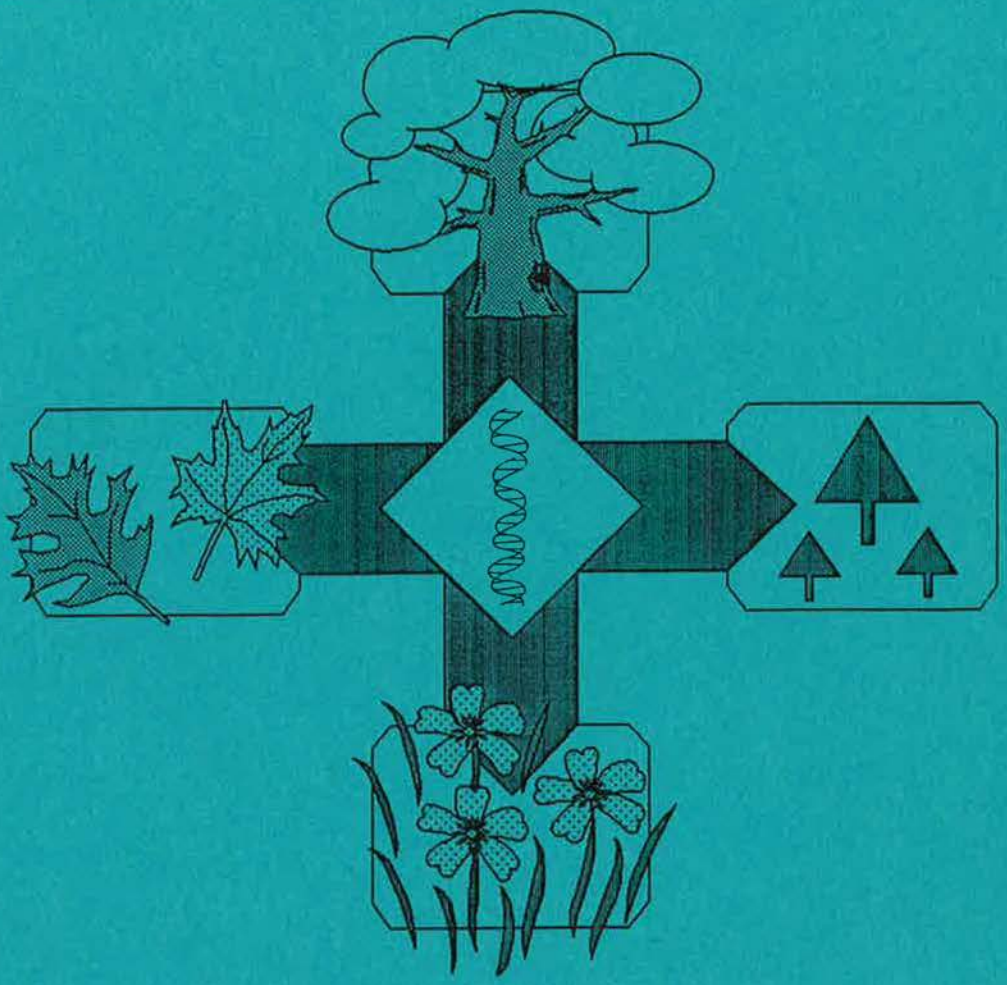

GENETIC MANAGEMENT OF PLANTS IN THE CALIFORNIA STATE PARKS: A PRIMER

A cooperative publication of the Pacific Southwest Research Station (USDA Forest Service) and the California Department of Parks and Recreation

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Preface

The idea for this primer was conceived in 1989, in joint recognition by the USDA Forest Service (Pacific Southwest Research Station) and the California Department of Parks and Recreation of the need for guidelines for long-term genetic management of lands controlled or influenced by the latter agency. This primer represents the first of five phases of a project developed to meet this objective.

Financial support for this project was provided by the two primary collaborators - USDA/FS (PSWRS) and CDP&R. The work was coordinated and the primer edited by Dr. Constance Millar, USDA/FS (PSWRS). Representative for the California Department of Parks and Recreation was Dr. Roy Woodward, (former) Senior Resource Ecologist, Resource Protection Division. Dr. Woodward provided input from the perspective of the target audience and edited the primer. The primer was written and produced by Deborah Rogers, Department of Forestry and Resource Management, University of California, Berkeley.

Appreciation is expressed to three other reviewers who made helpful suggestions for improving the primer. They are: Dr. William Libby, Department of Forestry and Resource Management, University of California, Berkeley; Marylee Guinon, Sycamore Associates, Lafayette, California; and Scott Cantrell, (former) Assistant Resource Ecologist, California Department of Parks and Recreation, Sacramento, California.

The intent of this primer is to inform: subjective interpretations should not be taken as recommendations or implied policy changes. Any opinions expressed herein are solely those of the author and editors and do not represent the views or policies of their employing agencies.

Technical Note: An asterisk appearing beside a word in the text indicates that the word is included in the glossary.

I. INTRODUCTION

Conservation biology, of which genetics is a major component, is receiving unprecedented attention in the management of natural resources. National fora on biological diversity, adoption by the World Bank of a strong wildland policy, and creation of new management strategies for species protection in our national parks all attest to the growing acceptance and application of this discipline. In applying conservation biology principles to vegetation management in California state parks, this discipline must be practical, usable, responsible and accessible to park managers and ecologists. Natural resource management, as it is practiced in state parks, is a professional endeavor with increasing demands on the discretionary and decision-making abilities of those involved. Thus, the background information contained in this publication has been collected in recognition of the fact that regardless of the current issues facing park professionals, their decisions will be better reasoned and supported if they are developed with an understanding of the genetic nature of the species under their stewardship.

The objective of this publication is to present, as clearly as possible, the biological principles related to genetic management of native plant species in California. These principles have been illustrated, where useful and possible, with examples from California's flora. Forest tree species may be over-represented in these examples relative to annual species for several reasons: 1) the high social profile they command; 2) the disproportionate amount of genetic information available for them; and 3) the critical roles they play in ecosystems. The guide has been organized to flow from the general to the more specific. The nature of genetic variation is first explained, followed by a description of its influences and how it is measured. Genetic conservation methods are then described. Finally, an annotated bibliography of genetic information for California native plant species is provided.

A few comments regarding terms and the tone of this publication will serve the reader in making more effective use of it. First, although genetic diversity is the foundation of all biodiversity*, it is not synonymous with biodiversity (Figure 1). Biodiversity encompasses the variety of life and living processes at all levels of organization, from genes to species to ecosystems to landscapes. Biodiversity at the genetic level refers to the amount and distribution of genetic variation. The usual context for genetic diversity, as used in this publication, is within a species. By contrast, species level biodiversity often is measured as a count of all species present in a given area, regardless of the genetic variation present within each species. Public exhibits at zoos are examples of high species diversity but low genetic diversity.

Second, the term 'natural' has been used here in a pre-European settlement context (i.e., pre-1500's). While acknowledging that Native Americans also influenced plant distributions, the use of 'natural' is not intended to imply anything about genetic variation except the lack of any significant modern human influence. Third, although it is an inherent bias of this guide that all plant species have intrinsic value, it is also recognized that priorities must be set for conservation purposes. Triage might be based on their status as keystone species*, rare or endangered species, critical-link species*, aesthetically or culturally valued species, etc. Fourth, an underlying assumption is that genetic management is most effective (perhaps only effective) when practiced when the species is 'genetically healthy' rather than nearing a crisis point. A critically endangered species is usually more vulnerable to immediate demographic problems, which genetic management may not help. Finally, this publication is not a 'how to' guide for either restoration or park management. Other substantial biological considerations, such as demography, are largely lacking herein, as are wildlife

principles and the influences of economics, law, policies and mandates. This guide is intended to be used as part of a rational decision-making process, and not as its replacement.

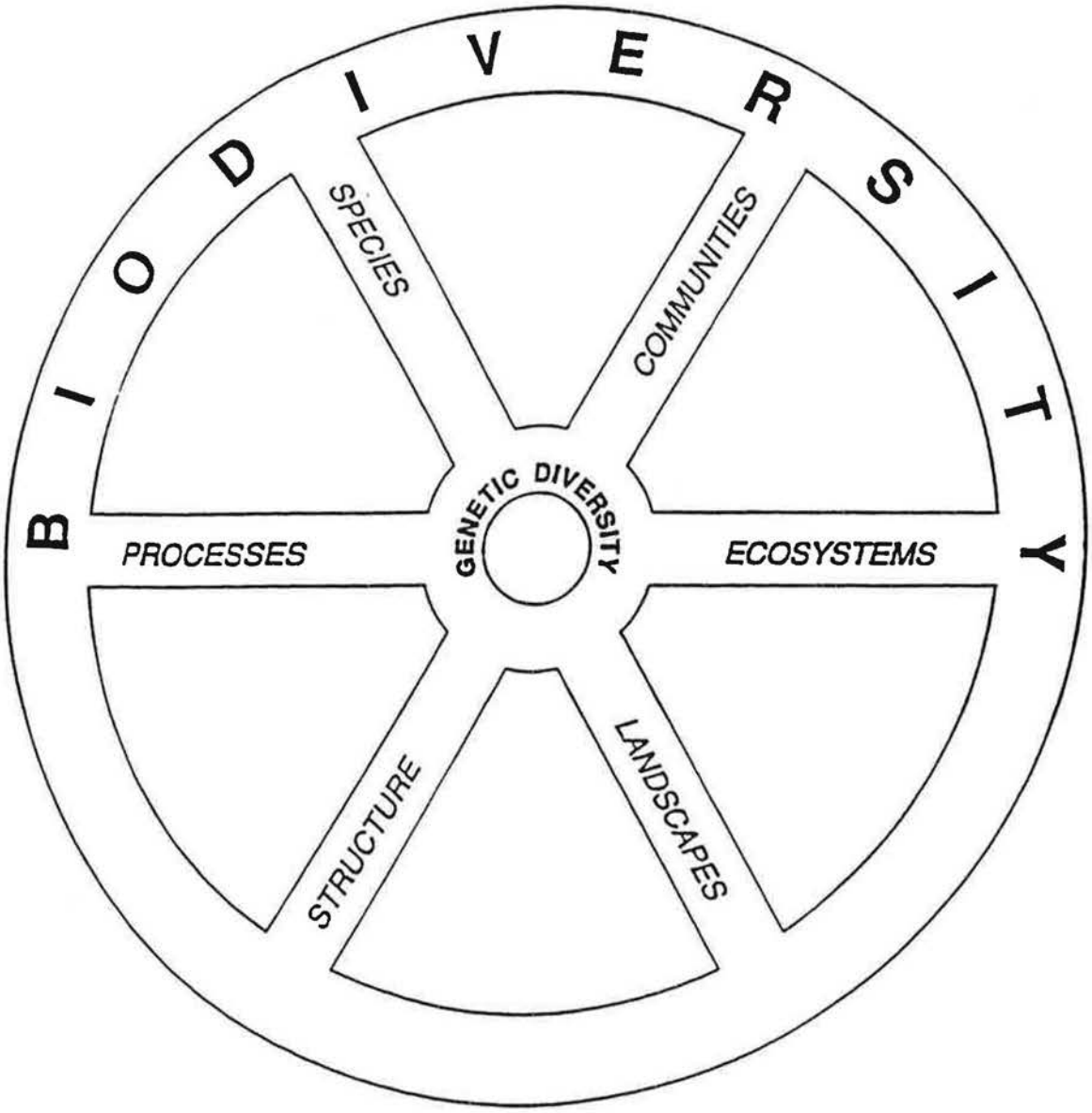

Figure 1. The relationship between biodiversity and genetic diversity (Ledig, 1991, unpublished USDA Forest Service figure)

II. GENETIC VARIATION: ITS NATURE AND SIGNIFICANCE

Nature vs Nurture

All natural variation in organisms, whether in form or function, is due to two interacting 'forces': the environment and the genetic constitution of the organism. The result of this interaction is commonly referred to as the 'phenotype'*. Plant species may differ not only in the total amount of variation that can be observed within the species, but in the relative proportions of genetic and environmental influence in this variation. One extreme example is found in western redcedar (Thuja plicata), a widespread western species that occupies diverse habitats ranging from northern (and eastern) British Columbia to northern California. Very little of the phenotypic variation it displays is due to underlying genetic variation. In this case, the species adjusts to environmental differences through developmental and physiological mechanisms. However, this situation is not representative of most northern hemisphere plants, especially conifers, which typically exhibit high levels of genetic variation.

The Significance of Genetic Variation

As it is possible for some species* to adjust to environmental changes with little genetic variation, one might question the importance of genetic variation more generally. There are two levels on which to address this issue: 1) the importance of genetic variation to the species; and 2) the importance to us. First, although some species show considerable (non-genetic) flexibility in adjusting to different environmental conditions, this is just one strategy - one, as previously mentioned, that is relatively rare among northern hemisphere plants. Low levels of genetic variation are usually indicative of lack of adaptive ability, and may lead to extinction. One extreme example is found in Torrey pine (Pinus torreyana), a species endemic to California which exists only as two small, discrete populations. This genetically depauperate species has been progressively shrinking in size over geological time and currently shows little evidence of successful reproduction.

More commonly, plant populations adjust to environmental changes in both time and space with changes in their genetic constitution. These changes originate with mutations (heritable changes) in the DNA (the genetic material of the plant) and may increase in frequency throughout the species if the mutations increase individual fitness. As genetic variation, unlike flexibility, is heritable, this variation accumulates over time. Thus, in the longterm, the potential to adapt to changing climatic and environmental conditions is dependent on the existence of genetic variation.

In addition to long term survival and success, genetic variation also influences short term or ecological performance of a species. First, genetic variation may allow efficient occupation of differing microhabitats within a species. For example, lodgepole pine (Pinus contorta), one of the most widespread of North American conifers, is extremely versatile with respect to the range of edaphic and climatic sites over which it commonly occurs. Four distinct and largely non-overlapping subspecies have been identified, three of which occur in California. Each occupies a different environmental zone, from shoreline to montane to serpentine barrens (Figure 2.1).

Second, there is evidence that genetic variation within a species is related to its ability to survive random environmental threats (such as pathogens or extremes in weather). For example, the genetic variation within sugar pine (Pinus lambertiana), a common forest tree species throughout the Sierra Nevada and northern coast of California, may hold the only hope for its survival in the face of a current fungal attack. White pine blister rust (Cronartium ribicola), a fungal, non-native pathogen fatal to sugar pine and many white pines, has been spreading throughout the Klamath Mountains and the Sierra Nevada for many years and is expected to

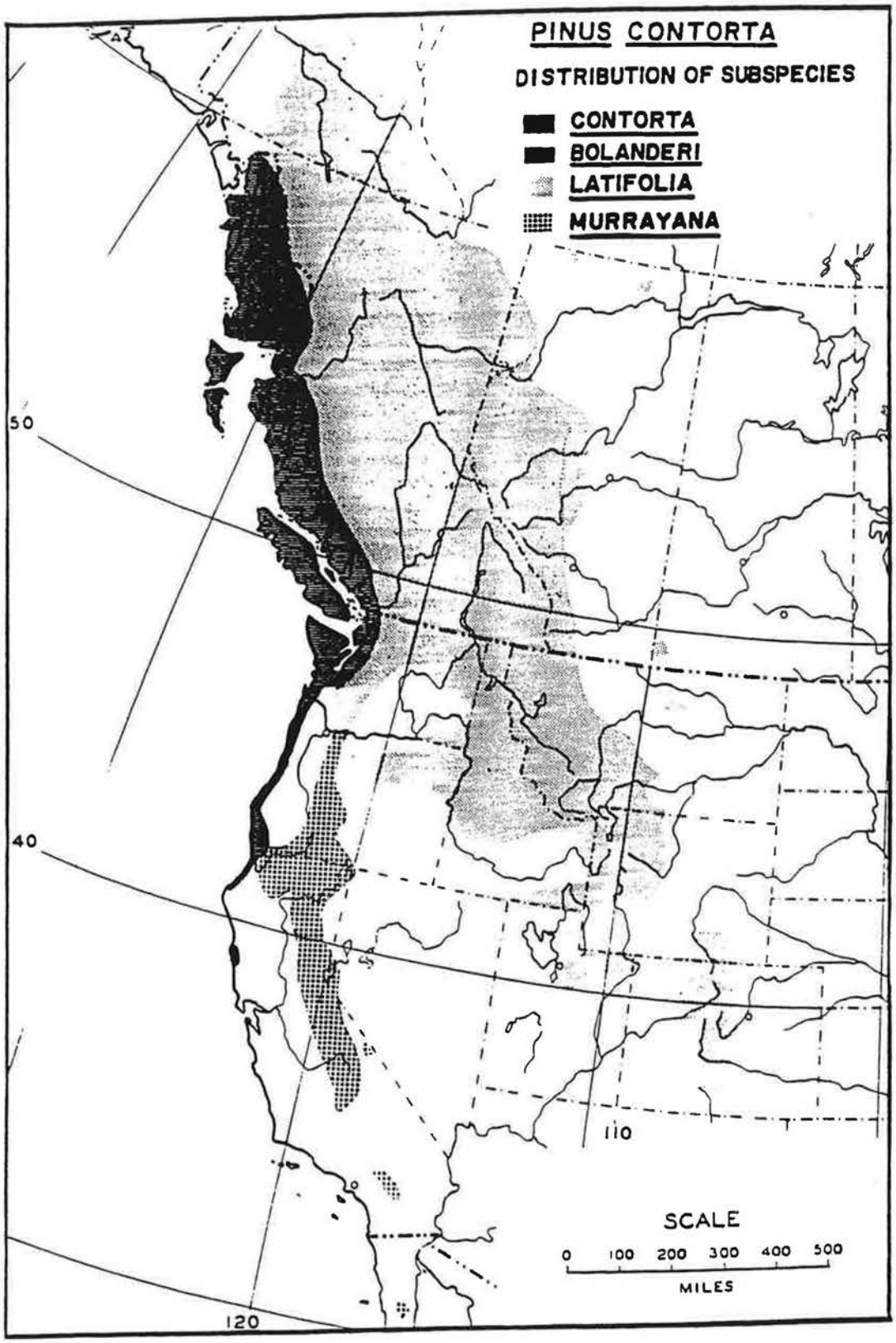

Figure 2.1 Geographical distribution of the four sub-species of Pinus contorta (from Critchfield, 1957).

reach epidemic proportions within the next 25 to 50 years. However, a naturally occurring rust-resistant gene occurs in low frequencies throughout the species range. Progeny from these trees, and from crosses among them, can be used to augment natural populations as they face the epidemic.

Third, genetic variation within a founding population* may influence the likelihood of success of that colonizing group. For example, individuals that colonized the current Torrey pine populations may have been low in variation themselves, setting the stage for the aforementioned problems in those populations. By contrast, in the California cypresses (Cupressus spp.), although the populations are often small and isolated their genetic variation is quite high. This suggests a high level of genetic variation in their colonizing ancestors. Cypress populations are generally robust.

There are many reasons for human interest in genetic variation of plant species, including economic and ecological. From an economic view, nature provides us with a wealth of commodities, both products and experiences. The World Commission on Environment and Development, in their 1987 'global agenda for change', states that "the genetic variability and germplasm material of species make contributions to agriculture, medicine and industry worth many billions of dollars per year ... This - the scope for species to make a fast-growing contribution to human welfare in myriad forms - is a major justification for expanded efforts to safeguard Earth's millions of species."

