in the chapter illustrate.

Principles of ecosystem management remind us that our attention should be focused on a broader array of species and environments than individual taxa targeted as high risk. Genetic conservation under ecosystem management ideally brings the best genetic management to all native species. Because of the enormous number of species this entails, the lack of genetic information for all but a minute fraction of these, and the expense and sophistication needed to gain that information, a general approach is needed for these remaining species. Under many circumstances, genetic diversity may be adequately maintained by focusing on species and habitat conservation, without further modification for genetic concerns. This is because natural genetic structure and function (i.e., evolutionary processes) occur when populations are functioning with

minimum human disturbance and in generally natural habitats. Thus, in many cases, species and ecosystem conservation serve as adequate surrogates for genetic conservation for the vast multitude of forest species.

### Genetic conservation for specific management situations

As described above, emphasis in genetic conservation is on protecting single species identified as high risk, mitigating certain management practices, and providing general protection to all species in an ecosystem management context. Examples of some approaches are described below.

#### GENETIC CONSERVATION IN PRODUCTION FORESTRY

Production forestry is one situation where genetic conservation goals are combined with others in a multiple-use landscape. Several silvicultural practices in the early days of forestry were potentially detrimental to tree gene pools. High-grading, or harvesting trees with superior growth and form traits and leaving poor quality trees to regenerate stands, was regularly practiced, and likely led to declines in growth and productivity in subsequent generations. In the early decades of planting, the genetic source of seedling stock was not considered, which contributed to plantation failure or poor performance, tree mortality, and decline in forest productivity. The ill effects of such early activities, seen in the light of modern information on genecology in forest trees, catalyzed the establishment of genetic practices to maintain productivity. For example, in 1934 a forest seed law was passed in Germany that called for the destruction of certain low productivity stands and forbade seed collection from 50% of the stands. Similar problems accumulated in the United States and many older plantations still exist on public and private lands where trees of unknown, but offsite, source essentially downgrade the sites due to poor performance. By 1939, the U.S. Department of Agriculture established policy on seed transfers for federal forests with the goal of maintaining local germplasm and representative diversity.

The California region of the U.S. Forest Service provides a more specific example (Kitzmillar 1976, 1990). A long-term objective is to maintain and promote broad adaptability of tree populations of all species, but the primary focus is on conifer species of highest commercial value, namely ponderosa and sugar pines (*Pinus ponderosa*, *P. lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Calocedrus decurrens*), and white fir

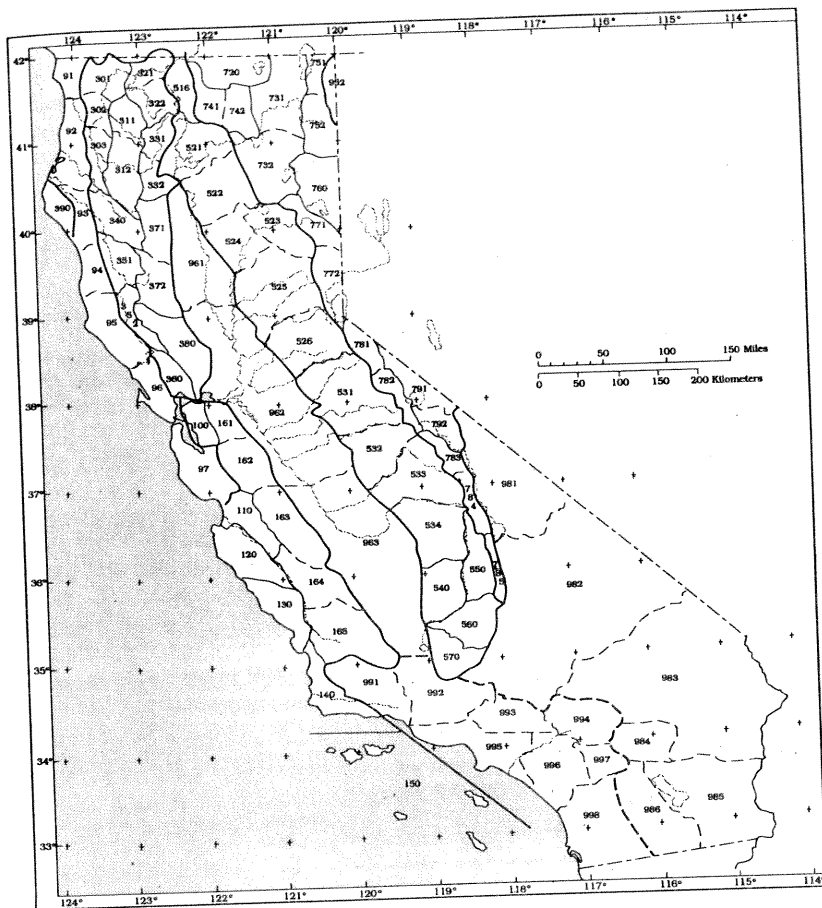


Fig. 14.4. Tree seed zones for forest genetic conservation in California. When harvested areas are planned for reforestation, seeds are collected within 150 m elevation of the planting site and within the same major zone. (From Buck et al. 1970, Kitzmiller 1990.)

(*Abies concolor*). The approach emphasizes in situ maintenance of genetic architecture by maintaining genetic standards (as described earlier in this chapter and Box 14.1) throughout harvest and planting regions. Scattered set-asides (reserve areas), designated for other conservation purposes, also contribute to maintaining population and ecotypic genetic diversity. Three elements compose the core of the program:

1. Tree seed zones. Forested ecosystems are divided into zones of general similarity in selection pressure (i.e., similarity in climate, forest types and species, soils, elevation, aspect) (Figures 14.2, 14.4). Movement of germplasm is restricted both within and among these zones. That is,

seed to be used for planting harvested sites is collected within the same zone and within the same 150 m elevation band as the planting site.

Zones for this map were first developed by a group of forest geneticists and foresters who based their estimates on general and anecdotal knowledge of land forms, elevation, and climatic zones (Buck *et al.* 1970). Little direct genetic information was available to inform those who drew the zone boundaries, although some elevation and latitudinal transect studies provided information. Subsequent analyses of genetic variation in these species (Figure 14.5), and ecological mapping of species and habitats, have shown that these early estimates of genecological provinces were surprisingly good.