Indeed, in California, plant resources are currently worth billions. A wild tomato species, sampled in 1962 from the Peruvian Andes and commercially utilized a decade later, provides a striking example of the economic potential of wild species. When crossed with domestic species, genes from the wild tomato increased soluble solids by almost 50% over the commercial variety. Adjusted to 1987 U.S. dollars, the value to the tomato industry of the genes found in this wild species was estimated to be about $8 million per year, assuming the genes were widely incorporated. Another lucrative genetic import was found in a single barley plant from Ethiopia. This plant was found to contain a gene that now protects California's annual barley crop (estimated value in 1985 ca. $160 million) from the lethal yellow dwarf virus.

Of all prescription drugs, 25% come directly from plants. The current investigation of natural compounds from Pacific yew (Taxus brevifolia) for cancer treatment is a local example of the pharmaceutical value of plants.

The advent of biotechnology has provided a means to screen large quantities of plants for useful, and potentially lucrative, substances. Syntex, a Bay Area pharmaceutical company, signed an agreement in 1991 under which science academies in China will supply it with up to 10,000 plant extracts a year for testing. With this approach, the odds of finding a useful genetic variant have been greatly improved.

Although the expression of the economic interests often rests ultimately at the species level, the value usually rests on the genetic variation within species, for at least two reasons. First, there is a strong relationship between the success and survival of most plant species and their level of intraspecific genetic variation. Second, the economically valuable traits are often products of genetic variants in the species, rather than a universal function of the species. This is particularly true in agricultural and forestry applications, where many plants may be screened for the desired trait - such as insect or disease resistance - before the appropriate variant is found. Although most current laws emphasize the species level (endangered species laws), others, such as the National Forest Management Act (1976), are general enough to support conservation of genetic diversity at the intraspecific level. Patenting laws refer to the gene, variety and line levels, and thus there are legal precedents for recognizing and protecting genetic variation at these levels.

Genetic diversity within a species, as already mentioned, contributes to the health and survival of the species in changing environments. Thus, by buffering species, genetic variation also helps to maintain the functioning of natural processes and the integrity of ecosystems. Variation within and among species determines the physical structure for the ecosystem - canopy layers, surfaces for evaporation and reflection, etc. This physical structure determines microclimate - which affects all species, plant and animal, and the cycling rate of resources. The genetic component of biodiversity also affects other ecosystem services such as soil stabilization and watershed protection, air filtering, atmospheric cooling, CO_2 reduction, soil fertilization, etc. Further, the species within an ecosystem are so interactive that the loss of critical species can have cascading effects which may disrupt whole ecosystems.

In California, in particular, we have both the opportunity and the responsibility to make a substantial impact on the genetic conservation of plants. This state has the greatest species richness and the highest rate of endemism* of any region in the continental United States. More than 5,000 vascular* plant species are native, a number that is more than that for the entire northeastern United States and Canada, an area ten times larger than California. At least a third of all the plants native to California are endemic - they occur naturally nowhere else on earth. The genera with the largest number of endemic species are Mimulus (monkey flowers), Astragalus (locoweeds), Lupinus (lupines), Eriogonum (wild buckwheats), Arctostaphylos (manzanitas), and Ceanothus (wild lilacs, etc.). The largest number of plant species endemic to the state is found in southern California, followed by the central coastal area. Relatively few endemics occur in the desert areas, the northern Sierra-Cascades, and the Central Valley.

Our responsibility to protect this natural wealth is emphasized by Harvard biologist E.O. Wilson, who warns, "The one process ongoing in the 1980s that will take millions of years to correct is the loss of genetic and species diversity by the destruction of natural habitats. This is the folly our descendants are least likely to forgive us."

The Genetic Basis of Diversity

Although a lengthy description of molecular genetics is outside the scope of this guide, it should be kept in mind that the 'genetic' variation discussed here refers to differences in the DNA (Deoxyribonucleic Acid) of plant species. These changes may or may not result in observable changes in the plants themselves. Second, public awareness of genetics and genetic issues is usually based on human models, and it is important to recognize the differences between plant and animal genetic systems. In general, plant species are more genetically variable than animal species. One reason for this is the necessity for plants to meet environmental challenges in place, whereas animal species have the additional advantage of mobility and other behavioral mechanisms for accommodation (Table 2.1).

Although all (new) genetic variation ultimately arises from mutation, it is the distribution of these mutations which determines the pattern of genetic variation within the species. There are five general processes that affect the distribution of genetic variation within a species:

1) Mutation - A mutation is any change in the genetic material which is heritable. One kind of mutation is simply a small point change in the DNA due to a replacement, duplication or deletion of one pair of nucleotides. Another class of mutations results from a fragment DNA breaking and rejoining the chromosome in a reverse configuration, so-called 'inversion' mutations.

Still another class of mutations occur when an unstable segment of DNA, called a 'transposable element', moves or transposes from one position on a chromosome to another position on the same chromosome

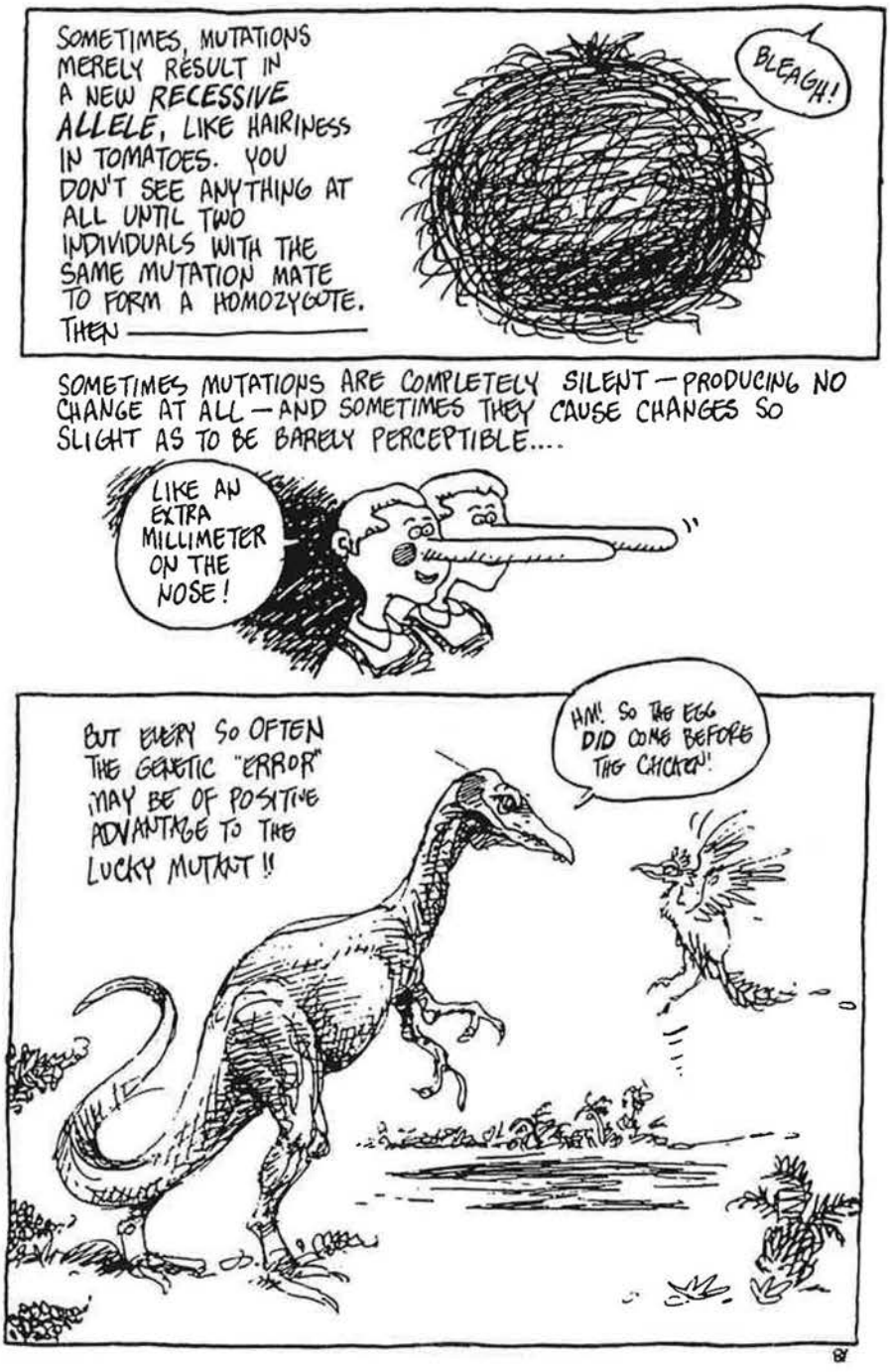

Figure 2.2 Some effects of mutations (Copyright 1983 by Larry Gonick and Mark Wheelis)

or even on a different chromosome. One example of this kind of mutation is the variegated flower color in the snapdragon (Antirrhinum majus). A red and white flower has been shown to be the result of unstable elements transposing out of the gene conferring red color: the earlier this occurs in the development of the flower, the larger the red spots or sections. Transposable elements also occur in animals, but in plants they occur in both somatic and germinal tissue. Once thought to be a property of only a few aberrant genes, transposable elements are now thought to be a property of many, possibly all, genes and could be the source of much of the genetic variation in natural populations.

In some cases, individual chromosomes or the whole genetic complement may become multiplied, leading to a change in 'ploidy*' and perhaps a new species. This was true in the case of coast redwood (Sequoia sempervirens), in which a basic chromosome number of 11, was eventually multiplied to the current chromosome number of 66 for the species (i.e., it is a 'hexaploid'). Another species displaying this tendency towards changes in ploidy is the Ash-gray Paintbrush (Castilleja cinerea), a fairly rare plant found in southwestern California. A hybrid variety which grows in the Big Bear Valley has twice the number of chromosomes of either parental (coastal or desert) variety.

A stellar example of the role of polyploidy in adaptation and evolution is in the grass (Gramineae) family, which contains higher percentages of species of polyploid origin than any other large family of angiosperms. More than 80% of its species have undergone polyploidy some time during their evolutionary history. Some studies of native California grass species have indicated a relationship between increased chromosome number and increased heat and drought tolerance.

Although certain environmental conditions can increase mutation rates, spontaneous mutations continually occur at low rates in nature. Both plants and animals have evolved a series of enzymatic systems that repair DNA in a variety of ways. Some systems remove or 'excise' the mutated segment of DNA; others act by blocking transcription* of the mutated DNA. Thus, all mutational events do not result in a heritable mutation in the DNA.

Those mutations which are not repaired continuously add to the genetic variability in natural populations. Many mutations are lethal or sub-lethal and are eventually removed from the population gene pool by mortality. Some mutations do not affect the immediate viability* (i.e., they have neutral value) and they may increase in frequency in the population by random effects. Occasionally, new mutations are superior to existing genes. These variants become part of the genetic variation of a species. One aforementioned example is the gene for resistance to white pine blister rust in sugar pine. Another advantageous mutation is that for resistance to the fir engraver (insect) in white fir.

Occasionally, an adaptively valuable mutation might mark the beginning of a new sub-species or species. For example, the most prominent differences among colombine species (Aquilegia spp.) are floral characteristics, such as nodding or erect position, and presence or absence of floral spurs. Both of these traits are due to single genes. These characters lead to the sub-division of the ancestral species as they adapt the species to pollination by different groups of insects and birds.

2) Recombination - This is an event that generally occurs during meiosis - the process of producing the plant spores or gametes by reducing the number of chromosomes by one-half. Although the chromosomes in the spores could be the 'parental type' (i.e., could resemble the genetic constitution of either maternal or paternal spore that produced the plant), often this is not so. Rather, a recombination or 'crossing over' event occurs between two

strands of two homologous* chromosomes, resulting in a novel array of genes within each chromosome. Thus, the resulting spores have neither lost nor gained any genes, but rather, have a different combination of maternally- and paternally-derived genes than before the recombination event. Since these events are quite common, the impact on the distribution of genetic variation is substantial.

3) Natural Selection - This is considered the most influential evolutionary process as all adaptive change is the result of natural selection. It operates through differential survival - better adapted individuals survive and reproduce in their current environment. There are many examples of selection causing adaptive genetic change in California plants, such as adaptation to differences in elevation, climate and soil. In ponderosa pine (Pinus ponderosa), for example, different ecotypes* on the west slope of the Sierra Nevada show adaptations to different elevational zones. Adaptive characteristics of higher elevation habitats include slower growth and frost-resistance features. Genetic differentiation in ponderosa pine also occurs between serpentine and non-serpentine soils, and in areas with different amounts of rainfall (e.g., gradient up the west flank of the Sierra Nevada).

Some of the earliest and most comprehensive studies of natural selection in plants were conducted in California by Clausen, Keck and Hiesey during 1920-38. Working with numerous native genera, they conducted transplant experiments, moving representatives along a California transect extending from the Pacific Ocean at Point Montara, across the Santa Cruz Mountains and the San Joaquin Valley to the Great Basin at Benton. Plant response to the great variation in elevation, rainfall, temperature and light encountered along this transect allowed insight into the nature of plant distribution in relation to environment, and in particular, the designation of various ecotypes. For example, four distinct ecotypes were recognized in the widespread species Potentilla glandulosa, corresponding to different elevational zones. The ecotypes differ in many morphological characteristics, and especially phenology.

There are many examples of natural selection in annual species adapted to elevation and soil conditions. A classic example of soil differentiation is the genetic determination of copper tolerance in grasses (e.g., Agrostis tenuis) growing on mine spoil dumps. Metal tolerance is seemingly omnipresent in mine populations, but almost completely lacking in adjacent populations growing on normal soils; despite gene flow across the abrupt environmental boundary, differentiation is maintained by selection. Sharp contrasts in soil pH in the southern San Joaquin Valley are matched by changes in species adapted to different levels of acidity. In the depressions, soils are heavily alkaline. Alkali-tolerant plants found here include shiny peppergrass (Lepidium nitidum), pineapple weed (Matricaria matricarioides), and a rare plant endemic of the upper San Joaquin alkali sink, the alkali larkspur (Delphinium recurvatum). Within just a few feet, there is another array of species, adapted to the neutral soil on the hummocks and low ridges. These include bird's-eye gilia (Gilia tricolor), chia (Salvia columbariae) and pine bluegrass (Poa scabrella).

It is important to keep in mind that natural selection acts in a retrospective manner - adaptation is always to previous environmental conditions. The plants that survive to reproductive maturity are those that are relatively well-adapted to current conditions, and their progeny will reflect adaptations to those same conditions. Changes in environmental conditions can be reflected in successive generations, but there is always a lag. An analogy from Alice in Wonderland is often used for this lagging feature of adaptation. The Red Queen, who runs as quickly as she can just to stay in the same place, is a reflection of a

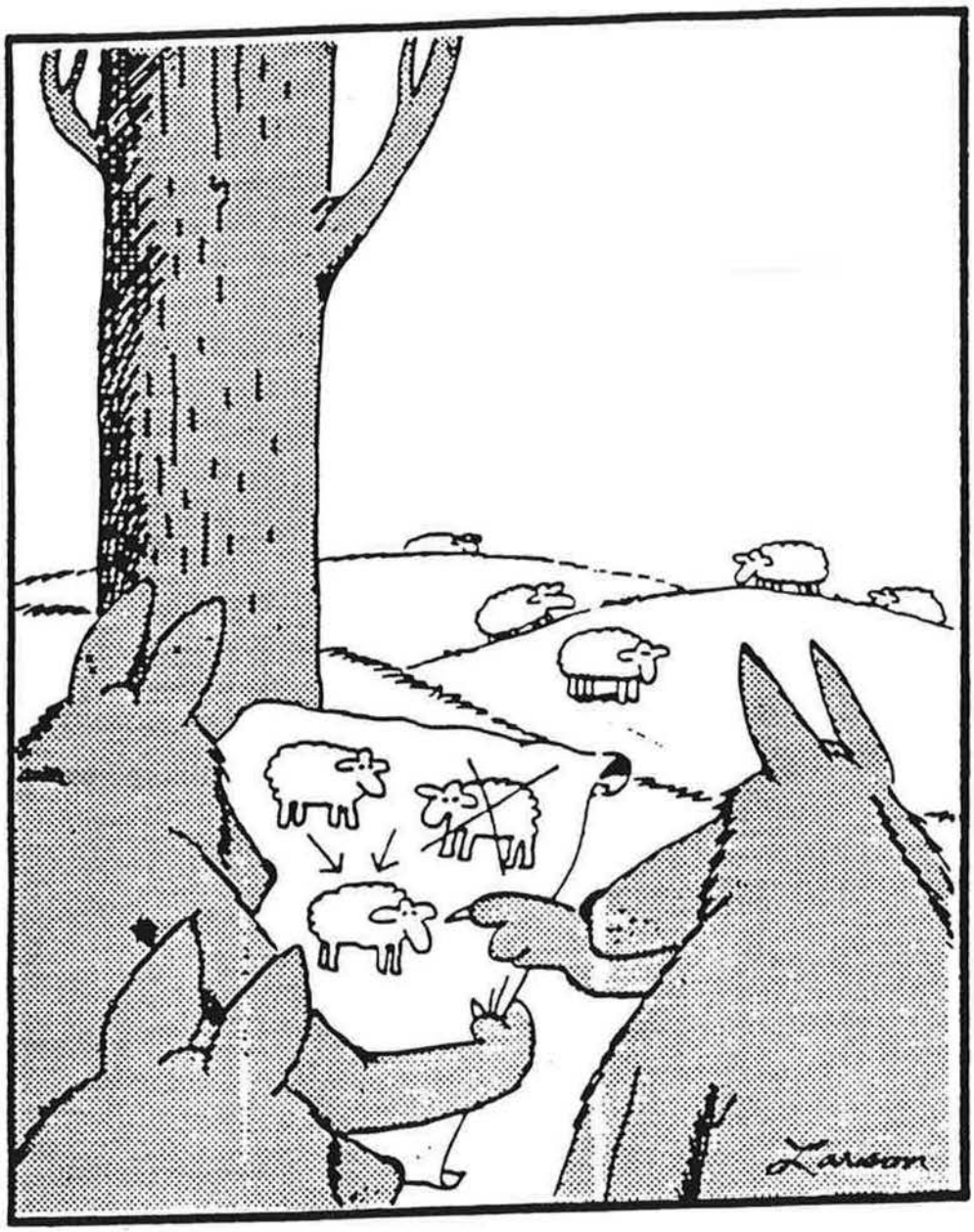

Figure 2.3 Natural selection at work (THE FAR SIDE copyright 1985 UNIVERSAL PRESS SYNDICATE. Reprinted with permission. All rights reserved.)