2. Seed collection and nursery practices. Once locations for seed collecting are determined, seed is collected from a minimum of 20 forest stands per zone, with one to many trees per stand serving as seed parents (Kitzmillar 1976, 1990). Equal contributions of seeds from each donor are sought to create bulked (combined) seedlots from each stand. Similarly, attempts are made to keep numbers of seeds and seedlings per tree and per stand equal throughout the nursery phases to maintain effective population sizes and thus favor high genetic diversity. During seed collection and culling operations in the nursery, slight selection is exerted toward traits of interest to production forestry (e.g., rapid height growth, stem straightness, flat branch angles). This latter practice integrates the objective for gains in productivity, whereas the other recommendations assure the retention of adequate adaptive genetic diversity.
3. Harvest practices. The main genetic conservation goal for tree harvest is to avoid systematic alterations in the gene pool, or high-grading. Thus, when partial-harvest methods are used, a mix of tree phenotypes is left rather than the best trees repeatedly being harvested and poor phenotypes being left as parents of natural regenerants. Federal laws (National Forest Management Act 1976) require that harvested sites be planted with the same mix and abundance of native species that existed on the site prior to harvest.

No formal monitoring exists within the California program, although research studies have shown that genetic diversity is similar in production seedlots and the native stands where seeds were collected.

#### GENETIC CONSERVATION AREAS

Sometimes genetic conservation goals are the primary emphasis in land management. Where activities occur that might significantly affect genetic diversity (such as those described earlier in this chapter), parcels of land may be chosen to conserve representative genetic diversity. Such *genetic conservation areas* (GCAs) have the goal of conserving allelic,

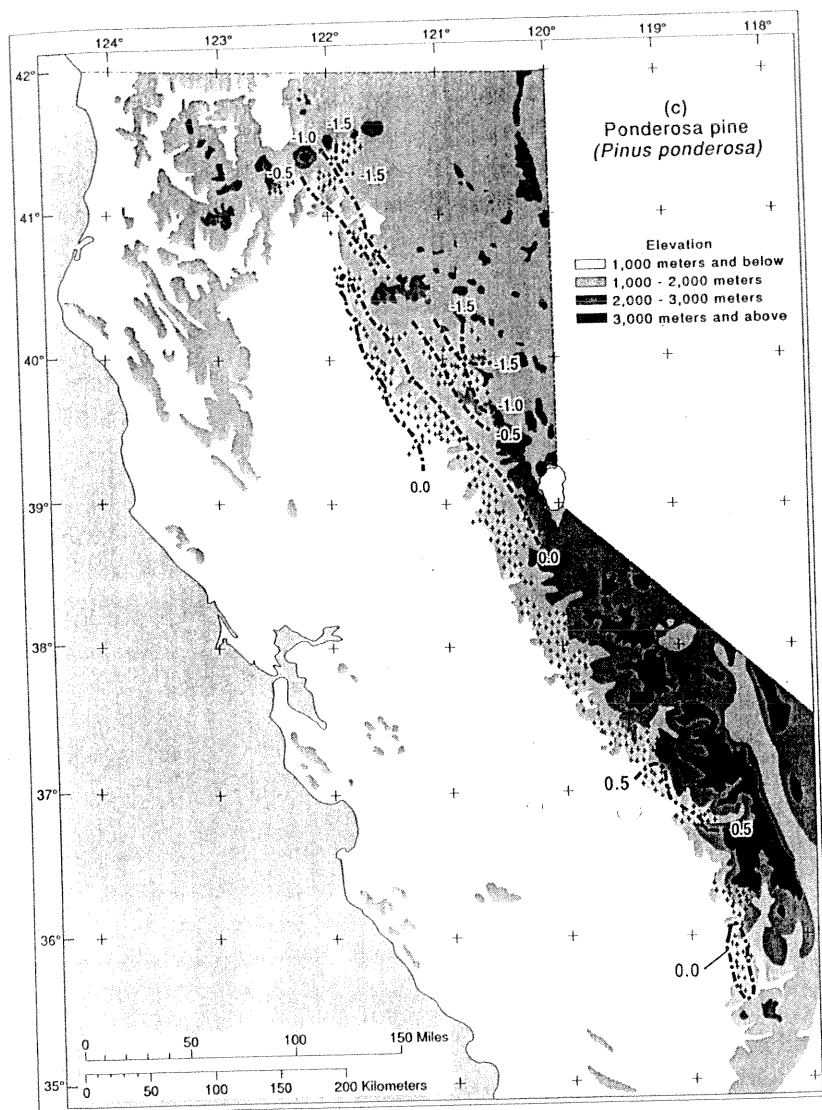


Fig. 14-5. Multi-locus contour maps of genetic variation among ponderosa pine (*Pinus ponderosa*) populations in the Sierra Nevada of California. Contours are derived from canonical trend surface analyses of many isozyme loci. Contour intervals are based on 0.50 standard deviation units from the analysis. Highly resolved genetic studies such as these provided refinement of original tree seed-zone boundaries. (From Westfall and Conkle 1992.)

genotypic, population, and species genetic variation through designation and genetic management of natural habitat distributed over the native range of target species. In addition to conserving *in situ* genetic diversity and genetic function, these GCAs can be used for genetic monitoring, serving as baselines against which manipulative treatments can be compared. Wilderness areas, national parks, nature reserves and natural areas, and other specific conservation areas (such as for rare or endangered species) often function effectively as GCAs. For rare species, there may be as few as one to several GCAs (Nabhan and Norman 1992), whereas for widespread species, networks of many GCAs are developed, ideally with individual units being carefully selected to represent important parts of genetic architecture (Wilson 1990, Arbez 1995). Whereas GCAs are usually managed similarly to strict nature reserves (with no manipulative activities allowed), they can be developed from areas where certain kinds of manipulation occur, as long as native species are maintained and land management priorities allow genetic standards to be maintained.