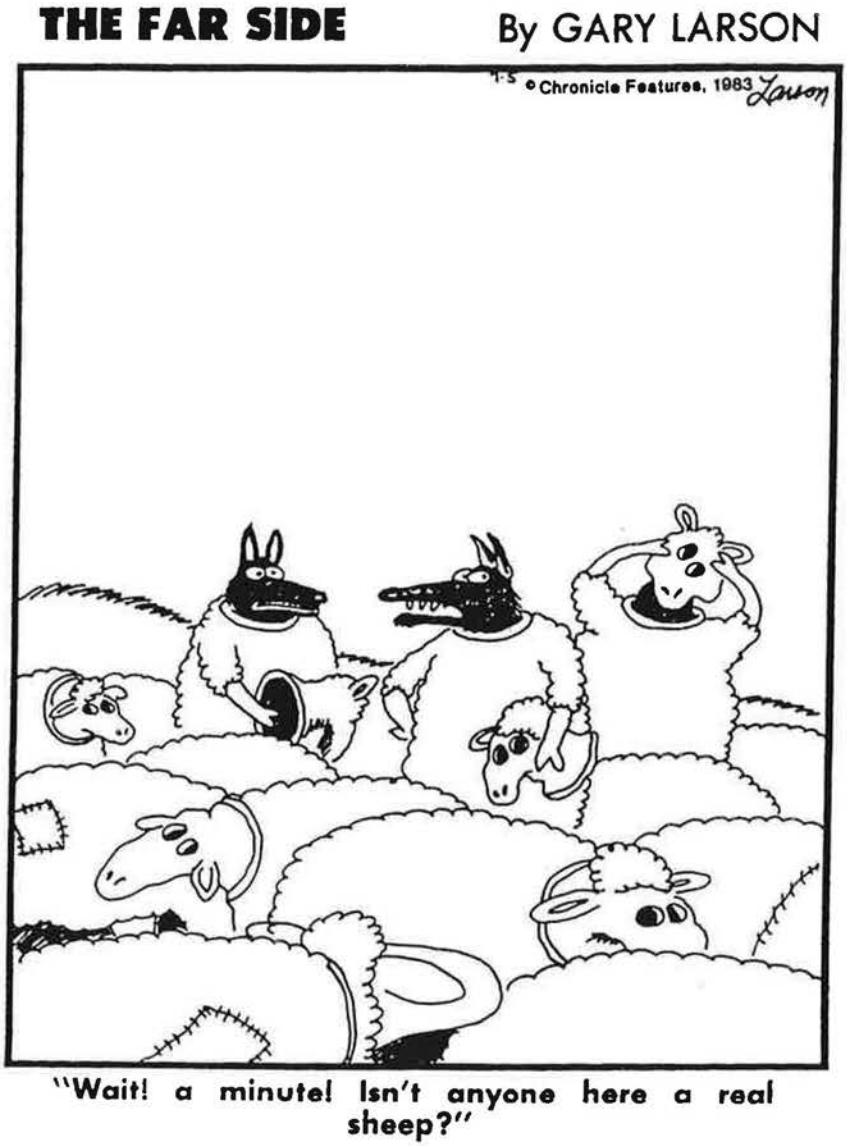

Figure 2.4 Natural selection gone awry. (The Far Side cartoon by Gary Larson is reprinted by permission of Chronicle Features, San Francisco, CA.)

species always 'chasing' the environment just to maintain a constant level of adaptation. One lesson here is that adaptations we see today may have evolved under conditions no longer present.

Finally, natural selection acts at every stage of a plant's life, from germination to seedling survival through reproductive maturity. During reproduction, natural selection influences not only which adult plants will contribute genetic material to the next generation, but also the genetic composition of the seed by influencing (differential) pollen survival and fertilization success.

4) Migration - Migration refers to the dispersal of genes through space and time. Spatially, plant genes 'migrate' as pollen or seeds. In the case of clonal plants, genes can also migrate by vegetative processes such as sprouting from the exposed cambium of a stump (e.g., coast redwood), rhizomes, root sprouting or even the rooting of fallen twigs (e.g., poplar spp.). Sexually reproducing plant species vary in their means of pollination (e.g., wind, insects), and whether seed dispersal is largely a function of gravity, wind, or animal transport. The method of pollination affects the pattern and distance of pollen migration, which influences genetic variation. Other factors that influence the range of pollen transport - from feet to miles - are pollen size, shape and density.

The temporal transmission of genes, from one generation to the next, is called the mating or breeding system. Plant species exhibit a large variety of such systems. The type of mating system common to the species plays a major role in adjusting the manner in which genetic variability is organized in populations. Furthermore, mating systems are under genetic control and themselves subject to selection.

Plant mating systems should be thought of as a continuum of possibilities rather than as discrete types. However, for most purposes, we can comfortably classify plant species as belonging to one of five major classes (Table 2.2). The main difference among these classes is the degree of inbreeding (versus outcrossing). Most plant species are predominantly outcrossing.

Plants show much variation in mating systems: closely related species or even subspecies may have different mating systems. For example, in the tetraploid species Clarkia gracilis, three of its subspecies are mostly outcrossing, but one subspecies reproduces predominantly by self-fertilization.

Although there are many exceptions, there is a general correlation between the type of mating system and the position of the species in ecological succession. This is a reasonable expectation since the mating system evolves as a workable compromise between the contradictory demands for fitness (i.e., maintaining, in an unaltered form, well-adapted genotypes) and flexibility in population variability. Thus, those species invading open or unstable habitats evolve towards self-fertilizing systems which minimizes the breakdown of any existing adaptive gene combinations. At the other end of the successional spectrum, in more closed habitats such as forests, more outbreeding is favored.

Mating systems influence the way genetic variation is structured, a topic explored in a later section. Basically, inbreeding leads to lower levels of genetic variation within populations, and more variation between. Outbreeding produces the opposite effect: variation within populations is high relative to that between populations.

Different types of mating systems may be exhibited within the same species. For example, Gilia ochroleuca, a diploid annual in southern California, occupies a fairly wide range of habitats, from coastal mountains to interior deserts and has accompanying changes in its mating system. The central area of relatively stable woodland communities is occupied by

populations which are bee-pollinated and partially outcrossing. The race in the Mojave desert on the eastern boundary of the species range, where the habitat is more open, is autogamous (self-pollinating). A local autogamous race also occurs on the extreme northwestern margin of the species range (Figure 2.5). One might expect the pattern of genetic variation to change accordingly.

5) Random Genetic Drift - This refers to the chance fluctuations in allele* frequency that occur as a result of random sampling among gametes*. Drift occurs in all populations but has significant effects in small populations. Any event that causes a severe reduction in the population size is also accompanied by genetic drift, as only a sample of the former population now dictates the genetic agenda. In general, genetic drift tends to decrease the genetic variation within populations, although it may result in increased variation among populations.

Genetic drift may also result in populations with unusual variation. Because of these random sampling effects, neutral or even non-adaptive genes can be established in populations. One example may be in Torrey pine, where the seeds germinate while still in the cones on the tree.

Two northwestern coniferous species, western white pine (Pinus monticola) and western redcedar (Thuja plicata), may owe their current genetic uniformity to genetic drift. Western redcedar, recently described as having "one of the lowest degrees of variability found thus far in northern North American conifer species", may have lost much of its variability during glaciations, when it was reduced to a small population far south of the glacial limits.

In the case of western white pine, the northern populations have far less genetic variation than do the more southern populations. It is speculated that the northern part of its range was reduced during glaciations to a small coastal population, whereas the southern populations in California were less restricted by ice and acted as multiple refugia. The genetic variability lost through this massive reduction in the northern part of the species range has not been regained even with the reoccupation of former habitats by migration of the coastal population.

Structure of Genetic Diversity

Genetic variation within natural populations of native species is structured, and we often refer to this structure as the 'genetic architecture' of the species. This refers to the hierarchical arrangement of genetic variation in species. Species differ not only in the total amount of genetic variation present, but in the way in which this variation is partitioned among these levels (Figure 2.6).

It is difficult to discuss the structure of genetic variation without first understanding how it is measured. This is the topic of Chapter IV. Thus, presented below is an introduction to the concept of genetic architecture, with further details provided in a later chapter.

1) Individual gene locus - One could describe the genetic variability from the perspective of a specific gene locus. Based on a sample of individuals from a population, one could find that there is no variation at this locus (i.e., locus is monomorphic) or that there are two or more variants (polymorphic).

2) Genome level - This refers to the ploidy level, or number of copies of each genetic locus per genome, discussed earlier. Thus, the ploidy level sets the upper limit for variation at a locus in an individual. For example, if a species is diploid, an individual can have, at most, two types of alleles at any locus.

3) Individual level - As each plant carries at least two copies of each gene (one on each chromosome) there are many ways for

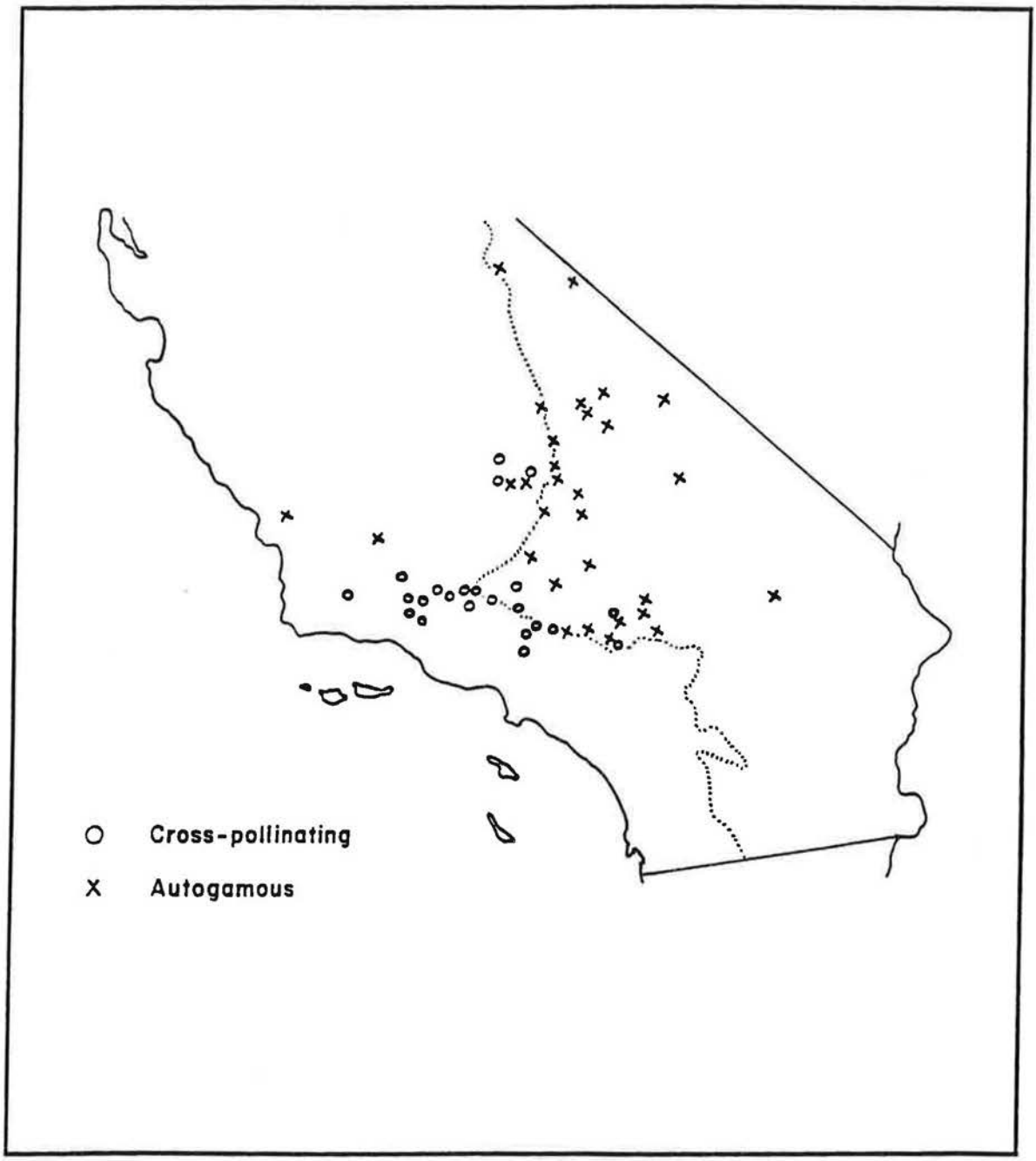

Figure 2.5 The geographical distribution of cross-pollinating and autogamous races of Gilia ochroleuca in southern California. The dotted line marks the western boundary of the desert (from Grant, 1975).

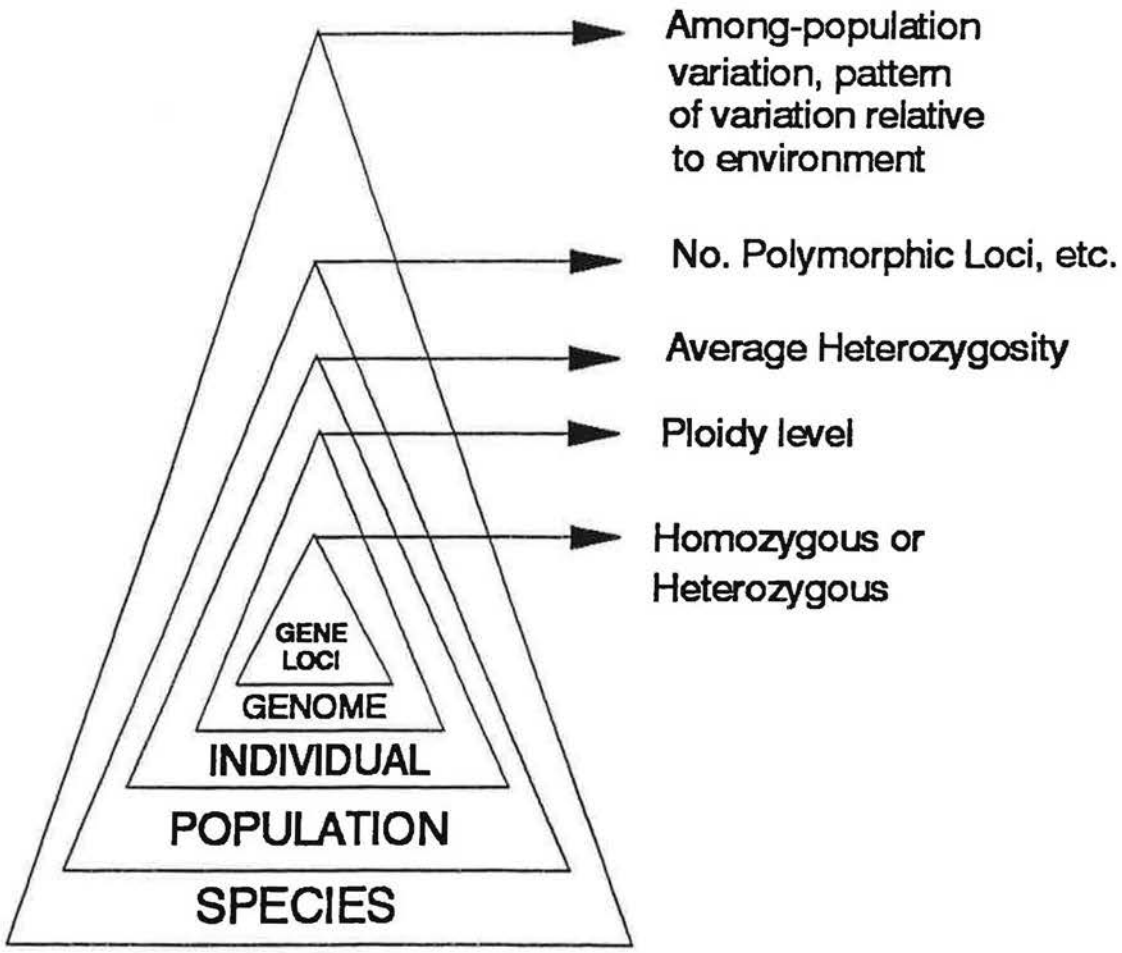

Figure 2.6 Five examples or levels of genetic variation

genetic variation to be represented. Each gene could have several variant forms (alleles) and the plant could possess one form (homozygous) or two forms (heterozygous) of each gene. Thus, one measure of genetic diversity is the degree of homozygosity* or heterozygosity* of an individual based on a sample of its loci.

4) Within-population level - If a number of individuals from a population are sampled, and their heterozygosity values are averaged, this mean heterozygosity can be used as a measure of within-population variation. Another measure is the number of polymorphic loci* (i.e., number of genes that have more than one form) and the number of alleles or mutants that can occur at each of these polymorphic loci. For example, no variation was detected in a study of nine genes of red pine (i.e., 0% polymorphic loci), while a study of 42 loci in lodgepole pine showed a range from 55 to 82% polymorphic loci. The number of alleles per locus is often quite low - normally between one and three. For example, in the same study of lodgepole pine, the average number of alleles per locus was approximately two. The low observed number of alleles per locus is probably often a sampling phenomenon - rare alleles would not often happen to be chosen for analysis. (These genetic measures will be discussed further in Chapter IV).

Another valid perspective for genetic variation is the 'genotype' frequency - the genotype being the 'package' in which the genes reside in an individual, or the genetic constitution of the individual. There are processes that, while not affecting the total amount of genetic variation in a species (i.e., number of polymorphic loci or number of alleles per locus), do affect the distribution (i.e., the genotypes) of that genetic variation in a significant manner. For example, inbreeding (mating of related individuals) alone does not affect the frequency of alleles in a population. However, relative to outbreeding, it does change the relative frequency of genotypes in the population. The frequency of homozygotes (the individual possesses only one form or allele of the gene) is increased, while the frequency of heterozygotes (the individual has typically two forms or alleles of the gene) is decreased. Another situation in which the distinction between genes and genotypes becomes apparent is in sampling schemes for genetic conservation. For example, if the objective is to conserve genes only, obviously a much smaller sample size is required than if the objective was to conserve genotypes.

The spatial arrangement of genetic variation within the population is largely a function of the mating system, as described earlier. Outcrossing, wind-pollinated species will tend to exhibit little within-population structure, while more inbreeding types will exhibit a 'family style' of structure. The pattern presented by the mating system will, of course, be influenced by natural selection.

5) Species (Among-population) level - Many of the measures used for within-population variation can also be used to compare the relative amount of genetic variation within and among a species' populations. For example, genetic studies of Torrey pine show this species to have little or no variation within its populations but significant differences between populations. In contrast, incense-cedar (Calocedrus decurrens, a widespread forest tree species common in the mixed conifer forests of California and Oregon, shows high variation within populations, but only minor genetic differences among its populations.