Although forest GCAs have long been discussed, they have been slow to be implemented. Several pilot networks are planned or developed for Norway spruce (*Picea abies*), cork oak (*Quercus suber*), and a few hardwood species in western Europe (Arbez 1995). In Malaysia, a network for hardwood species is being developed (Tsai and Yuan 1995). The Turkish government has established a national genetic conservation area program that provides a model for other countries (see case study below).

Determining the size and locations of individual units within GCA networks has been approached in several different ways. In the state of Washington, USA, over 100 GCAs (there called gene pool reserves) for Douglas-fir were designated in each 152 m elevation band within every seed zone. Reserves were selected to be 10 ha and containing at least 400 dominant or co-dominant trees (Wilson 1990). These reserves are withdrawn from timber harvest and managed strictly for genetic-conservation purposes.

In Europe, 31 countries, the European Community, and four international organizations approved six resolutions in 1990 pertinent to forest genetic conservation (Arbez 1995). One emphasized the development of *in situ* methods, including the development of pilot GCA programs and eventual comprehensive networks. For European silver fir (*Abies alba*) in France, available genetic information was used to select 20 populations considered to be representative of the important genetic variation in the region. The total area of this network covers about 200 ha, less than 1% of the species distribution in France. Each stand is about 10–15 ha, ensuring

at least 600 tree from gene conta with the general constrain wood

In California, in the Sierra Nev genetic informa Libby 1991). The species of the Si Douglas-fir, and are subject to tim vation practices forestry above. T back-up and insu also as baseline fi

Siting and size genetic data can network. Areas v compile genetic d models and analy combine all five regular intervals : areas where all sp classes, and where activities (e.g., mi pression or catast plans that prescrib and restrictions on

Recommended sidering the size of sizes into the futu large enough to av buffer against poll mended sizes ra ditions of the sites

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at least 600 trees. An additional 90 ha isolation zone protects the stands from gene contamination. Genetic management guidelines are integrated with the general management plans for each area, and do not significantly constrain wood production goals for these areas.

In California, USA, a research GCA project for key conifers was initiated in the Sierra Nevada which demonstrated a quantitative approach to using genetic information in designing GCA size and placement (Millar and Libby 1991). The focus of this GCA project was the five commercial conifer species of the Sierra Nevada (ponderosa pine, sugar pine, incense-cedar, Douglas-fir, and white fir). Throughout most of their ranges, these species are subject to timber harvest, and also conserved under the genetic conservation practices of the U.S. Forest Service described for production forestry above. The development of a GCA network was proposed as a back-up and insurance to the operational gene conservation practices, and also as baseline for assessing the efficacy of those operational guidelines.

Siting and size decisions about the individual units demonstrate how genetic data can be used to improve the efficiency of designing a GCA network. Areas were selected according to four generalized steps: (1) compile genetic data for multiple traits; (2) develop multivariate statistical models and analyses to locate alternative network designs for GCAs that combine all five species and represent genetic diversity gradients at regular intervals across the landscape; (3) survey on-the-ground to find areas where all species represented are in appropriate conditions and age classes, and where natural processes have been least disrupted by human activities (e.g., minimal history of timber harvest, road building, fire suppression or catastrophic fire); (4) develop and implement management plans that prescribe goals, restricted and permitted activities, monitoring, and restrictions on adjacent land use.

Recommended size of each GCA in this project was calculated by considering the size of an area that would maintain stable effective population sizes into the future (i.e., no decline in genetic diversity). Areas must be large enough to avoid inbreeding, retard loss of diversity due to drift, and buffer against pollen contamination from neighboring stands. The recommended sizes ranged from 500 ha to 3000 ha, depending on stand conditions of the sites and management of adjacent areas.

Management plans for this GCA network would emphasize natural structure and process, including ecologically appropriate mixes of species, age classes, and densities, as well as appropriate fire and natural insect/pathogen regimes. Carefully controlled harvest, artificial regeneration, and other manipulative practices could occur if genetic considera-

tions were given highest priority. This arguably diminishes or obviates their usefulness as baseline areas for comparison with harvested areas. In most parts of the world, however, undisturbed (by human influence) forest doesn't exist. In light of this, the best approach is to choose areas with least historic disturbance, greatest record of past effect, and highest likelihood of achieving genetic standards and practices in future management.

#### ENDANGERED SPECIES MANAGEMENT

Much conservation activity is focused on endangered species. Protection of these species can be both preventative, in minimizing or halting the activities that eroded or contaminated genetic diversity, and restorative, in reintroducing allelic, genotypic, and ecotypic diversity. Often a management decision hinges on determining how much genetic diversity is enough; that is, whether a rare population or species' gene pool would be 'significantly impaired' by a proposed management project (e.g., timber harvest, trail-building, grazing allocations, fire). Significant genetic change is difficult to interpret even with monitoring, and thus it is difficult to determine what constitutes a threat, especially to small or weakened populations.

One way to evaluate the significance of proposed actions involving endangered species is to model or predict the implications on short- and long-term genetic diversity and population viability. An example comes from sugar pine, an ecologically and commercially important species of western North America. Sugar pine, along with other white pines native to North America, is threatened by an exotic pathogen, *Cronartium ribicola*, which causes the fatal white pine blister-rust disease (Smith 1996). White pine blister rust was introduced into North America in 1910 on a shipment of infested eastern white pine (*Pinus strobus*) from France, and has spread with variable speed through sugar pine and other white pine forests in western and eastern parts of the continent.

Sugar pine is highly susceptible to blister rust. Seedlings and young trees are killed outright, while old trees die more slowly, losing portions of their crowns over many years. A major gene for resistance, which appears to be widely distributed in sugar pine populations at very low levels, was found almost 30 years ago (Figure 14.6, Kinloch *et al.* 1970, Kinloch 1992). Threat of population or species extinction from blister rust is attenuated by sugar pine's naturally low stand densities, which were further reduced as a result of heavy harvest during the settlement period in California (late nineteenth century).

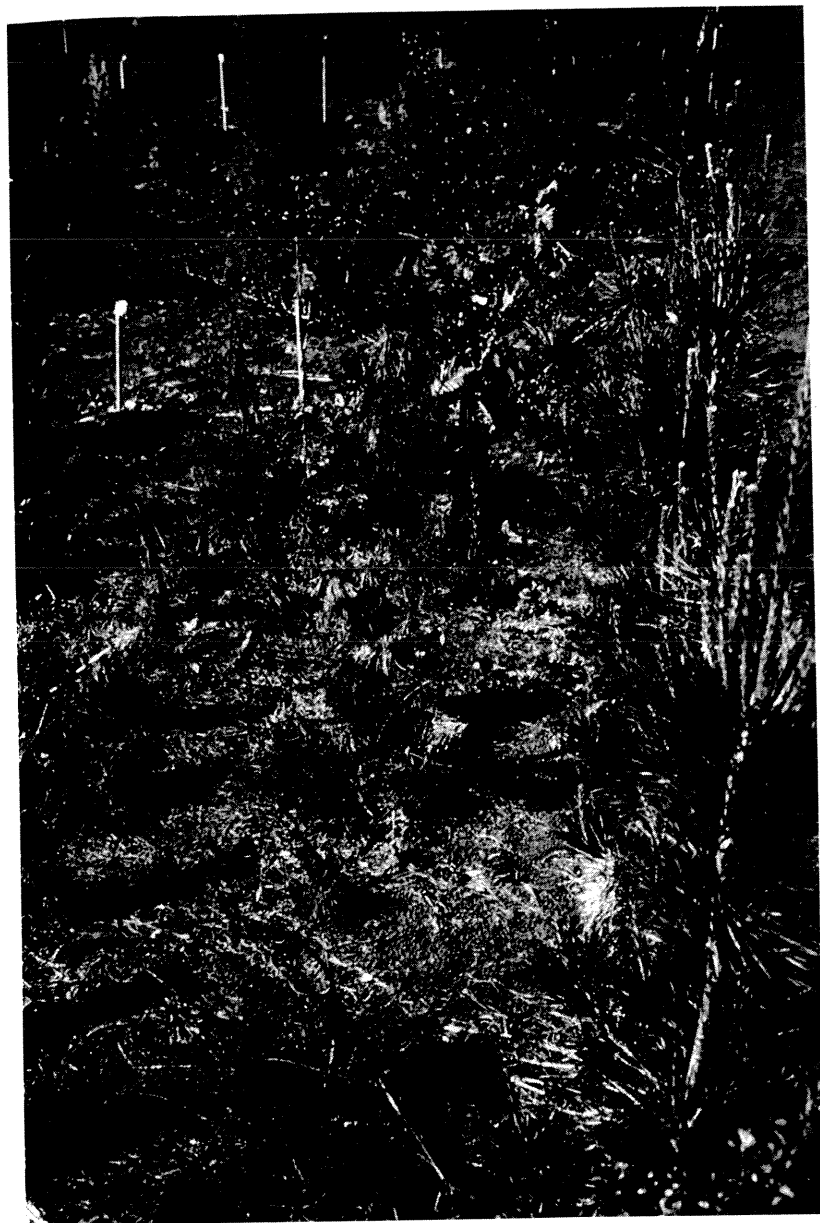


Fig. 14.6. A single dominant gene in sugar pine (*Pinus lambertiana*) confers resistance from white pine blister-rust disease to individuals that carry the gene (right). Individuals carrying the normal allele die when exposed to the pathogen (left). Frequencies of the resistant gene vary in sugar pine forests from absent to about 10%. (From Kinloch et al. 1970, Kinloch 1992.) (B.B. Kinloch photo)

Models have been developed to predict changes in genetic diversity and to assess long-term population viability in sugar pine (Millar *et al.* 1996). The assessment focused on the rate and geographic extent of the spread of the rust, the effects on sugar pine populations as the epidemic reached all parts of the species' range, and the consequences to the species at populations, ecotypic, and species levels. In modeling, effective population size was tracked as the key marker of genetic diversity during the predicted rust epidemic. Effective population size ( $N_e$ ) is similar to the census size of a population (the actual count of individuals) but is adjusted to represent the number of genetically effective individuals.  $N_e$  is equal to the actual census only when mating is random, all parents contribute offspring equally, where sex ratios are equal, and population sizes remain unchanging over time.

Following effective population size in sugar pine shows some surprising results (Figure 14.7). As blister rust becomes epidemic, sugar pine populations decline rapidly in size. A few individuals in most populations are likely to survive due to the resistance gene. These individuals produce resistant progeny. In subsequent generations, populations increase rapidly in size due to strong selection for the resistance gene (Figure 14.7). An important outcome from modeling, however, is the significant and long-lasting decline in  $N_e$ . This suggests that a large portion of genetic diversity in sugar pine populations will be lost even though the populations recover in size. Without its complement of genetic diversity, however, the long-term stability of sugar pine is hampered since the species would lose resilience to meet future environmental changes.

Comprehensive management programs have tackled the blister-rust problem in sugar pine for several decades (Kitzmilller 1976). Most recently, a breeding program is developing resistant sugar pine seedlings to outplant after timber harvest (Samman and Kitzmilller 1996). Seeds are collected from known resistant trees in wild stands, and resistant seedlings are returned to reforestation sites within the same adaptive zone. This augmentation of resistant stock should significantly improve sugar pine's chances for successfully passing through the epidemic and maintaining genetic diversity as well.