In species with high levels of genetic variation both within and among populations, there is one further classification - that of discontinuous or continuous geographic variation. In the former, the genetic differences among populations are abrupt. If these differences appear to be adaptations to abrupt environmental differences, the populations are labelled 'ecotypes'. Major ecotypes have

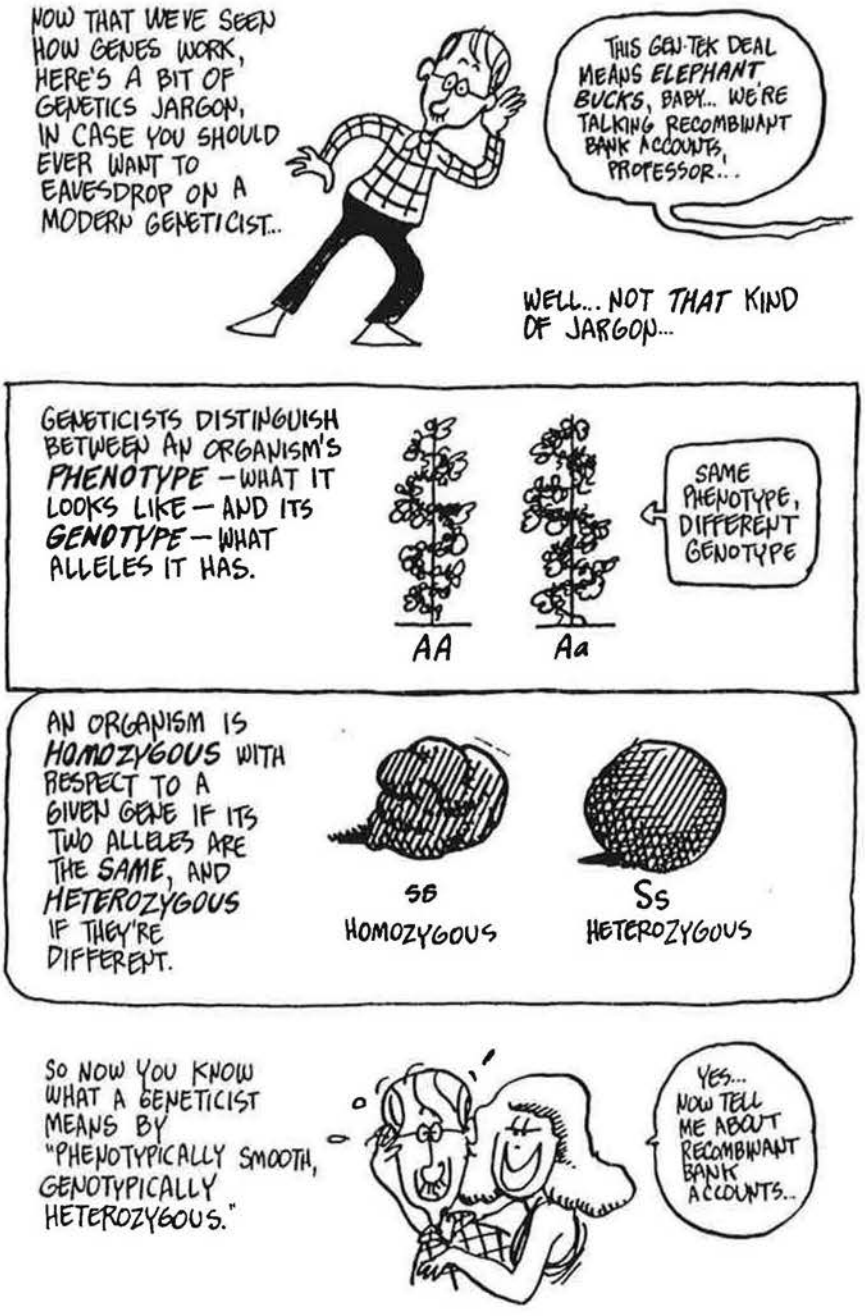

Figure 2.7 Some genetics jargon made simple! (Copyright 1983 by Larry Gonick and Mark Wheelis)

been described, for example, bishop pine (Pinus muricata) and ponderosa pine. (Figure 2.8). Alternatively, where the genetic variation occurs gradually, the pattern is described as 'clinal'. There are many examples of clinal variation in California's flora, where gradients in some environmental factor(s) are reflected in a genetic gradient. For example, early height growth in white fir (Abies concolor) and incense-cedar appears to increase clinally from south to north in California. The pattern of variation may vary in different traits within the same species. For example, in white fir, although early height growth appears to vary clinally, differences in adaxial stomata rows have an ecotypic pattern of variation (Figure 2.9).

The five forces influencing genetic variation (mutation, recombination, natural selection, migration and genetic drift) act within the constructs of this hierarchical arrangement. For example, natural selection acts primarily at the individual level. Mutation, recombination and random genetic drift can be regarded as forces that change gene frequencies within populations. Migration, as an interpopulation force, usually causes the genetic constitution of several populations to converge, depending on the strength of the migration. Selection and random genetic drift may oppose the homogenizing influence of migration by causing populations to differentiate from one another. The complex interplay of these four evolutionary forces determines the genetic constitution of a species and, ultimately, whether new species will emerge from the genetic division of a pre-existing species owing to the emergence of reproductive isolation barriers.

In conclusion, although the ultimate origin of genetic variation is rather straightforward, its nature within plant species is rather complex. This has two important implications. First, although there are certainly some generalities among plant groups, each species has a rather unique genetic signature - the amount and architecture of its genetic variation. Second, in any discussion of genetic variation, the context is all important. An appropriate context should consider a temporal reference point, the genetic architecture of the species, and the specific genes or traits whose variability is under discussion. The latter point, in particular, is important as the variability in one gene or trait of a species may bear little resemblance to the genetic variability in others.

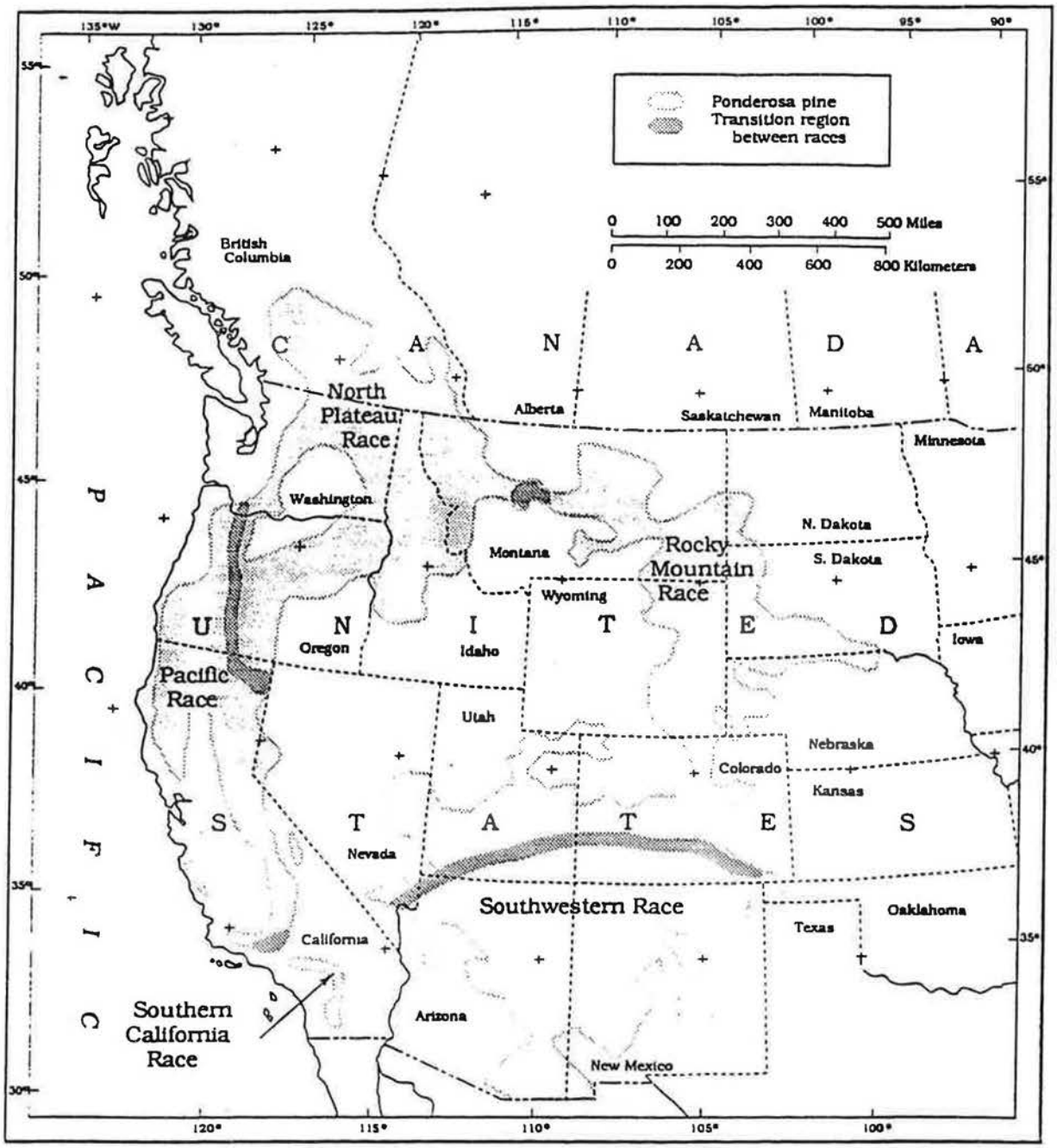

Figure 2.8 Major ecotypes of Ponderosa pine (from Millar and Libby, 1991)

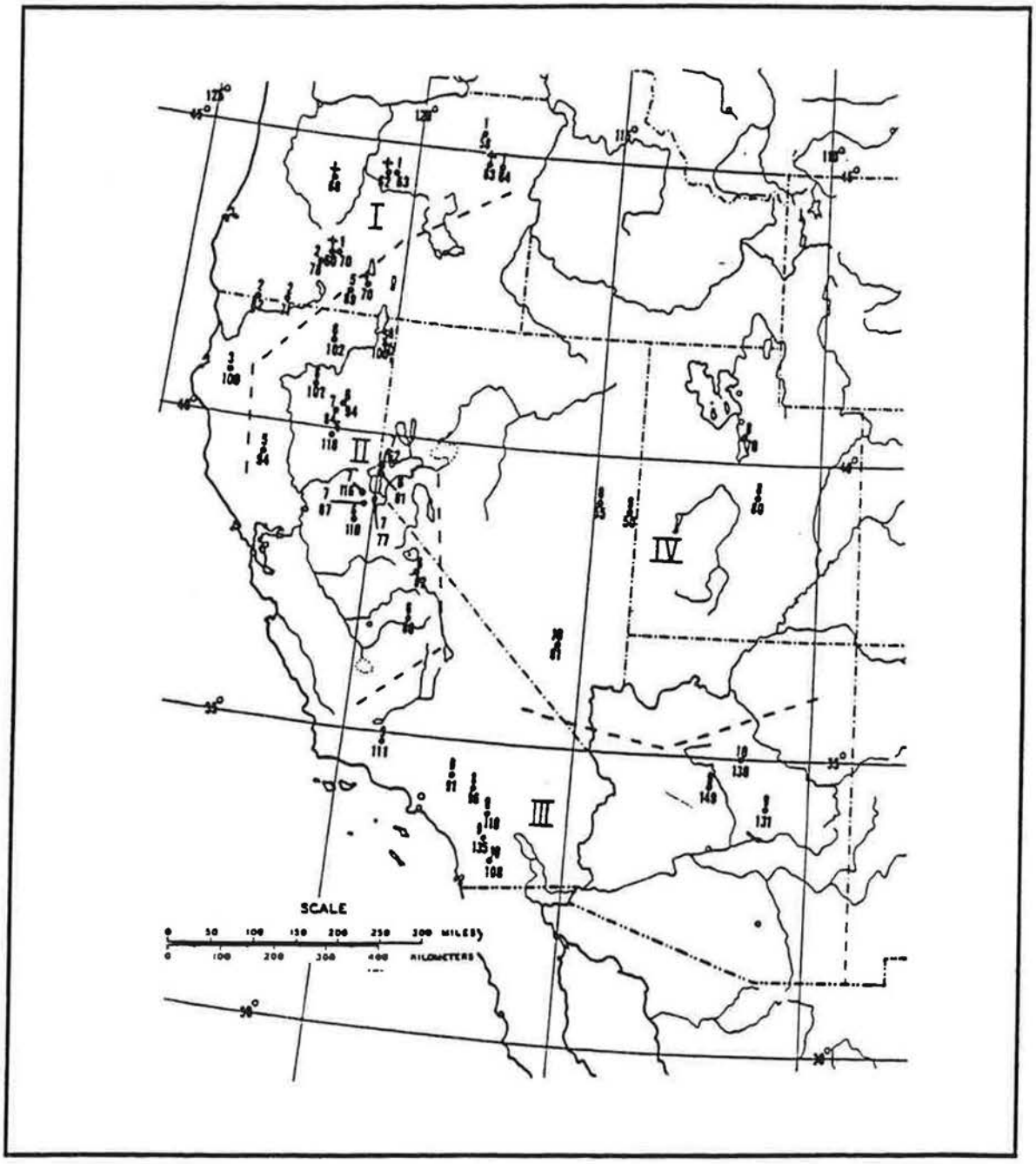

Figure 2.9 Clinal variation in second-year height (numbers above dots) and ecotypic variation in adaxial stomatal rows (numbers below dots) in white fir. Roman numerals specify the four regional groups that have been indicated on the basis of nine traits (from Hamrick and Libby, 1972).

Table 2.1 Some basic differences between genetic systems in plants and animals

FEATURE	PLANTS	ANIMALS
Breeding system:		
Selfing/inbreeding	Common	Uncommon
Monoecy*	Common	Uncommon
Location of DNA	Nucleus, mitochondria, Chloroplasts	Nucleus, mitochondria
Stability of chromosome number	Wide range in number, even among species within same genus	Very stable
Size of chromosomes	Wide range in sizes, even among species within same family	Lower range in sizes
Somatic* variation in chromosome number	Not uncommon; known as 'genetic mosaic'	Extremely rare
Ploidy* level	Changes among species are quite common, even among species of the same genus	Conservative, less variation

Table 2.2. The major types of plant mating systems

MATING SYSTEM	DESCRIPTION	EXAMPLE
Predominantly selfing	About 20% of all plant species fall into this category. In populations of these species the majority of seeds are produced by self-fertilization	Lupines; Camouflaged campion
Predominantly outcrossing	Includes the majority of plant species. Rarely, if ever, self-fertilizes.	Most forest tree species e.g., jeffrey pine
Mixed selfing and crossing	Species which exhibit an intermediate or variable amount of outcrossing	Some clover species; Primroses
Apomixis	Species that form seed without meiosis or fertilization. It is a uniparental form of reproduction.	Dandelions, hawkweeds
Haploid selfing	The (haploid) gametophyte self-fertilizes, thus producing a homozygous plant in one step	Some ferns

III. HUMAN INFLUENCES ON GENETIC VARIATION

Although natural processes are continually shaping the genetic variation of plants, as described in Chapter II, they are dramatically upstaged by human impact. The nature of the impact can be quantitative and/or qualitative. A quantitative impact must be assessed within an appropriate context: more genetic variation is not necessarily better; less genetic variation is not necessarily worse. While natural processes tend to work in many (often balancing) directions, and in a gradual and cumulative manner, human influences may cause dramatic unidirectional (either increases or decreases) shifts in genetic variation. An impact can also qualitatively affect genetic diversity: although the total amount of genetic variation may remain unchanged, there may be changes to the genetic architecture, type of alleles present (e.g., well-adapted or foreign), or the distribution of alleles (e.g., amount of homozygosity in the population), any of which may affect fitness*.

Anthropogenic effects can be classified as direct - such as removal of a plant population by harvesting, or indirect - such as polluting the air, thereby creating selection pressure for pollution-tolerant genotypes. Land conversion effects, where whole populations are completely obliterated, are direct, immediate and obvious, and will be discussed only for their effects on fragmentation. The direct impacts will be addressed under the headings of **genetic contamination, fragmentation, and vegetation management** (Figure 3.1). Here, management includes most of the intentional, normal park activities, such as maintaining or restoring natural communities. The indirect effects on genetic variation caused by **climatic change** and **air pollution** will then be reviewed. Finally, the genetic consequences of **fire** will be discussed, recognizing that this phenomenon could be classified as either natural or anthropogenic.

Genetic Contamination

This term refers to the introduction of individuals or genes from exotic (i.e., non-native) species or non-local populations of native species. It has been estimated that more than 10% (>3,000 species) of all spontaneously growing (i.e., non-agricultural) plants growing in the state are exotic; for our grasslands, the figure is closer to 90%. A common example of genetic contamination by an exotic species is the introduction to California of Eucalyptus species from Australia. Approximately 75 species have been introduced, including red ironbark (E. sideroxylon), manna gum (E. viminalis), and bluegum (E. globulus). These species serve to demonstrate the potential problem of exotics: they have quickly become established, even to the point of displacing some native species and changing the entire ecology of some grasslands to forest cover. However, because they are not adapted to the climate of California, they can suffer heavy mortality with extreme years, as was seen following the 1972 and 1990 frosts in this state.

A European immigrant that arrived in California in 1860 currently infests 7.9 million acres (12,344 square miles) or 8% of California's land. Yellow star thistle (Centaurea solstitialis), growing in dense stands in parks, grasslands and along streams, chokes out native vegetation and its presence on rangeland renders it unfit for grazing as the thistle is toxic to horses.

Domination by alien annuals has changed the nature of many Californian grassland communities. In the southeastern San Joaquin Valley, European annual grasses, such as Red Brome (Bromus rubens), soft chess (Bromus mollis), foxtail Fescue (Festuca megaleura), and hare barley (Hordeum leporinum) are stiff competition for the native annual grasses such as alkali barley (Hordeum depressum) and few-flowered fescue (Festuca reflexa). Here, contamination is characterized by low

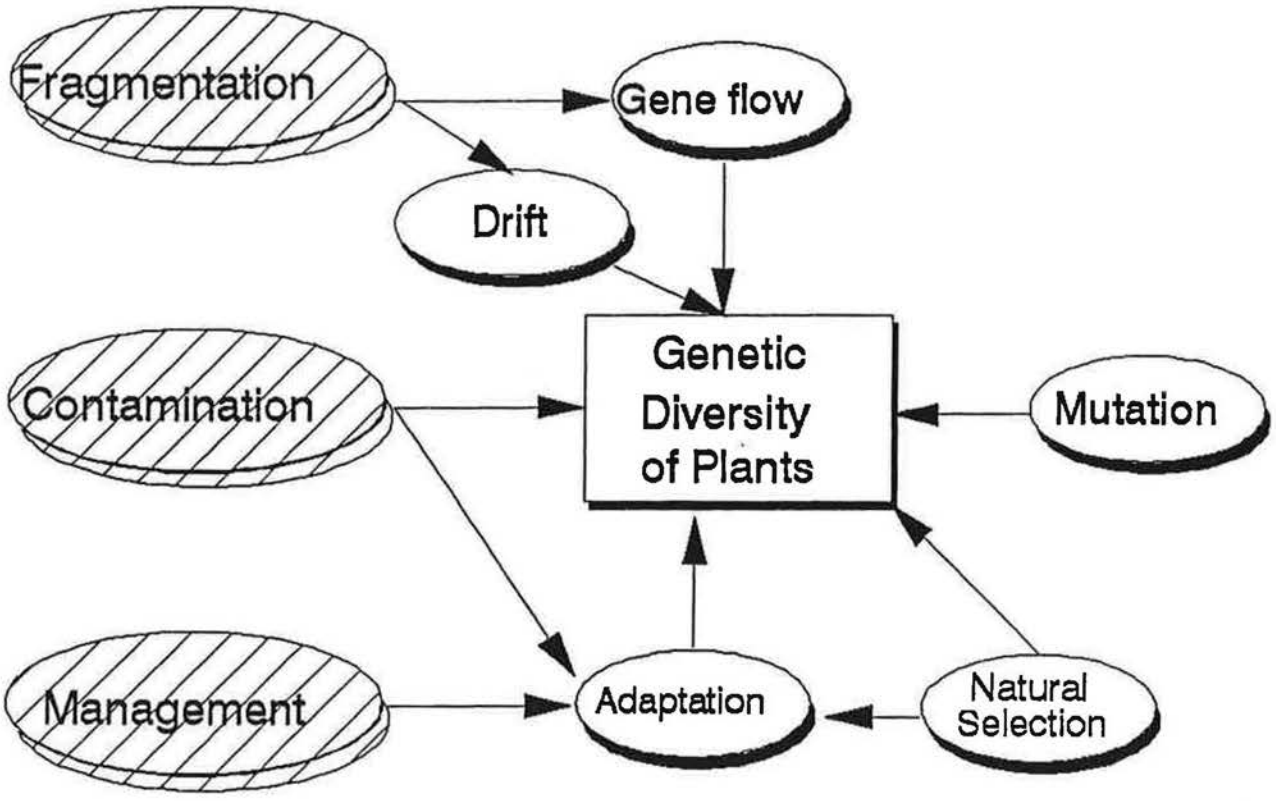

Figure 3.1 Quantitative impacts on genetic variation within populations. Human impacts (cross-hatched ellipses) interact with natural processes. Some relationships are straightforward. For example, fragmentation generally increases genetic drift, which reduces genetic variation within, and increases genetic variation between, populations. Other relationships are more context-specific. For example, natural selection sometimes increases, other times decreases, genetic variation within populations.

species diversity and low abundance of native species.