A less obvious implication from the modeling is the effect that harvesting genetically susceptible old-growth sugar pine individuals would have on long-term loss of genetic diversity. Although it might seem that these genotypes are extraneous to the population since they will likely be killed by the rust, in fact as long as trees with susceptible genotypes are alive (and many may take years to die), they contribute genes through pollen to

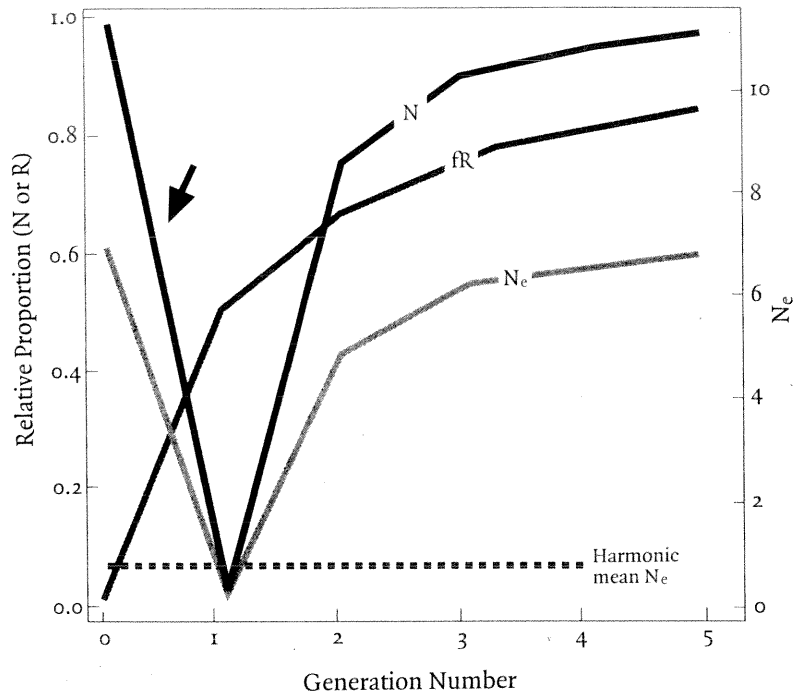


Fig. 14.7. Evaluating impacts to genetic diversity in sugar pine from white pine blister rust with predictive models. The model shows the effect of five generations of blister rust on population size ( $N$ ) of sugar pines, frequency of the sugar pine resistant allele ( $fR$ ), effective population size in sugar pine ( $N_e$ ) over five generations, and harmonic mean  $N_e$ . Harmonic mean  $N_e$  is the average effective population size over the five generations and is used to evaluate effect on genetic diversity. With a mean  $N_e$  of 0.2, in five generations approximately 95% of sugar pine's genetic diversity could be lost. (From Millar et al. 1996.)

resistant mother trees. They also can bear resistant seeds themselves through pollination from resistant father trees. The genetic diversity they contribute at genes other than the blister rust gene is significant, and emphasizes why it is so important that these trees be kept alive during the epidemic.

This example demonstrates how projections that focus only on population numbers can be misleading: although a population may appear to be stable or recovering in census size, significant undesired impacts may be accruing, as in the case of sugar pine, to long-term genetic diversity, which could impair long-term resilience and adaptability in the species. Preventative and proactive management approaches that 'load the dice' genetically can be chosen where practical.

## GENETIC MONITORING

Although the importance of ecological monitoring extends to the genetic level, genetic diversity is difficult to assess, requiring costly laboratory methods or time-consuming field studies for detection. The genetic structure of several forest tree and fish species have been studied in many places, but few if any studies have been repeated, and time trends are unavailable. With no long-term studies, we have little understanding of natural fluctuations or response to ecological disturbances, and thus no patterns of temporal or spatial variability to use as a baseline. A related barrier to genetic monitoring is the difficulty in interpreting changes in diversity relative to adaptability, resilience, and vigor. With current techniques, by the time we could detect significant changes in genetic diversity, populations and species may already be irretrievably in demographic decline. New approaches combining molecular with physiological techniques, such as quantitative trait locus (QTL) monitoring, are encouraging (Neale and Harry 1994), but these techniques are not yet available for conservation use. In sum, although genetic theory provides expectations about changes in diversity, we have not yet developed a meaningful approach to genetic monitoring because we do not know whether increases, decreases, or other changes we may measure are significant for a particular species or population. For now we can advance the objectives of genetic monitoring by understanding ecological contexts within which genetic trend data are collected, integrating genetic diversity measurements with other ecological monitoring data, and using ecological surrogates for genetic inference (Bawa and Menon 1995, Boyle and Boontawee 1995).

**Case study: preserving a priceless legacy of genes in Turkey**

An ambitious and comprehensive project is under way to conserve the rich genetic resources of native plants and wild relatives of important crop, medicinal, and ornamental plants of Turkey (Global Environment Facility 1995, Adams *et al.* in press). The program is jointly administered by the Turkish Ministry of Agriculture and Rural Affairs, Ministry of Forestry, and Ministry for the Environment and funded by the Global Environment Facility of the World Bank. Turkey is one of the richest countries in plant genetic resources. Over 30% of its 9000 species are endemic. Turkey has a unique biogeographical setting located at the junction of the Euro-

Siberian, Mediterranean, and Irano-Turanian floristic regions. Diverse environmental and climatic conditions contribute to making Turkey a major center of origin for globally important plant genetic resources and the native home of widely used domesticated plants.

This project is the first of its kind in the world to protect both woody and non-woody wild crop relatives through the development of *in situ* multi-species genetic conservation areas. Whereas many nations have undertaken some form of *ex situ* genetic conservation (seed storage, primarily), Turkey is the first to integrate *ex situ* with *in situ* methods in a national program for the management of genetic resources. In addition to identifying and establishing gene conservation areas, a project goal is to strengthen the institutional capacity in Turkey for implementing an ongoing national program for genetic conservation and integrating with other current conservation efforts in the country.

The project includes five major components: surveys and inventories, gene conservation areas (called gene management zones in this project), data management, a national plan for a larger network of *in situ* conservation areas, and institutional strengthening for gene conservation. This pioneering program began in March 1993 with a three-year pilot phase that emphasized development of eco-geographic surveys and inventories of species and genetic diversity (isozyme and common garden studies) of tree and crop relative species across the country to determine appropriate locations for genetic conservation areas. These areas would be located to preserve unique genetic resources as well as conserve areas of high species diversity. The number of areas and their size would vary with site and species richness. Areas will be selected that contain more than one population of target species, and that contain core areas (center of the zone) and buffer zones. The pilot program focused on areas within Kazdagi National Park, Ceylanpinar State Farm, and the Anatolian Diagonal.