The second type of contamination is the introduction of non-local sources of (native) plant species, which could have a range of effects. Ill-adapted individuals will be selected against fairly quickly but others may survive past reproductive maturity, thereby 'contaminating' adjacent natural populations with their seeds and pollen. Genetic contamination of locals will not occur if the species is an obligate self-pollinator. But if the species is either facultatively or obligately outcrossing, the flowering members of the introduced non-local populations may massively contaminate the flowers of the truly native plants with their pollen. The full consequences of this kind of contamination are not well known. However, there are certainly many examples of non-local introductions. Non-local Monterey pine has been planted at Monterey and Cambria, CA, near two of the three endemic populations of that species. Non-local bishop pine (Pinus muricata) has been planted at Sea Ranch, CA, which is unique in being the meeting place for two divergent races of that species.

An example of a revegetation effort that combined both kinds of genetic contamination was the re-seeding effort of the Berkeley-Oakland Hills, following the fire of October, 1991. Over a ton of a grass seed mixture was broadcast over the area. The mixture consisted of six species, three of which were non-native. All three native species represented non-local populations.

A third type of human-vector contamination is the introduction of diseases and insects to the native vegetation. Dutch elm disease and gypsy moth are notorious examples. At the most extreme, this could obliterate the species. More often, it introduces a new selection pressure that confers advantage to individuals with tolerance or resistance to the pest. White pine blister rust, a fungal disease, was apparently introduced to Western North America in the early 1900's, and has spread widely through white pines across the country. Now a significant pathogen of eastern white pine, western white pine, and sugar pine, it is still expanding southward throughout the range of sugar pine in southern California. Strong selection pressure for resistance or tolerance will tend to reduce genetic variation more generally.

In another example, populations of Port-Orford-cedar (Chamaecyparis lawsoniana) are being threatened by a fatal root disease caused by the fungus Phytophthora lateralis. Genetic variation in Port-Orford-cedar is being directly and indirectly affected due to the effects of the spreading infestation of P. lateralis (presumed to be an exotic pathogen). Genetic resistance in Port-Orford-cedar is low or absent, suggesting that the epidemic will have a much different genetic effect on the species than in sugar pine, where genetic resistance is not uncommon.

Fragmentation

The patchwork removal of natural vegetation and installation of large-scale transportation and communication corridors results in the fragmentation of habitats and reduction of genetic variation within the remaining populations. This break up of natural populations is often described with 'island' analogies as the consequences of isolation are similar. This issue is especially important for the state parks, as they are likely to increasingly become natural islands in a human-altered landscape.

There are several major impacts on genetic variation from fragmentation. First, fragmentation interrupts the natural gene flow by disrupting the continuity in pollen flow and seed dispersal. The 'artificial' populations thus created, depending on size, site, and other factors, may experience more inbreeding and lose genetic variability over time. Second, smaller populations are more vulnerable to the effects of genetic

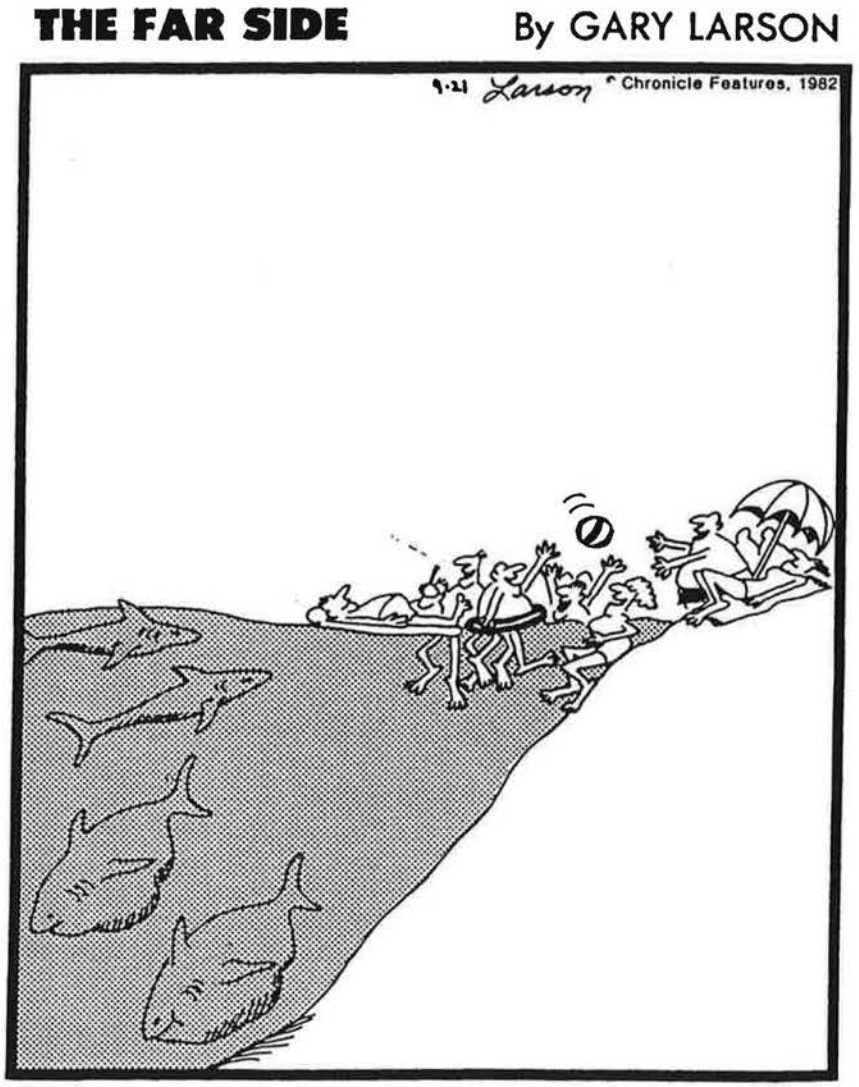

Figure 3.2 One impact of fragmentation: "edge effects". (The Far Side cartoon by Gary Larson is reprinted by permission of Chronicle Features, San Francisco, CA.)

drift. As discussed in Chapter II, this generally leads to loss of genetic variation. Third, by increasing edge effects and reducing the size of the natural area, fragmentation creates new microenvironments by changing the wind patterns, temperature, light and relative humidity within the fragment. Since these new selection pressures are created quickly, the effect on plants can be devastating.

The degree of impact of fragmentation is closely linked to the pattern and scale of genetic architecture of the species relative to the scale of fragmentation. Thus, breaking up sub-populations that are closely adapted to an environmental gradient such as slope, may have different genetic consequences than fragmentation of large, genetically variable populations. The severity of effect will also be related to the breeding system. If the species is mainly outbreeding, then fragmentation may result in a serious level of inbreeding depression.

Vegetation Management

With this term, we refer to the activities normally associated with the management of natural vegetation in parks. Such activities may involve general or selective removal of plants and vegetation restoration via natural or artificial regeneration. Vegetation management in state parks is based on risk, compromise and information (Figure 3.3). The goal is to minimize the risk of introducing plants that are ill-adapted over either the short- or long-term. The risk is the smallest when local sources are used for restoration. Management decisions also involve compromise, among different aspects of the state parks' mandate, and between biological and administrative (e.g., budget) concerns. Information is key to the success of the management activity. The more that is known about the target species - the amount and distribution of its genetic variation - the lower the risk. The more information available , the more efficient can be the management activity. For example, what sources may be considered 'local' will depend on how genetic variation is related to environmental differences. The best and worst possible outcomes from vegetation management are summarized in Table 1.2.

1) Vegetation removal - The selective removal of plants with a common characteristic, as long as it is genetically based, will decrease genetic variation for that trait. For example, selective removal of the better timber trees was an early logging practice, otherwise known as 'dysgenic selection' that resulted in loss of genetic variation for growth. Alternatively, random removal of individual plants is a 'genetically neutral' event, until the numbers removed are so large as to start removing rare alleles. Again, it is important here to keep in mind the context. For example, removal of exotic vegetation, while perhaps reducing overall genetic variability in an area, provides the opportunity for reinvasion by better-adapted, native, species.

Ice plant (Carpobrotus spp.) is an example of an exotic species that has negatively influenced native species in several different ecological settings. Thus, it is being removed from the dunes at Asilomar State Beach where it competes with Menzies' wallflower (Erysimum menziesii) and Tidestrom's lupine (Lupinus tidestromii var. tidestromii). Hand removal is being used to control ice plant in the Monterey pine - coastal bluff area at Point Lobos State Reserve. Here, it is directly competing with the dune eriogonum (Eriogonum parvifolum var. lucidum). It has also been removed from the understory of Torrey and Monterey pine stands where it appears to be competing for moisture, adding stress to the pines especially during drought years.

Vegetation removal, especially by prescribed burning, can be used to mimic natural processes, and encourage the growth of native plants and retard alien species. This approach is particularly useful in grassland communities, where the

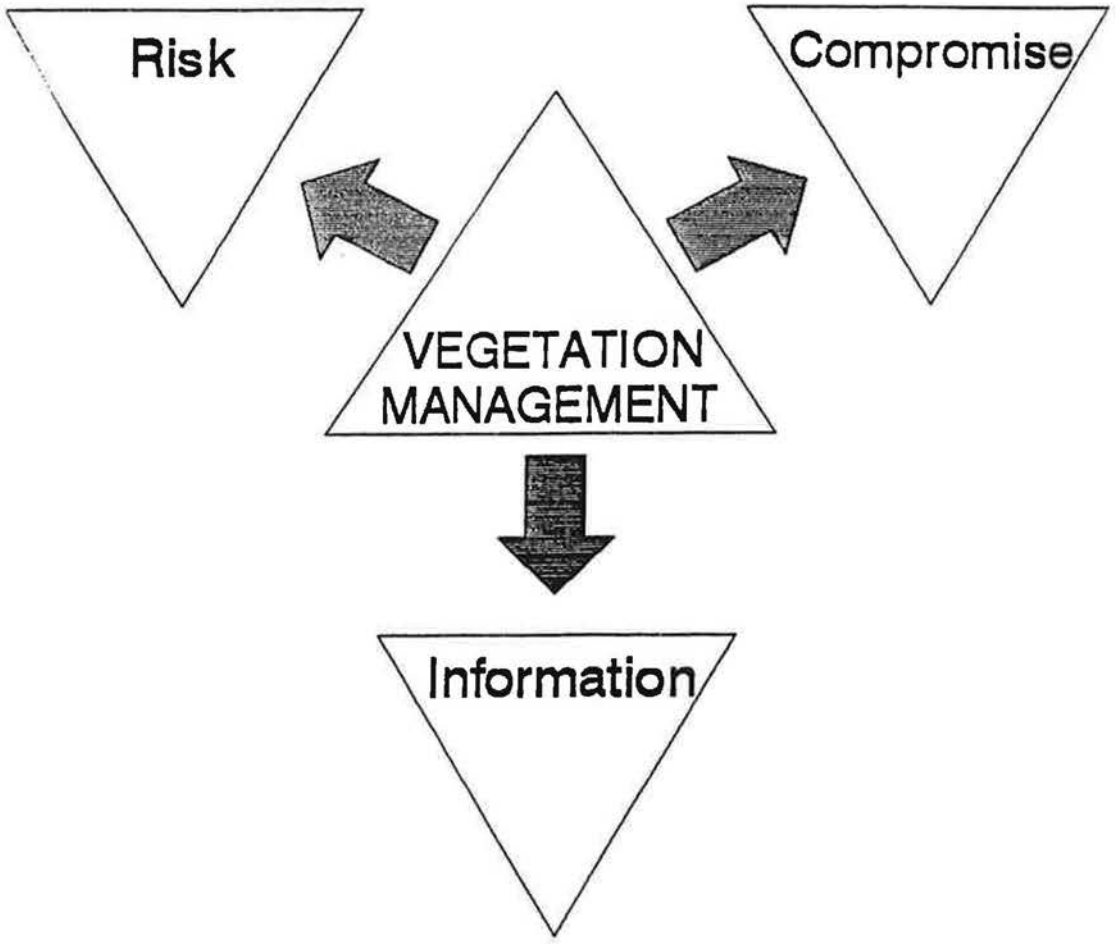

Figure 3.3 Vegetation management in state parks is based on the assessment of risk involved, the information available and the compromise struck among biological, fiscal and administrative concerns.

build-up of mulch and its consequent modification of the microenvironment can prevent the germination of native grass species. More information on the influences of fire on genetic variation will be presented in a later section.

2) Restoration - Following vegetation removal, an area may be left to regenerate naturally if the desired species is within proximity or has recently occupied the area. If there is an available in situ, natural, seed bank (i.e., reserve of viable seeds in the soil) this may be the most desirable restoration method as the resulting plants should be well adapted. If the seed bank was derived from a large, healthy, population then the level of genetic diversity should be sufficient to launch a new sustainable population. However, there is a disadvantage to natural regeneration when the seed source is from a small number of residual plants. In theory, this would tend to reduce genetic variability in the resulting new population due to inbreeding and genetic drift.

If natural regeneration is not appropriate, then the action normally taken is to seed the area directly or to transfer individual plants. In either case, there are three decisions involved, each with attendant impacts on genetic variation. They are: what source of genetic material to use, how to sample the source, and which propagule type to use.

The guiding principle in both selecting and sampling suitable genetic materials is to match, as closely as possible, the quality and pattern of environmental variation in the restoration site. Site quality factors are more influential than the size of the restoration site.

i) Source of genetic material: The effects of introducing an exotic species have already been discussed. The risk is that of failure, due to maladaptation, or, even worse, complete domination by the new species at the expense of native populations. In the longer term, this might result in catastrophic failure, and would undoubtedly result in lower genetic diversity in the area.

If native species but non-local sources are used, this would again probably result in maladaptation of the transferred material. Further, if the plants survived to reproductive maturity, this could result in the worsened situation of genetic contamination of any native populations in the vicinity. Deciding which source may be considered 'local' requires information on both the qualitative and quantitative aspects of genetic variation in the species. For example, if genetic variation corresponds with an environmental gradient such as elevation, soil moisture, temperature, or soil pH, the source must be matched with the restoration site or else there is a substantial risk of maladaptation. Alternatively, if the species is genetically depauperate (e.g., Torrey pine), then the source may be of little consequence and this information would allow the most cost-saving approach to obtaining materials.

The choice of an appropriate genetic source of material is important not only for the short-term survival of the restored vegetation, but for its longer term sustainability. First, maladaptation may not be immediately obvious. For example, variability in local weather patterns may allow ill-adapted plants to survive for several years before finally succumbing to unfamiliar environmental pressures. This generally represents a greater financial loss than if the failure had been immediate. Second, a correct match of genetic material also maximizes the probability that the other biological cofactors of long term survival will also be present at the restoration site. These cofactors might include mycorrhizal associations, specific types of soil bacteria, or pollinating vectors such as specific species of insects.

ii) Sampling the source: Whether the materials collected are seeds, whole plants or self-sustaining plant parts, information on the pattern and amount of genetic

variation in the species is required to sample the source appropriately. For example, if the genetic architecture of the species was such that the genetic variation within populations was very large relative to that among populations, then a fairly large number of individuals within the appropriate population(s) should be sampled. Transferring genetic material from just a few individuals in this case, even if it was from a region well matched to the restoration site, may result in a depression of genetic variability. If, on the other hand, most of the genetic variation of the species is distributed among populations, then the sampling strategy should be geared towards fewer individuals per population and more populations.

Some knowledge of the nature of genetic variation in the species also helps to determine the spatial collection of samples. For example, in a very large population of a widely-outcrossing species, it may be acceptable to collect many seeds per plant as long as the individual plants that were sampled are separated from one another. However, if there were just a few individuals of this same species in a remote, disjunct population, then there is a good chance that many of the seeds would result in plants exhibiting symptoms of inbreeding depression. Knowledge of reproductive biology of the species (for example, how far pollen is likely to travel) can serve as a guide for how far apart samples should be located in order to avoid collecting related individuals.

iii) Propagule type: The type of propagule chosen for use in restoration (for example, seeds, seedlings, or clonal materials) is largely a function of the biology of the species and characteristics of special interest. Some species (e.g., grasses) establish well from direct seeding, while others (e.g., coast redwood) are more likely to become successfully established when planted as seedlings or rooted cuttings. If part of the restoration objective is to increase or duplicate a certain plant trait (for example, known resistance to a certain pathogen) then this may dictate that the propagule be a product of asexual reproduction (i.e., from a parent plant known to possess the resistance).

When seeds from an appropriate source are used, the impact on genetic variation may be quite small. Since natural selection can act at a very early stage, the resulting plant population may be very similar to one resulting from natural regeneration. However, if the seeds have been stored for a time long enough to show some decline in percentage germination then 'artificial selection pressures' (i.e., those related to storeability characteristics) may have already modified the genetic composition of the seed collection. In any case, there are two features which would distinguish this 'restored' population from a natural condition. First, the demographic structure has been disrupted - with an even-aged population resulting. Secondly, the pattern of genetic architecture may have been significantly altered, depending on the pattern and the scale at which the regeneration activities were undertaken.

When seedlings are planted, the genetic implications increase. First, seedlings have been grown in an artificial environment, so the selection pressures have not necessarily been those that would operate in the natural environment. Certain genotypes may be lost due to selection at almost every stage of the nursery process, including seed storage, germination, culture, lifting, sorting and cold storage. Nursery practices that maximize seedling percent (percentage of seeds sown that develop to plantable seedlings) and seedling survival after outplanting will minimize changes in the genotypic mixture of a seedlot and preserve the maximum potential genetic diversity. Nurseries and species with large nursery factors (high seedling losses) undergo the greatest genetic change. Thus, using restoration materials purchased from a commercial nursery would tend to increase the risk of impact on genetic variation, unless the nursery practices were known and considered to be appropriate.

Occasionally, the seedlings chosen for restoration purposes may be the result of selection for certain characteristics, such as rapid growth, and thus may represent much less genetic variation than would the natural gene pool. The decrease in genetic variation is directly related to how strongly the selection pressure has been applied (e.g., number of parent trees), how the seeds were produced, and the heritability* of the trait being selected. Thus, there is a sliding scale of impact on genetic variation, with seedlings grown from 'unimproved' bulk seed collections representing the least impact, and highly 'genetically selected' seedlings (e.g., horticultural strains), the most. Further, whenever planting density is lower (e.g., individual plants were expensive) the opportunity is less for competition and other types of natural selection.

A third type of commonly used propagules is those that have been vegetatively reproduced (e.g., grafted plants, rooted cuttings, tissue-culture plantlets). As this implies that one genotype or 'clone' could be represented several or many times, the use of this material could potentially decrease genetic variation significantly. However, the impact will depend on the number of clones used, the number of copies per clone and the genetic variation among the clones. Vegetative propagation is most commonly used with species that would normally reproduce asexually in a natural state, and with rare and/or high value material that is well known, such as horticultural varieties. For many species, it is also often the quickest and least expensive method of propagation. Thus, caution needs to be taken to ensure adequate genetic representation in the planting stock.

3) Landscape management - In general, this term refers to consideration of the broader spatial scales at which populations, species and ecosystems reside. This involves recognition of both genetic-ecological connections and the relationships among distinctive ecosystems. Basic to these considerations is the understanding that ecosystems are inter-connected forming an 'ecological mosaic'.

Although conservation activities are often planned and discussed under the rubric of 'ecosystem, species or niche management' the effects are not confined to these levels. Influences on the genetic composition of a plant population will influence some other species (both plant and animal) directly and all others indirectly through inter-relationships with the common media of air, soil and water. The influence of scale limits the generalization of these impacts. Processes and parameters important at one scale may not be as important at another scale. For example, the distribution of oak seedlings is explained differently at different scales. Seedling mortality at local scales increases with decreasing precipitation, whereas mortality at regional scales is lowest in the drier latitudes.

The relationship between the environment and genetic diversity at the landscape level is a function of both environmental variability and the geometrical configuration of the environment. The former refers to the range of values of a particular environmental variable (spatial variability) and the latter to the continuity or distance decay of the variable (heterogeneity). Fractal geometry, with its characteristic parameter of 'fractal dimension' (D), is commonly used to explore the effects of environmental patterns of variability. Soils variables associated with hardwood forests often have fairly high fractal dimensions (i.e., tendency towards patchiness). Other important environmental variables, such as soil moisture in slightly sloping land, often have low fractal dimensions (i.e., gradual, continuous pattern of variation). In general, increases in either the spatial variability or heterogeneity of the environment are accompanied by increases in species richness*. However, the relationship with heterogeneity is more complex.

Two of the most significant decisions at the

landscape level of organization are those pertaining to park boundaries and transfers of genetic materials. Many of the associated ideas have already been discussed under the headings of fragmentation and vegetation management.

There is an ongoing need for management of genetic resources, after the more major and dramatic activities of vegetation removal and restoration are finished. This is required because both natural and anthropogenic influences will continue to shape the genetic composition of the population. In addition to the influences and activities already described, one further activity associated with longterm management is the preventative function of genetic monitoring (e.g., via isoenzyme analysis) to detect problems in the genetic health of the populations before they become catastrophic.

Climatic Change

1) The nature of climatic change - Although climatic change is normal, the rate of climatic change in the post-industrial era is such that it must be considered in current conservation strategies for plant genetic resources. The so-called greenhouse gases have either come into being (e.g., chlorofluorocarbons) or risen dramatically (e.g., CO_2, CH_4) since the middle of the twentieth century. The build-up of these gases has direct climatic implications, the most commonly predicted being a warming trend. A conservative estimate of mean global warming by 2030 is 1.5 to 2.5° C. from nineteenth century levels, with a further warming of up to 1.3° C. by 2050. (This is a conservative estimate as the ocean's thermal inertia has been taken into account.) Other predicted changes, associated with this warming trend are: increases in mean global precipitation and evaporation, and sea levels.

Even if the global predictions are accurate, local responses may vary considerably. It has been suggested that during the transient phase of climate change the middle of continents, middle of oceans and high latitude oceans will all be evolving toward new equilibrium temperatures at different rates. This means that the temperature differences from land to sea and equator to pole will shift over time, which suggests that regional climatic anomalies associated with global warming will not necessarily be uniformly increasing over time, but could have a transient character very different from the long-term equilibrium character. Thus, not only may local climates vary significantly from the overall global change (for example, there are some predictions that the California coast is experiencing longer and colder fog seasons) but the local patterns are much less predictable than the global ones.

2) Implications for vegetation - Predicting vegetation response to these climatic changes is complicated by the uncertainty of local climatic changes and the complexity of ecosystems. Further, the type of selection pressure exerted by climatic change is likely to be species-specific, and depend on the local mix of climatic variables. For example, an increase in temperature will increase transpiration thereby increasing water stress, but the accompanying increase in CO_2 concentration will tend to increase the water use efficiency of plants. Thus, the net effect in this case will depend on the species and the relative increases in temperature and CO_2 at the local level. In spite of the uncertainty, the effects of climatic change on plant genetic resources can be characterized as two types: 1) Gradual selection pressure, resulting in in situ adaptation and changes in relative abundances of plant species, and 2) Species migrations, including expansion or shrinking of total range and even extinction. Probably the former effect will be the more common, with extinctions and species boundary changes being more related to extreme years in climate.

The most commonly predicted migration pattern in response to climate change is that species will shift their boundaries

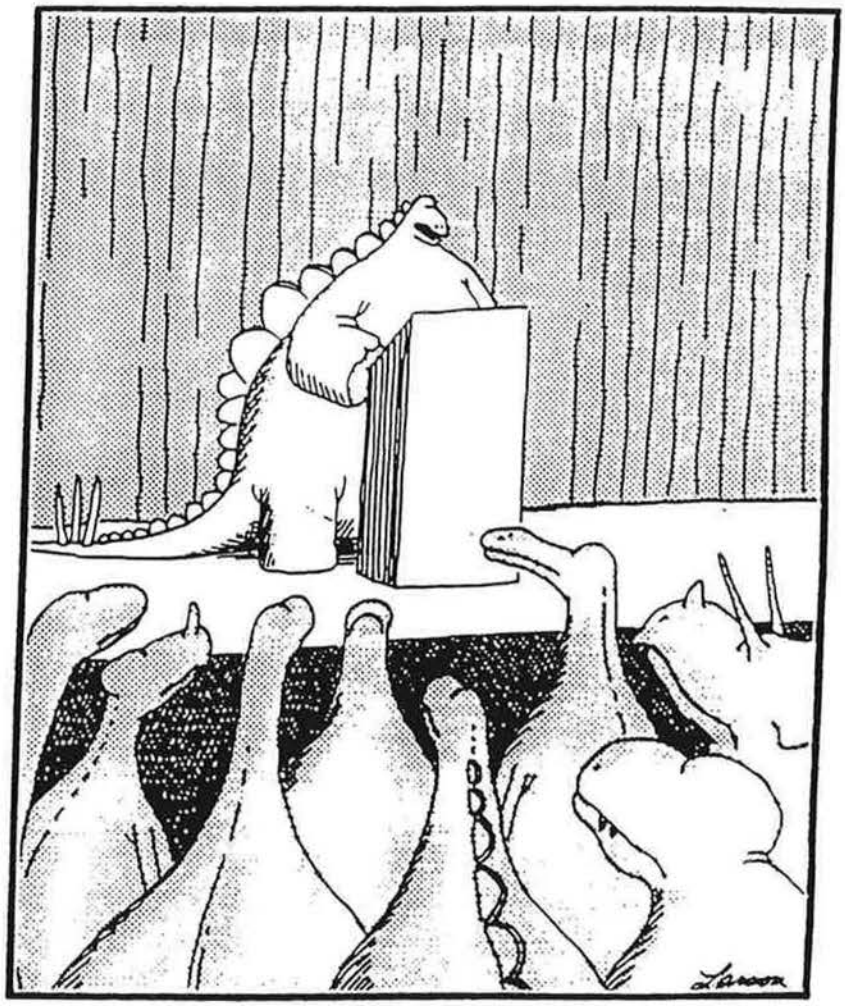

Figure 3.4 Climatic change is a timely theme for conferences (THE FAR SIDE copyright 1985 UNIVERSAL PRESS SYNDICATE. Reprinted with permission. All rights reserved.)

northward and/or upward in elevation. For example, loblolly pine (Pinus taeda) is limited currently on its southern border by moisture stress on seedlings. It has been projected that its southern range limit would move 350 km northward in response to a 3° C. increase in temperature. However, this scenario rests on three rather questionable assumptions. The first assumption is that there are no restrictions on movement other than climate. Plant species migrations have been compared with bird migrations. However, a key limitation in this analogy is that birds can fly over great distances of unfavorable habitat, while a plant species requires favorable and fairly contiguous habitat in order to 'migrate'. Thus, depending on pollen and seed dispersal distances, migration could be limited by such obstacles as mountains, lakes or oceans, or unsuitable soils. Further, human-induced fragmentation caused by activities such as mining, agriculture and other developments severely limits the ability for plants to migrate.

The use of artificial migration corridors among park 'islands' is one option park managers have to mitigate the effects of the compounded stresses of fragmentation and climatic change. Corridors are generally believed to provide such benefits as enhanced biotic movement and refuges during disturbances, although there are also potential disadvantages such as facilitating the spread of diseases, insects and fire, and the high cost of maintaining linear remnants with high edge:area ratios. The relative merits of corridors and their required characteristics (e.g., width, composition) will vary from place to place and will depend on the target species.

Second, it assumes that other climatic factors will vary in the same way as temperature, such that a move northward would simply be an expansion into a familiar environment that itself has moved. However, it is more likely that entirely new environments will be created, rather than just shifting the boundaries of the current ones. This is likely because, while mean temperatures and CO_2 concentrations are increasing globally, the solar radiation regime and often the rainfall will continue to be controlled largely by latitude. Thus, climates will be created which have no precedent. Finally, there is the assumption that necessary and co-adapted biotic components of the plant species will survive and migrate in the same direction and manner. Thus, insect-pollinated plant species depend on the coordinated migration of their pollinators.

Climatic effects on genetic variation may also be mediated by effects on the ecosystem, which are even more difficult to predict than are species effects. For example, in the desert and chaparral, one might expect plants to grow larger and more quickly as the concentration of CO_2 increases. However, this will also increase the rate of fuel accumulation, and hence the chaparral may burn more frequently under elevated CO_2 levels. Thus, climatic change may act both directly and indirectly as a selection pressure on plant species.

Finally, the most significant factor in determining vegetation response to climate change is the rate of climatic change relative to the potential rates of adaptation and migration. The fastest rate of migration estimated for any North American forest tree species (i.e., spruce, Picea species) (under favorable wind conditions, 9000 years ago) was 200 km per century. This rate will vary according to habitat conditions, management and the life-histories and reproductive biology of the constituent species. The faster the rate of climatic change, the less likely are adaptation or migration to be effective in maintaining the plant species.

Given the uncertainty of how climatic change will influence plant populations, there is little opportunity to predict which genotypes will be most successful in the future environments. Initially, individuals with higher levels of plasticity may be favored, but if climatic conditions stabilize

and/or continue to change in the same direction, more specifically adapted genotypes will be ultimately favored.

There are three implications for genetic conservation based on this uncertainty. First, the most conservative approach, directed at maintaining as much genetic diversity as possible, is indicated. Second, in situ populations should be supported with ex situ collections (discussed in Chapter VI). Third, as the environment changes, so too must our ideas of what is 'native' and 'exotic'. The transfer of genetic materials must be considered within this context.

In summary, although there is controversy regarding the rate, extent and direction of climatic change, it behooves natural resource managers to make the conservative assumption that it is a reality and is contributing to the selection pressures on plant populations. These changes will probably result in environments which have no precedent, and which will vary considerably at the local level. One traditional survival response of plant species, that of migration, has been severely curtailed due to the excessive, human-induced fragmentation of plant populations. For these reasons, the maintenance of genetic diversity is absolutely essential in order to allow plants the opportunity to adjust to these novel conditions in situ.

Air Pollution and Acid Rain

These refer to the general phenomenon of atmospheric deposition, normally anthropogenic. There are three major mechanisms for transfer of substances from the atmosphere into ecosystems: (1) absorption and adsorption of gases; (2) impaction and gravitational settling of fine aerosols and coarse particles, and (3) precipitation (rain, snow, hail, dew, fog and frost) containing both dissolved substances and particles removed from the atmosphere. Acid precipitation, in particular, has received considerable attention: there is incontrovertible evidence that changes have occurred in the acidity of precipitation in North America since industrialization began. (Acid precipitation is arbitrarily defined as precipitation with a pH value below 5.6). As the acidity of precipitation reflects the balance between all the major cations and anions in solution, plus the impact of temperature on the chemical reactions, there is to be expected some natural variation in the pH of precipitation. However, variation due to such natural changes in conditions is completely dwarfed by that due to anthropogenic influences.

There is considerable evidence that air pollution and acid rain are having genetic impacts on natural plant populations. These stresses can act at many levels on individual plants and ecosystems, affecting leaf cuticles (and hence photosynthesis and water balance), soil pH (and hence nutrient uptake), as well as direct toxic effects. When the stress is large, all individuals of the population may succumb. This may occur in particular where the plant populations are already under heavy stress from other factors. Alternatively, and more commonly, the stress acts as a selection pressure as some individuals are more sensitive than others to the effects of acid rain and air pollution. Thus, as sensitive genotypes are eliminated, so are their genetic contributions to the population. Alleles that are exclusively present in the susceptible genotypes may be lost in one generation! The major effects, though, are reduction in overall genetic diversity and selection for tolerance.

Genetic variability in tolerance to air pollutant stress has been demonstrated for many forest tree species (e.g., ponderosa pine, Scots pine, Douglas-fir, Norway spruce, white birch, yellow birch, beech species, poplar species). This feature is being exploited in some tree improvement programs, where trees tolerant to industrial emissions are selected, but the genetic basis for the tolerance is not understood. In spite of a few specific cases, such as these, little

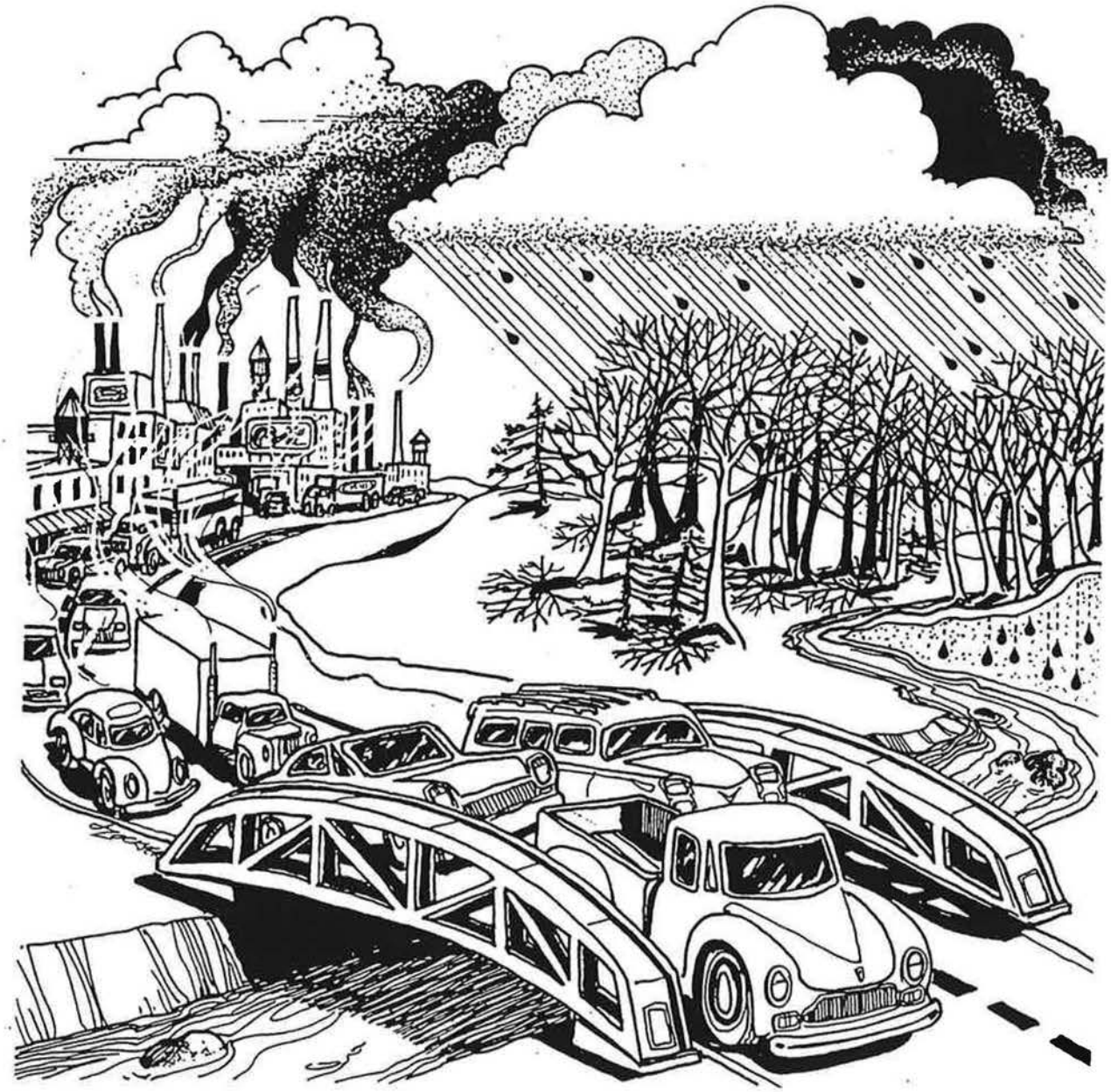

Figure 3.5 One of the park/urban interfaces is represented by the impact of air pollution and acid rain on native plants (From Hornbeck, 1981).

optimism has been expressed that adaptation could be a very likely or satisfactory response to acid rain or air pollution. First, the stress may simply be too great and result in decline and death. Second, these stresses typically have multiple impacts and simultaneous, coordinated adaptation in many plant traits would be required. Although mitigation is the only reasonable longterm solution to pollution stress, there does at least appear to be some progress in the development of diagnostic methods to identify sensitive and tolerant plant groups with respect to air pollutant susceptibility.

In summary, air pollution and acid rain, like climatic change, pose additional stresses or selection pressures on plants. The best opportunity for the survival of extant plant populations under these conditions is the promotion and maintenance of genetic diversity.

Fire

Fire, whether of natural or anthropogenic origin, can be a major selective force in determining plant species composition and even genetic characteristics within a species. In order to allow adaptation there must be a genetic basis for the traits that render some individuals more fit than others with respect to fire. Some plant traits considered adaptive to fire are: fire-resistant roots, bark and/or fruit; bud protection and resprouting; fire-stimulated flowering; seed storage on the plant and fire-stimulated dispersal; seed storage in the soil with fire-stimulated germination. Thus, different species may adapt to fires in different, but effective, ways. Further, species frequently display multiple fire-adaptive strategies. Also, morphologic and physiologic changes are usual as plants age, particularly if they are long-lived perennials. In short, complexity rather than simplicity should be expected in the adaptations of plants to ecosystems where fire is expected.

Controlled burn studies with three rare California plant species have shown that these species are fire-adapted, each in a somewhat different way. Roderick buckbrush (Ceanothus roderickii), although completely consumed by fire, regenerates profusely from fire-stimulated germination of its seedbank. Seedling germination and survival are apparently much greater than under non-burned conditions. Pine Hill flannelbush (Fremontodendron decumbens) resprouts after a fire, leaving the original population virtually unchanged. Its seedbank, too, is stimulated to germinate by fire. Eldorado mule-ears (Wyethia reticulata, a candidate for state-listing as rare) is apparently well-adapted to episodes of fire. Unlike the other two species it does not exhibit fire-stimulated germination from a seedbank. Instead, there is a major increase in flowering and subsequent seed production the first year after the fire. Additionally, plants are stimulated to reproduce vegetatively the second season after a fire, leading to an increase in the population over pre-fire levels.

Common examples of fire-adapted trees are bishop and Monterey pine (Pinus muricata and P. radiata, respectively). The serotinous cone habit (i.e., resin-bonded cone scales open at 45-50° C., releasing seeds) is the major mechanism enabling these pines to become established at the expense of associated species. A contrasting adaptation to fire is found in many annual grass species. Their seeds lie dormant under a layer of mulch until a fire removes it. Germination is then triggered by light which can now be sensed by the seeds.