Each GCA designated in the Turkish network will have a separate management plan, and a scientific and technical team from several government agencies will implement and review conservation activities of each site. Management will emphasize non-manipulative uses initially, especially in core areas. Cessation of grazing will be the most important management action. For areas that have endangered species, recovery plans will be written and implemented but the focus emphasizes restoring ecosystem function not just species representation. Removal of invasive plants and feral animals and fertilization of some parts of the GCA may be needed. Permanent sampling and monitoring plots will be established to monitor baseline biotic and physical environmental changes. Plots will be

resampled every 3–5 years, and ecological research will be encouraged in these areas. These GCAs of forest and crop species are intended to serve as the core of a much larger network of conservation areas that will comprehensively cover all plant species in Turkey.

### Summary

Genetic variation is the fundamental source of all biological diversity. Without genetic variation, adaptation to changing environments would not occur. Because species are subject to natural selection, gene flow, chance events of genetic drift, and other evolutionary forces that shape their genetic composition, they have evolved highly structured patterns among individuals, populations, and widely separated portions of native ranges. No two species are alike in their genetic architecture, although some species that are similar in mating systems (e.g., inbreeders vs. outbreeders), geographic distribution (e.g., widespread vs. rare), or longevity (e.g., annual vs. perennial) may share similar general patterns in genetic diversity. Much of this variation has evolved as a consequence of natural selection fine-tuning populations for adaptation to local environments, although many ecosystem forces alter the genetic structure of species in random ways as well. Human actions also influence genetic diversity, in both beneficial and detrimental ways.

Genetic conservation is a component of land management that aims to maintain the ecological and evolutionary potential of species' gene pools. Traditionally genetic considerations have been limited to a very few taxa (commercial forest species) and a few aspects of forest management (tree improvement or reforestation). General guidelines and strategic genetic plans that aim to maintain and restore genetic diversity need to be more widely integrated across suites of taxa in forest planning. Where the management goal is to maintain biodiversity, genetic objectives can be aided by actions that maintain native genetic diversity and function, and avoid genetic contamination. These include using local germplasm of native species (in projects like tree planting, fish stocking, ecological restoration, or rare species reintroduction); maintaining natural population sizes, distributions, and connectivity; ensuring that parents of future generations are genetically representative of current generations when individuals are removed (e.g., in tree harvest, hunting and fishing); providing sources of back-up genes in storage in case of emergency needs (e.g., seeds in a seedbank, frozen sperm); and promoting natural disturbance

agents that act as selection agents (e.g., fire and native insects/pathogens). Specific genetic conservation prescriptions may be needed when genetic diversity seems at risk; these include germplasm collection and transfer rules, minimum population size guidelines, genetic conservation areas, and guidelines on selection of individuals for removal or introduction.

### Further readings

Hartl (1988), Hartl & Clark (1989) and Hedrick (1983) develop the basic population-genetic theory that underlies conservation genetics. Early conservation biology treatments, such as Soule and Wilcox (1980) and Frankel and Soule (1981), set the stage for important conservation genetic precepts. These are further developed generally in Oldfield (1984) and Soule (1987), while Ledig (1988), Schoenewald-Cox et al. (1983), Falk & Holsinger (1991) and National Research Council (1991) take up genetic conservation within specific management contexts. More recent treatments include Hedrick and Miller (1992), Rogers and Ledig (1996), and Friedman (1997).

### Literature cited

- Adams, W. T., S. H. Strauss, D. L. Copes, and A. R. Griffin (eds). 1992. *Population Genetics of Forest Trees*. Kluwer Academic Publishers. Boston.
- Adams, W. T., Y. Anikster, Z. Keya, N. Zencirci (eds). (In press). In situ genetic conservation in Turkey: National programs and scientific bases. *Proceedings from the Symposium on In Situ Conservation of Genetic Resources in Turkey*. November 1996. Antalya, Turkey.
- Antonovics, J., A. D. Bradshaw, and J. Turner. 1971. Heavy metal tolerance in plants. *Advances in Ecological Research* 7:1-85.
- Arbez, M. 1995. A federative plan for the conservation of forest genetic resources in Europe. Pp. 465-72 in Ph. Baradat, W. T. Adams, and G. Mueller-Starck (eds). *Population Genetics and Genetic Conservation of Forest Trees*. SPB Academic Publishing, Amsterdam.
- Asins, M. J. and E. A. Carbonell. 1987. Concepts involved in measuring genetic variability and its importance in conservation of plant genetic resources. *Evolutionary Trends in Plants* 1(1):51-62.
- Baradat, Ph., W. T. Adams, and G. Mueller-Starck (eds). 1995. *Population Genetics and Genetic Conservation of Forest Trees*. SPB Academic Publishing, Amsterdam.
- Barrett, S. C. and J. R. Kohn. 1991. Genetic and evolutionary consequences of