Fire not only plays a role in determining species distribution at the landscape level, but the spatial distribution and genetic composition of populations within fire-influenced ecosystems. For example, when the burn is patchy (e.g., Klamath fires of 1987) the remaining plant 'islands' are subject to effects of genetic drift and other effects, as previously discussed, which result from fragmentation.

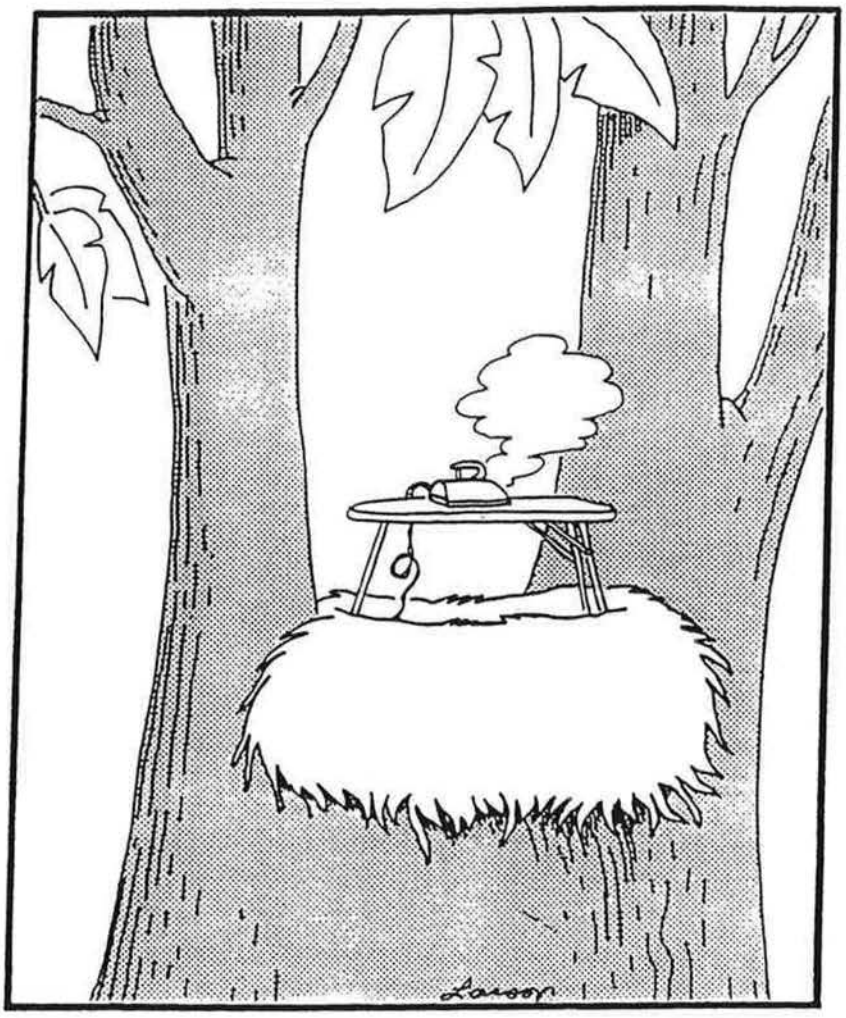

Figure 3.6 Some native plants exhibit adaptations to fires of 'natural' origin. (THE FAR SIDE copyright 1985 UNIVERSAL PRESS SYNDICATE. Reprinted with permission. All rights reserved.)

Within the natural range of fire-adapted species, there is evidence that fire has influenced the genetic composition of different populations. For example, cone serotiny in lodgepole pine (Pinus contorta) can vary greatly between populations. Cones of the coastal populations are fragile, symmetrical, open and deciduous, while many of the northern Rocky Mountain populations and the Mendocino pygmy forests are hard, asymmetrical, serotinous and persistent. This correlates well with the fire characteristics of these areas, being severe and widespread in the Rocky Mountains, and low-intensity and frequent close to the coast. This is consistent with a model in which cone serotiny in the species is governed by a single gene and two alleles. This hypothesis attributes trees with a preponderance of either open or serotinous cones to the homozygotes, but the phenotype of the heterozygote would bear both types of cones.

There is also some evidence that age of tree may influence serotiny. It has been observed that young stands tend to bear open cones, and towards age 20-30 years, this may change to a preponderance of closed cones. Thus, there may be a complex interaction of ontological and genetic factors influencing serotiny in this pine species.

Two other comments regarding fire as a selection agent are worth noting. First, a trait which is seemingly adaptive to fire, such as vegetative survival through bud protection and resprouting, may be adaptive to other environmental variables as well (e.g., insect attack, shade, disease). Thus, the relative influence of fire in shaping the adaptation may be difficult to ascertain. Second, fires vary in frequency, intensity, size and other features, each of which can affect the type of selection pressure exerted on the plants. Thus, adaptation must be considered within the context of the usual, local fire regime: type (i.e., peat or above-ground), season, frequency and intensity.

Table 3.1 The best and worst possible outcomes of vegetation management activities

ACTIVITY	NEGATIVE OUTCOME	POSITIVE OUTCOME
Vegetation Removal	Undesirable selection pressures; Loss of genetic diversity	Removal of exotic species or ill-adapted, non-local populations
Restoration	Death of transferred materials; Genetic contamination of local populations; Introduced exotics dominate landscape	Restoration of well-adapted, local populations of native species
Landscape Management	Undesirable selection pressures; Loss of genetic variation	Maintenance or promotion of genetic variation in well-adapted populations

IV. DIRECT ASSESSMENT OF GENETIC DIVERSITY

Given the importance of genetic diversity, we need a means by which to measure it. A well-known geneticist once referred to this as 'the struggle to measure variation', hinting at the complexity and multiplicity of this issue. There are many ways to assess genetic variation, the most appropriate one depending on the intended use of the information. The kind of genetic variation of interest to conservation biologists can be measured as the amount and structure of genetic diversity within and among populations.

The actual measurements of genetic diversity mean little in themselves: they require an appropriate context for interpretation. Genetic structure is addressed by using an appropriate sampling design and then comparing amounts of variation at different hierarchical levels, such as the individual, population and species. As such, this discussion will begin with a summary of contextual considerations, proceed with a consideration of sampling strategies, and concentrate on approaches to quantifying genetic diversity.

Context for interpretation

The meaningful interpretation of values of genetic diversity requires an appropriate context.

i) Genetic architecture - As discussed in Chapter II, genetic variation in plant populations is arranged in a hierarchical structure. Thus, measures of genetic variation of a plant species should be discussed in relation to this structure. Also, many measures of diversity only have meaning relative to other species - their absolute value is meaningless. For example, it has been suggested that the number of alleles in a population relative to the total number of alleles present in all populations of its species (i.e., rather than the absolute number of alleles) may constitute the best single estimate of the relative potential of the population for adaptive evolutionary change.

ii) Comparison species - To judge a species as relatively genetically variable or invariable, a suitable comparison species is required. For example, it would not be reasonable to compare the genetic variability of a grass species with that of a conifer, if the objective was to focus on the genetic variability of that one particular grass species. A suitable comparison species is generally one that has the same taxonomic status (i.e., gymnosperm, monocot or dicot angiosperm), life form (e.g., annual, long-lived herbaceous perennial), geographic range, breeding system and successional status.

iii) Traits assessed - A genetic analysis based on height comparisons will not necessarily yield the same picture of genetic variation within the species as one based on the protein level (isozyme analysis) or the DNA level (RFLP analysis). For example, in one comparison between isozyme loci and quantitative traits* in Douglas-fir, no significant associations were found. On the other hand, a similar comparison among several populations of ponderosa pine did reveal significant associations. Thus, genetic variability must be discussed in the context of the trait(s) measured. Ideally, different kinds of traits should be assessed and the information combined to form a composite view of genetic variation for the species.

iv) Temporal context - As genetic assessment is a relatively recent activity, there is little chronological information available on patterns of genetic variation. Sometimes two generations are simultaneously assessed by assaying (i.e., isozyme or RFLP analysis) both parental tissues and seeds. However, establishing baseline levels of genetic variation is key to monitoring changes in diversity. Thus, an assessment of genetic variation should not be considered a static genetic 'fingerprint' of a species, but rather, a temporal sample of

its genetic history.

A second aspect of temporal influence, already discussed, is that techniques may be strongly associated with the timeframe in which the genetic variation occurred.

Sampling Strategies

For all but the rarest species or populations genetic assessment is based on a sample of the total genetic resource of a species. Thus, the proportion of the variation sampled (i.e., proportion of genes and individuals) will influence the assessment. As well, there is the 'catch 22' situation that the most effective and efficient sampling design requires a priori information about the genetic structure of the species. If nothing is known about a species, some direction about probable genetic architecture of the species may be gained from its other general characteristics (see Indirect Assessment of Genetic Diversity - Chapter V).

There are rules of thumb that can be helpful in sampling for genetic assessments. These rules have the underlying assumption that all populations have essentially similar levels of variation. Under this assumption, the optimum sampling strategy is: i) to collect 50-100 randomly distributed individuals per site, ii) to sample as many sites as possible with the time and resources available, and iii) to ensure that sampling sites represent as broad a range of environments as possible, within the target area.

The efficiency of this sampling strategy declines with departures from the assumption of evenly distributed genetic variation.

Approaches to Assessing Genetic Diversity

Measuring genetic diversity, although trivial in principle (i.e., counting different types of genes), is difficult in practice. This is a consequence of at least three characteristics. First, genetic variation may be measured at various scales, including genes, genotypes, and populations. Second, it may be measured at various biological levels from the molecular (e.g., nucleotides, genes), to protein, to phenotypical (e.g., physiological, developmental, morphological) levels. Third, regardless of the type of measurement chosen, the resulting statistics must be interpreted within an appropriate context. As the first two of these are interdependent, they will be considered together in this section. Following is a consideration of the appropriate context for interpreting the quantitative assessment.

1) Phenotypic approach - As discussed in Chapter II, the diversity we perceive results from the interplay between both genetic and environmental influences. Thus, although the least expensive and complicated approach to assessing genetic diversity would be to take measurements under natural conditions, this is not often appropriate. Normally, we can't separate the variation we see into that part which is due to environmental influences and that which is due to underlying genetic variation.

Situations in which direct observation of genetic variation may be possible are those where environmental conditions do not affect the expression of the trait. An example of such a trait might be insect-resistance or disease-resistance where resistant plants growing among other severely affected neighbors may suggest a genetic cause. Sugar pines resistant to white pine blister rust can be detected in this way. In these cases it is assumed that all the plants were exposed to the pest and thus the basis for resistance must be genetic. Also, the expression of the genetic difference is clearly visible.

More often though, the genetic differences are more subtle (i.e., the environment affects the phenotype). For example, measuring the heights of some perennial grasses in two different areas would not be

informative. The difference in heights between the two areas could be due to genetic differences between the plants, microsite differences such as water or nutrient availability, or a combination of the two. In these cases genetic diversity can only be measured with appropriate controls and techniques.

One of the simplest (and time-honored) approaches to measuring genetic variation is to sample the species, often by collecting seeds or cuttings, and to grow the seedlings in a homogeneous test environment. By growing the plants in such a common environment (called a common-garden study), the variation observed is assumed to be genetic because all the plants are subject to the same environment. The sampling design for the plants in the study allows comparisons of genetic variation within and among the various hierarchical levels - e.g., individual, family, population, and region. The characteristics measured are most often morphological (e.g., growth, leaf size or color), phenological (e.g., rate or timing of vegetative or reproductive growth), or physiological (e.g., drought, frost tolerance, rate of photosynthesis or respiration).

Statistical procedures are applied to these measurements in such a way (i.e., analysis of variance) as to separate genetic and environmental variation. This separation is not possible with measurements taken from wild-growing plants as the environment in which all the plants are growing can not be assumed to be common to all. Thus, the results from this type of genetic assessment are expressed in terms of the percentage of genetic variation that contributes to total phenotypic variation and the percentage that is expressed at each level of the genetic hierarchy. Finally, this level of variation typically reflects relatively recent genetic differences, and often is interpreted to reflect adaptive variation.

As an example, a common garden study of six populations of incense-cedar was established near Foresthill, California, in 1981. After twelve years there are major differences between the southern-most population (S. California) and the other five populations in terms of average height and diameter and the shape of the crown* (Figure 4.1). This population also is more variable than the other five.

The advantages and disadvantages of the phenotypic approach are summarized in Table 4.1. The phenotypic approach is attractive in that it is relatively simple to design, install, analyze and interpret. Once installed, the field studies can be used for many other purposes. The characteristics measured are biologically meaningful. However, as the expression of the traits of interest may vary with the age of the plants and with the growing environment, it is often necessary to replicate the tests on several sites and to monitor them over several or many years. This makes the experiments expensive to establish, and also, due to the large amount of space and time they occupy, they are at risk.

2) Allozymes - Since the late 1960's, the application of a biochemical technique known as electrophoresis has provided the most abundant source of information regarding genetic diversity in natural plant populations. This type of study is also commonly known as isozyme or isoenzyme analysis. This technique distinguishes genetic variation that is expressed in different ('allelic') forms of a protein. Proteins obtained from tissues of individual plants are placed side by side on a suitable medium, such as a starch gel, and are subjected to an electric current. The proteins migrate at differential rates, depending on their size and charge. Using suitable stains, the protein migration positions can be detected and compared, thus allowing protein differences to be determined. This technique, therefore, detects a subset of molecular variation that may exist among the individuals studied. The genetic variation detectable here is within those genes that code for soluble enzymes, and whose variations produce differences in electrophoretic mobility.

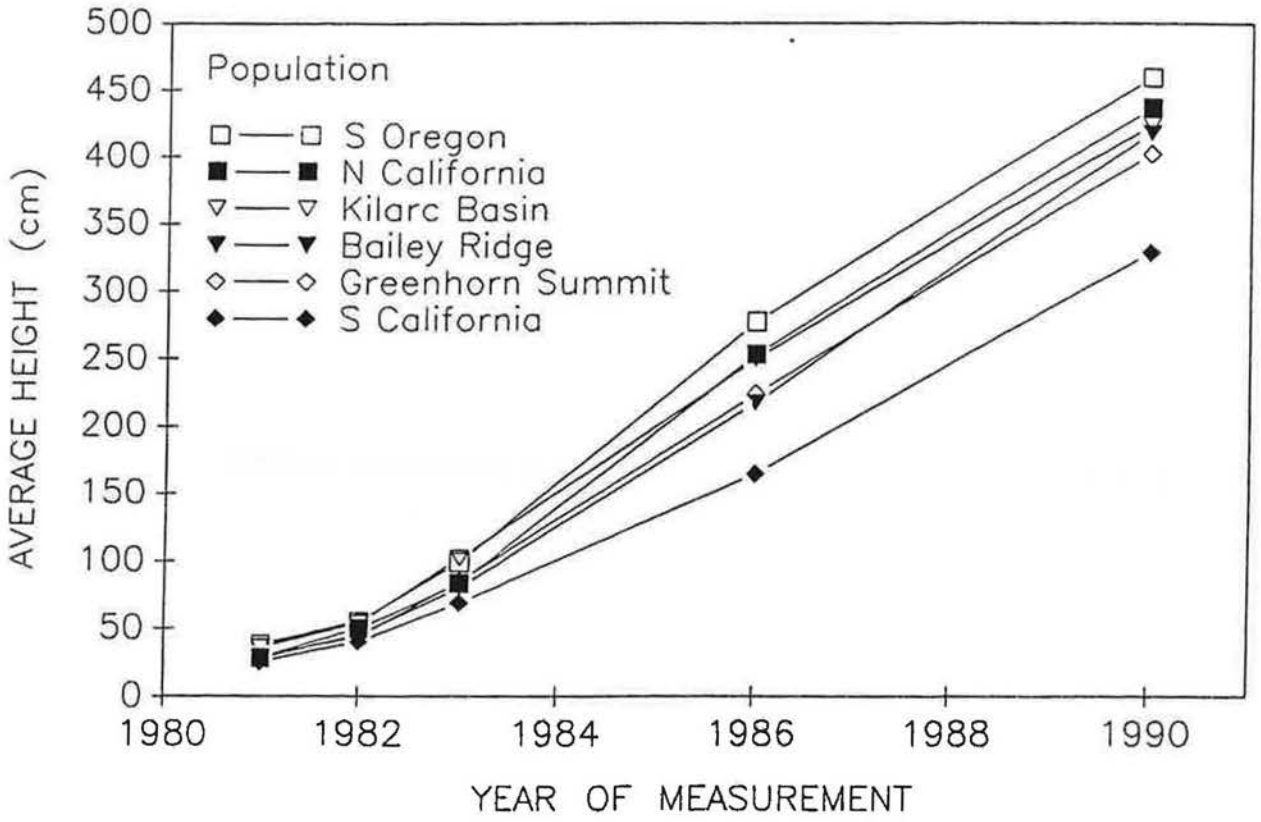

Figure 4.1 Population mean heights at 3 (1981), 4 (1982), 5 (1983), 8 (1986) and 12 (1990) years of age for six populations of incense-cedar growing in a common-garden study near Foresthill, California (From Rogers, Harry and Libby, 1992.)

Table 4.1. A comparison among common garden, allozyme and molecular methods for the detection and measurement of genetic diversity.

CRITERION	COMMON-GARDEN STUDIES	ALLOZYMES	MOLECULAR METHODS
Proportion of genome sampled	Large	Typically fairly small (i.e., 15-20 loci)	Typically very small but potentially large
Efficiency	Dependent on growing time required and traits measured (but typically low efficiency)	Several hundred plants per day[1]	Approx. 20 plants per day[1]
Cost	Very trait-dependent, but usually high	Unit cost moderate[1]	Unit cost high[1]
Detection of variants	Only those variants that lead to a change in phenotype	Limited to amino acid substitutions that cause a change in mobility in an electric field	All types of mutations detectable
Technical difficulty	Usually simple	Experience required, but fairly simple	More difficult; expertise required, required, especially interpretation

[1] After Clegg, 1990

The interpretation given to allozyme analyses is different from that of phenotypic studies. As the relationship between allozyme variation and plant functions is not known, we can interpret allozyme variation as adaptive variation only when the allozyme pattern closely and consistently follows an environmental gradient. Rather, allozymes are considered most useful in tracking non-adaptive genetic variation, that which occurred more than 10,000 years ago. The history reflected in allozyme variability can provide insight into the cumulative effects of such processes as genetic drift and inbreeding.

Allozyme analysis is now the most commonly employed method of measuring genetic diversity of plants. Unlike some phenological approaches, it measures standard plant products and thus can be used to relate differences among closely related species and, in some cases, genera. It is relatively quick and inexpensive, allowing a large number of plants to be analyzed. The efficiency of the method also allows a large number of individuals to be surveyed (although the number of loci sampled may be a very small proportion of the genome). Finally, as the analysis is usually undertaken without any prior knowledge of the genetic variation present, in this sense it is an unbiased sample of the structural genes in the population.