- small population size in plants: Implications for conservation. Pp. 3-30 in Falk, D. and K. Holsinger (eds). *Genetics and Conservation of Rare Plants*. Oxford University Press, New York.
- Bawa, K. S. and S. Menon. 1995. Biodiversity monitoring: the missing element. *Trends in Ecology and Evolution* 12(1):42.
- Bonner, F. 1990. Storage of seeds: potential and limitations for germplasm conservation. *Forest Ecology and Management* 35(1,2):35-44.
- Boyle, T. J. and B. Boontawee (eds). 1995. Measuring and monitoring biodiversity in tropical and temperate forests. *Proceedings of a IUFRO Symposium held at Chiang Mai, Thailand, August 27-September 2, 1994*. Center for International Forestry Research, Bogor, Indonesia.
- Brown, A. H. D. and J. D. Briggs. 1991. Sampling strategies for genetic variation in ex situ collections of endangered plant species. Pp. 99-122 in Falk, D. and K. Holsinger (eds). *Genetics and Conservation of Rare Plants*. Oxford University Press, New York.
- Buck, J. M., et al. 1970. *California tree seed zones*. Miscellaneous Publication. USDA Forest Service.
- Campbell, R. K. and F. C. Sorenson. 1984. Genetic implications of nursery practices. Pp. 183-91 in M. L. Duryea and T. D. Landis (eds). *Forest Nursery Manual: Production of Bareroot Seedlings*. Martinus Nijhoff/Dr W. Junk Publishers, Boston.
- Center for Plant Conservation. 1991. Genetic sampling guidelines for conservation collections of endangered plants. Pp. 225-38 in Falk, D. and K. Holsinger (eds). *Genetics and Conservation of Rare Plants*. Oxford University Press, New York.
- Clausen, J., D. D. Keck, and W. M. Heisey. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Institution of Washington Publication No. 520.
- Clegg, M. T. 1990. Molecular evaluation of plant genetic resources. Pp. 13-17 in B. Fraleigh (ed.). *Proceedings of a workshop on the genetic evaluation of plant genetic resources, 1988*, Ottawa, Ontario.
- Conkle, M. T. 1986. Tree genetics and improvement. *Journal of Forestry* 84(1):34-6.
- Daly, J. C. and J. L. Patton. 1990. Dispersal, gene flow, and allelic diversity between local populations of *Thomomys bottae* pocket gophers in the coastal ranges of California. *Evolution* 44(5):1283-94.
- Dobzhansky, T. 1970. *Genetics of the Evolutionary Process*. Columbia University Press. New York.
- Eriksson, G. 1995. Which traits should be used to guide sampling for gene resources? Pp. 349-59 in Ph. Baradat, W. T. Adams, and G. Mueller-Starck (eds). *Population Genetics and Genetic Conservation of Forest Trees*. SPB Academic Publishing, Amsterdam.
- Falk, D. and K. Holsinger (eds). 1991. *Genetics and Conservation of Rare Plants*. Oxford University Press, New York.
- Falk, D., C. I. Millar, and P. O. Olwell (eds). 1996. *Restoring Diversity: Reintroduction of Rare and Endangered Plants*. Island Press, Washington D.C.

- Frankel, O. H. and M. E. Soule 1981. *Conservation and Evolution*. Cambridge University Press, Cambridge.
- Friedman, S. 1997. Forest genetics for ecosystem management. Pp. 203-212 in K. Kohm and J. F. Franklin (eds). *Creating a Forestry for the 21st Century, The Science of Ecosystem Management*. Island Press, Washington D.C.
- Global Environment Facility. 1995. In-situ conservation of genetic diversity in Turkey. Agricultural Research, Turkish Ministry of Agriculture and Rural Affairs. *Global Environment Facility Newsletter* 1:1-4.
- Hamrick, J. L. 1983. The distribution of genetic variation within and among natural plant populations. Pp. 335-48 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas (eds). *Genetics and Conservation*. Benjamin/Cummings Co. Inc. Menlo Park, California.
- Hamrick, J. L. and M. J. W. Godt. 1990. Allozyme diversity in plant species. Pp. 43-63 in A. H. D. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir (eds). *Plant Population Genetics, Breeding, and Genetic Resources*. Sinauer Associates Inc., Massachusetts.
- Hamrick, J. L., Y. B. Linhart, and J. B. Mitton. 1979. Relationships between life history characteristics and electrophoretically-detectable genetic variation in plants. *Annual Review of Ecology and Systematics* 10:173-200.
- Hartl, D. L. 1988. *A primer of Population Genetics*. Sinauer, Sunderland, Massachusetts.
- Hartl, D. L. and A. G. Clark 1989. *Principles of Population Genetics*, 2nd edition. Sinauer, Sunderland, Massachusetts.
- Hedrick, P. 1983. *Genetics of Populations*. Science Books International, Boston.
- Hedrick, P. and P. Miller. 1992. Conservation genetics: techniques and fundamentals. *Ecological Applications* 2(1):30-46.
- Hertel, H. and C. Ewald. 1995. Conservation of genetic diversity in SO<sub>2</sub>-polluted stands of Norway spruce (*Picea abies*). Pp. 413-20 in Ph. Baradat, W. T. Adams, and G. Mueller-Starck (eds). *Population Genetics and Genetic Conservation of Forest Trees*. SPB Academic Publishing, Amsterdam.
- Holsinger, K. E. and L. D. Gottlieb. 1991. Conservation of rare and endangered plants: principles and prospects. Pp. 195-208 in Falk, D. and K. Holsinger (eds). *Genetics and Conservation of Rare Plants*. Oxford University Press, New York.
- Hudson, W. E. 1991. *Landscape Linkages and Biodiversity*. Defenders of Wildlife, Washington DC.
- Hunter, M. L. 1996. *Fundamentals of Conservation Biology*. Blackwell Science, Cambridge, Massachusetts.
- Ingram, 1996. Integration of in-situ conservation of plant genetic resources into landscape and regional planning. Pp. 454-76 in R. C. Szaro and D. W. Johnston (eds). *Biodiversity in Managed Landscapes*. Oxford University Press, New York.
- Kinloch, B. B. 1992. Distribution and frequency of a gene for resistance to white pine blister rust in natural populations of sugar pine. *Canadian Journal of Botany* 70(7):1319-23.

- Kinloch, B. B., G. K. Parks, and C. W. Fowler. 1970. White pine blister rust: simply inherited resistance in sugar pine. *Science* **167**:193-95.
- Kitzmiller, J. H. 1976. *Tree Improvement Master Plan for the California Region*. USDA Forest Service, San Francisco.
1990. Managing genetic diversity in a tree improvement program. *Forest Ecology & Management* **35**(1-2):131-49.
- Knapp, E. and K. Rice. 1994. Starting from seed: Genetic issues in using native grasses for restoration. *Restoration Management & Notes* **12**(1):40-5.
- Ledig, F. T. 1986. Heterozygosity, heterosis, and fitness in outcrossing plants. Pp. 77-104 in M. E. Soulé (ed.). *Conservation Biology: the Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, Massachusetts.
1988. Conservation of diversity in forest trees: Why and how should genes be conserved? *BioScience* **38**:471-9.
1991. Human impacts on genetic diversity in forest ecosystems. *Oikos* **63**:87-108.
- Libby, W. J. 1973. Domestication strategies for forest trees. *Canadian Journal of Forest Research* **3**:265-76.
- Libby, W. J., K. Isik, and J. P. King. 1980. Variation in flushing time among white fir population samples. *Annales Forestales* **8**(6):123-38.
- Millar, C. I. 1993. Conservation of germplasm in forest trees. Pp. 42-65 in W. J. Libby and R. Ahuja (eds). *Clonal Forestry II. Conservation and Application*. 2. Springer-Verlag, Berlin.
- Millar, C. I. and W. J. Libby. 1990. Disneyland or native ecosystem: The genetic purity question. *Restoration Management* **7**(1):18-23.
- Millar, C. I. and W. J. Libby. 1991. Strategies for conserving clinal, ecotypic and disjunct population diversity in widespread species. Pp. 149-70 in D. Falk and K. Holsinger (eds). *Genetics and Conservation of Rare Plants*. Oxford University Press, New York.
- Millar, C. I., B. B. Kinloch, and R. D. Westfall. 1996. Conservation of biodiversity in sugar pine: Effects of the blister rust epidemic on genetic diversity. Pp. 190-99 in B. B. Kinloch, M. Marosy, and M. Huddleston (eds). *Sugar pine; status, values, and roles in ecosystems*. Proceedings of a symposium presented by the California Sugar Pine Management Committee, March 30-April 1, 1992, University of California, Davis, CA. University of California, Division of Agriculture and Natural Resources, Publication 3362.
- Nabhan, G. and D. Norman. 1992. *A proposal for natural area designation in the Tumacacori Mountains of the Coronado National Forest as a genetic reserve to protect plants of economic importance*. Miscellaneous publication of Native Seeds/SEARCH. Tucson AZ. 42 pp.
- National Research Council. 1991. *Forest Trees*. Committee on managing global genetic resources: agricultural imperatives. National Academy Press, Washington D.C.
- Neale, D. G. and D. E. Harry. 1994. Genetic mapping in forest trees: RFLPs, RAPDs, and beyond. *AgBiotech News and Information* **6**(5):107N-114N.

- Nei, M. 1987. *Molecular Evolutionary Genetics*. Colombia University Press. New York.
- Oldfield, M. L. 1984. *The value of conserving genetic resources*. USDI National Park Service Washington D.C.
- Patton, J. L. and J. H. Feder. 1981. Microspatial genetic heterogeneity in pocket gophers: Non-random breeding and drift. *Evolution* 35(5):912-20.
- Rogers, D. L. and F. T. Ledig (eds). 1996. *The status of North American temperate forest genetic resources*. Report No. 15. Genetic Resources Conservation Program, University of California, Davis, California.
- Russell, J. R., F. Hosein, E. Johnson, W. T. G. Van Der Ven, R. Waugh, and W. Powell. 1995. The use of RAPD markers to genetically differentiate between Cocoa (*Theobroma cacao*) populations. Pp.s 135-8 in Ph. Baradat, W. T. Adams, and G. Mueller-Starck (eds). *Population Genetics and Genetic Conservation of Forest Trees*. SPB Academic Publishing, Amsterdam.
- Samman, S. and J. Kitzmiller. 1996. The sugar pine program for development of resistance to blister rust in the Pacific Southwest Region. Pp. 162-70 in B. B. Kinloch, M. Marosy, and M. Huddleston (eds). *Sugar pine; status, values, and roles in ecosystems*. Proceedings of a symposium presented by the California Sugar Pine Management Committee, March 30-April 1, 1992, University of California, Davis, CA. University of California, Division of Agriculture and Natural Resources, Publication 3362.
- Savolainen, O. and K. Karkkainen. 1991. Effect of forest management on gene pools. Pp. 329-46 in W. T. Adams, S. H. Strauss, D. L. Copes, and A. R. Griffin (eds). *Population Genetics of Forest Trees*. Kluwer Academic Publishers. Boston, Massachusetts.
- Schonewald-Cox, C. M., S. M. Chambers, B. MacBryde, and W. L. Thomas (eds). 1983. *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*. Benjamin/Cummings Co. Inc. Menlo Park, California.
- Smith, R. S. 1996. Spread and intensification of blister rust in the range of sugar pine. Pp. 112-24 in B. B. Kinloch, M. Marosy, and M. Huddleston (eds). *Sugar pine; status, values, and roles in ecosystems*. Proceedings of a symposium presented by the California Sugar Pine Management Committee, March 30-April 1, 1992, University of California, Davis, CA. University of California, Division of Agriculture and Natural Resources, Publication 3362.
- Soulé, M. E. (ed.). 1987. *Viable Populations for Conservation*. Cambridge University Press, New York.
- Soulé, M. E. and B. A. Wilcox (eds). 1980. *Conservation Biology, An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, Massachusetts.
- Stern, K. and L. Roche. 1974. *Genetics of Forest Ecosystems*. Springer-Verlag, Berlin.
- Tsai, L. M. and C. T. Yuan. 1995. A practical approach to conservation of genetic diversity in Malaysia: genetic resource areas. Pp.s 207-18 in T. J. Boyle, and B. Boontawee (eds). *Measuring and monitoring biodiversity in tropical and temperate forests*. Proceedings of a IUFRO Symposium held at Chiang Mai, Thailand, August 27-September 2, 1994. Center for International Forestry Research, Bogor, Indonesia.

- Westfall, R. D. and M. T. Conkle. 1992. Allozyme makers in breeding zone designation. *New Forests* 6:279-309.
- Wheeler, N. C. 1996. The Pacific yew: minor species or cancer remedy? Pp. 23-4 in D. L. Rogers and F. T. Ledig (eds). *The status of North American temperate forest genetic resources*. Report No. 15. Genetic Resources Conservation Program, University of California, Davis, California.
- Wilson, B. C. 1990. Gene pool reserves of Douglas-fir. *Forest Ecology and Management* 35(1-2):121-30.
- Wright, S. 1978. *Evolution and the Genetics of Populations*. University of Chicago Press, Chicago.
- Zobel, B. 1977. Gene conservation - as viewed by a tree breeder. *Forest Ecology and Management* 1:339-44.