In spite of its popularity, there are a few weaknesses of the technique. The most common criticism is the limitation of the technique to selectively neutral structural genes, thus not providing a measure of the genetic variation which is adaptive. For this reason, results from allozyme analysis are often supplemented with other types of assessment, especially morphological data. Allozymes give quick results with good information on direct genetic events; common-garden studies give longterm results of apparently adaptive variation but without direct (genomic) information. Second, this technique requires more specialized skill and facilities than typical phenotypic studies and is particularly difficult to apply with polyploid species.

i) Allozyme variation within populations - Based on allozyme differences, the amount of genetic variation within a population may be characterized in several ways (Figure 4.2). One common measure is to simply determine the fraction of various allozyme loci (i.e., genes) that are polymorphic (i.e., show more than one form of protein). Alternatively, one could determine, for each individual plant sampled, the proportion of heterozygous loci of those assayed. (A diploid plant is said to be heterozygous at a locus when it carries two different forms of the protein encoded by the gene at that locus.) This value is then averaged over all individuals sampled in the population and expressed as the heterozygosity for that population. Average heterozygosity is probably the most commonly used expression of genetic diversity within plant populations. For example, the average heterozygosity of individuals within coastal populations of Douglas-fir in California is 0.33 (i.e., 33% of loci expected to be heterozygous for any given individual), while for individuals in a British Columbia population it is only 0.15.

A third type of measurement is the average number of alleles per locus. This measurement tends to represent more of the allelic diversity, but clouds the issue of how that diversity is distributed. From this measurement alone, it would not be possible to distinguish between a mainly monomorphic population with a few loci with many alleles, and one in which most loci were polymorphic but with only two or three alleles per locus. For this reason, often allelic diversity is represented as a frequency distribution - with the population represented by a table or histogram showing the relative frequency in three or four allele classes, ranging from highly polymorphic to monomorphic.

One final and common measure of genetic diversity within a population is the level of inbreeding*. This does not reflect the allelic diversity per se, but rather how the alleles

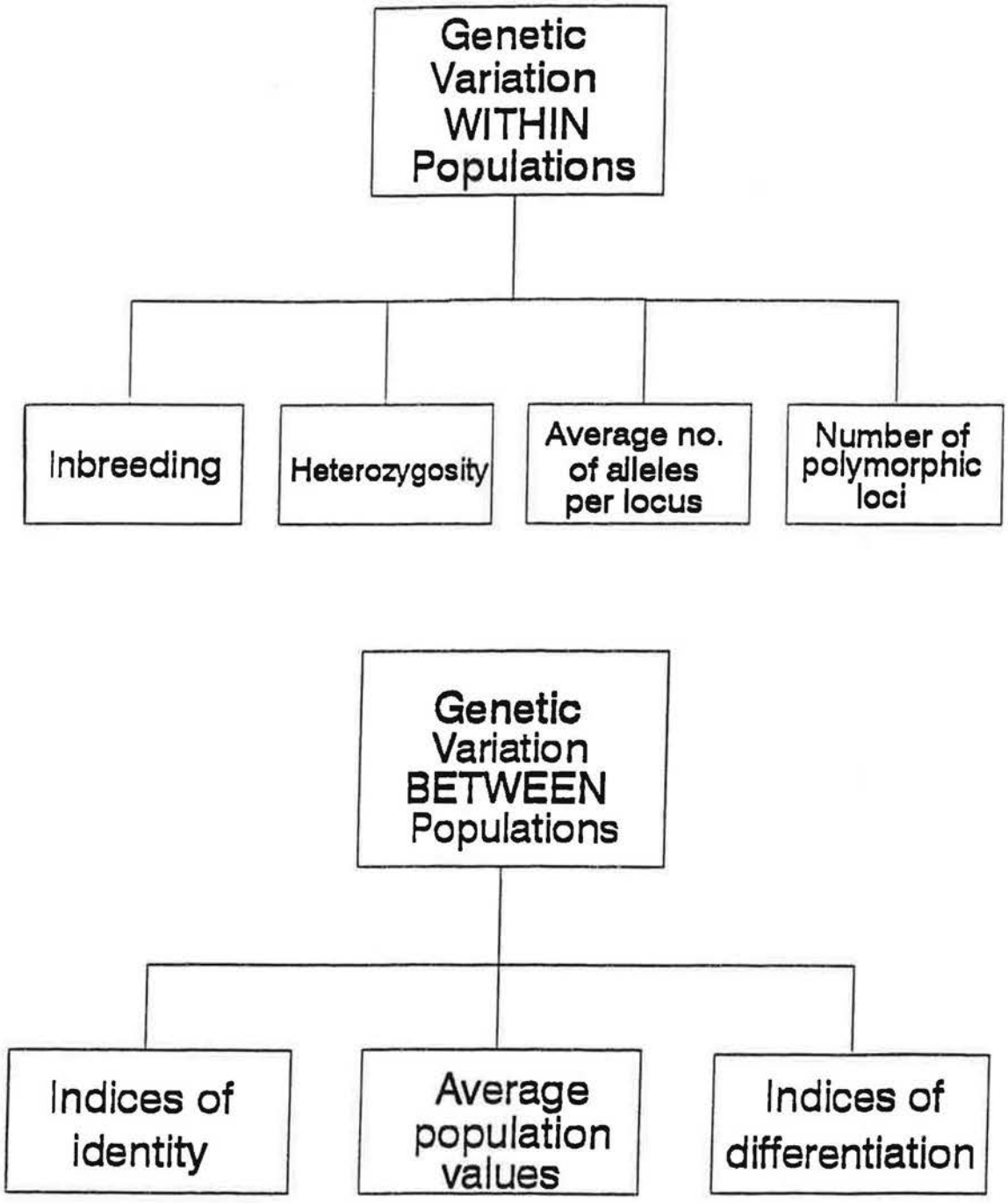

Figure 4.2 Measuring allozyme variation within and between populations.

are distributed within individuals. It is a measure of the expected level of homozygosity in the population under the assumption of random mating relative to the observed level of homozygosity. It is represented by the 'inbreeding coefficient' (F), which ranges from zero (expected levels of homozygosity and heterozygosity) to one (no heterozygotes, high level of inbreeding.) Note that in a completely outbreeding and randomly mating population, we still expect a certain level of homozygosity.

ii) Allozyme variation between populations - When the objective is the comparison of the genetic composition between two or more populations, several methods may be used (Figure 4.2). The first is simply to present, often in tabular or graphical form, the average values for all the within-population measurements for each population. This provides a sense of the pattern of allozyme variation, but without quantification. Summary statistics may be used to quantify the between-population differences. These are especially useful when numerous populations are being compared and average population values become unwieldy. There are various summary statistics but the two most common types are indices of identity and indices of differentiation. Indices of identity are the most widely used for comparing allele frequencies. The value for this statistic varies from zero (no alleles in common) to one (equal allele frequencies for all genes compared in both populations). The index of differentiation also varies from zero (where allelic frequencies are identical in all compared populations) to one (maximum variation among populations).

Regardless of the measurement chosen, several trends have been noticed. Allozyme variation is typically higher in vascular plants than in vertebrate or invertebrate species. Among plant species, there is great variation in the amount of allozyme diversity. For example, the average heterozygosity for Torrey pine (Pinus torreyana) is zero, while the average for 11 populations of Stephanomeria exigua is 0.30. Some species, such as Douglas-fir and ponderosa pine, even display large differences among populations. The range in heterozygosity in a species is greatly influenced by its breeding system. The wild oat (Avena barbata), a predominantly inbreeding species, has population heterozygosity values ranging from 0 to 0.48. The range for Stephanomeria exigua, a self incompatible species, is only 0.22 - 0.38 (Table 4.2).

3) DNA fragments - A third and more recent approach to measuring plant genetic diversity involves molecular techniques. These are the most direct types of genetic assessment as they can determine minor differences in DNA structure, regardless of whether or not the differences lead to a change in proteins produced or in the organism's phenotype. The technique commonly applied to the analysis of molecular diversity is called 'RFLP' analysis (Restriction Fragment Length Polymorphisms). This technique involves taking selected segments of DNA from a plant sample and identifying the variation in DNA sequences among plants by comparing these segments with specific DNA sequences called 'probes'. The key to this technique is that the enzymes used to cut the DNA do so in specific places, producing DNA segments that can be identified with known similar segments.

At the DNA level, the extent of genetic variability is most conveniently measured by nucleotide diversity, which is defined as the number of nucleotide differences, averaged across the total number of comparisons available. This value varies from 0.75 (maximum diversity) to zero.

The main advantage of this method over the isozyme method is that it can be used to detect variation in almost any part of the genome, whereas the isozyme method may be restricted to as little as 5% of the total genome. The RFLP method also allows detection of relatively minor DNA differences, which may not cause a protein difference detectable by the isozyme

Table 4.2 Heterozygosities of some common California plant species

SPECIES	SOURCE	HETEROZYGOSITY
Monterey cypress[1]	California range	0.18
Torrey pine[2]	California range	0
Douglas-fir[3]	Sierra Nevada	0.190
Douglas-fir	Northwest CA	0.267
Ponderosa pine	Southern CA	0.082
Ponderosa pine	Northwest CA	0.183
Wild oat[4]	CA (16 populations)	0.070 (Range: 0 - 0.48)
S. exigua[4]	CA (11 populations)	0.300 (Range: 0.22-0.38)

Sources:

[1] Conkle, 1987
[2] Ledig and Conkle, 1983
[3] All Douglas-fir and ponderosa pine data are from Millar and Libby, 1991
[4] Brown, 1978

technique. Thus, the RFLP method is relatively unbiased and much more powerful than the allozyme method in assessing genetic diversity.

There are, however, some significant disadvantages of this technique. It is relatively expensive in labor and in reagents. More importantly, there is considerable uncertainty concerning the interpretations of fragment differences. Once again, the relationship between DNA variants and phenotypic variation is unknown. Important questions for which there are currently no generally accepted answers include: How do DNA variants relate to adaptive variation? What is the general significance of these variants? What time-scale of genetic differentiation do they reflect?

Summary - Phenotypic, allozyme and DNA techniques all provide valid measures of genetic variation, although they preferentially detect different types of variation. Given that isozyme analysis is relatively fast, cheap, and simple, this might be the preferred technique for rapid genetic analysis of a species in which large numbers of samples would be screened. Phenotypic studies could be used to evaluate specific adaptive genetic variation. RFLP's could then be used to resolve more specific questions of genetic variation. However, the high costs and current uncertainty surrounding interpretation currently limit the use of molecular techniques. This situation may change in the future. Economies of scale are possible with RFLP's, particularly once panels of probes and/or tester lines are established. The cost per test of RFLP analysis goes down dramatically as the number of tests per plant increases. Also, technical advances are likely to continue to reduce costs. Thus, there are advantages and disadvantages of all methods of genetic assessment. The ideal genetic study would involve all methods.

V. INDIRECT ASSESSMENT OF GENETIC DIVERSITY

Sufficient genetic information often will not be available when management decisions are pending. In these cases, insight into the genetic variation of a species may be gained by extrapolation from other characteristics. This is a statistical approach to genetic assessment, as it is based on the correlation between genetic variation and certain species features across a wide range of plant species for which there are some direct genetic measurements. Because it is based on average correlations, predicting patterns of genetic variation for an individual species is risky, but when information is lacking, it may be the only source of information for making management decisions.

The most comprehensive and recent study of characteristics correlated with genetic variation in plants is by Hamrick and Godt (1990). This study reviews variation in 449 plant species and examines their patterns of genetic variation for correlation with eight plant traits (Figure 5.1). Due to the large number of species involved the correlations discovered are quite convincing. However, the study is based entirely on allozyme data and thus may not reflect all aspects of genetic variation. Certain traits are better indicators than others. Also, the eight traits together accounted for less than 50% of the total genetic variation and thus are not perfect indicators, even on average. Most of this chapter is a summary of their findings, unless otherwise indicated.

As discussed in Chapters II and IV, genetic variation is described within a hierarchical frame-work, and correlated features also differ depending upon the hierarchical level of genetic variation. Thus, the trait correlations are presented separately for the species, among-population and within-population levels.

Variation at the species level

At the species level, geographic range has the strongest relationship with genetic diversity, as measured by allozyme variation. Widespread species have the most allozyme diversity: 47% more than narrowly-distributed species and 35% more than regionally-distributed species. Endemic species have the least genetic diversity - less than 50% that of widespread species. Three other features are significantly associated with genetic variation at the species level: taxonomic status, life form, and means of seed dispersal. For instance, gymnosperms are more genetically diverse than monocots, on average, and monocots more than dicots. Longevity of the species is also correlated with genetic variation. Long-lived perennials generally have higher levels of genetic variation than short-lived perennials. Annuals tend to have high levels also, similar to long-lived perennials. Finally, seed dispersal mechanisms offer one more correlate at the species level. Species whose seeds are dispersed by hitchhiking on animals or humans have the highest levels of genetic variation. Species with explosively dispersed seeds have the lowest genetic diversity while gravity-dispersed, animal ingested and wind-dispersed species have intermediate values. The other four traits examined have mild correlations with genetic variation (Table 5.1).

Another generalization is available for Californian conifers, a group for which there is a relatively large amount of genetic information. From a comparison of over 25 species, it is apparent that California coastal conifers have lower levels of variability than those from the Sierra Nevada or those that are distributed in both the outer and inner coastal ranges. Species restricted to the outer coast ranges (e.g., Monterey pine, Torrey pine, Bishop pine, Santa Lucia fir, Monterey cypress) average 0.08 in heterozygosity, compared with 0.19 for the others (e.g., incense-cedar, Jeffrey pine, sugar pine).

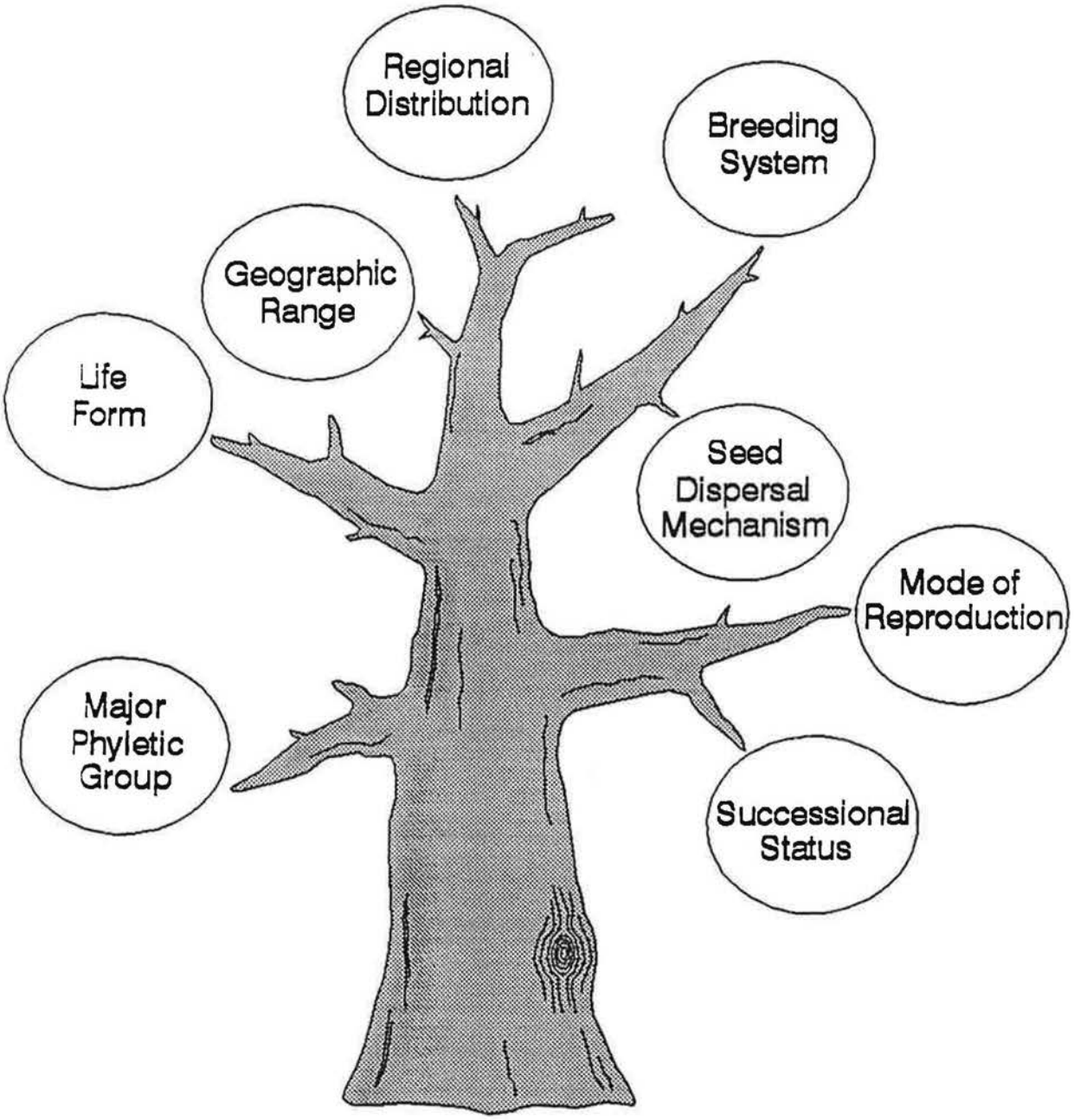

Figure 5.1 Eight plant traits commonly associated with genetic variation.

Table 5.1[1] Correlates with genetic variation within plant species

Trait	Highest level	Lowest level
Geographic range	Widespread	Endemic
Life form	Long-lived, woody perennials	Short-lived perennials
Breeding system	Mixed mating, wind-pollinated	Mixed mating, animal-pollinated
Seed dispersal	Attached	Explosive
Taxonomic status	Gymnosperms	Dicots
Regional distribution	Boreal-temperate	Tropical or temperate
Mode of reproduction	Sexual	Sexual and asexual
Successional status	Late	Mid-successional

[1] Traits are arranged in approximate order of their strength of correlation with genetic variation. Thus, geographic range is very strongly correlated with genetic variation within a species, but successional status is almost insignificant.

Variation among populations

A useful statistic for making comparisons of genetic variation among populations within species is the ratio of among population variation to total genetic variation. Considering an array of plant species, from highly diverse among populations to no diversity among populations, allozyme variation shows a different array of correlates than for species level variation (Table 5.2). Breeding system and life form are most closely associated with genetic diversity among plant populations. In selfing species, approximately 50% of the total genetic variation, on average, is among populations. This is significantly higher than species with mixed or out-crossing breeding systems, whether wind- or animal-pollinated. Less than 10% of the allozyme variation in wind-pollinated outcrossing species resides among populations, on average.

When life form is considered, annuals are found to have a significantly higher proportion of their genetic variation among populations than either short-lived or long-lived perennials. Annuals, on average, have been found to have 36% of their total genetic variation residing among populations, as compared with long-lived, woody perennials that average less than 8%.

To a lesser degree than either breeding system or life form, several other attributes have also been found to correlate with the level of genetic variation among plant populations. Angiosperms, both dicots and monocots, tend to have more genetic variation among populations than do gymnosperms. This pattern may be a function of the breeding system correlation, due to the presence of many selfing species among the angiosperms, and many wind-pollinated outcrossing species among the gymnosperms in the data base. Regional distribution shows some relationship with the partitioning of genetic variation, boreal-temperate species tending to have a lower proportion of among-population variation than temperate, temperate-tropical or tropical species.

Seed dispersal mechanisms also show some correlation with allozyme variation, with gravity-dispersed species having the highest, and gravity-attached species the lowest, proportions of among-population variation. Finally, species of early and mid-successional stages tend to have higher proportions of among-population variation than do late successional species.

It is interesting to note that geographic range was not significantly associated with variation among populations. Although endemic and widespread species have different average levels of genetic variation, their among-population variation is partitioned in much the same way.

Variation within populations

Breeding systems and geographic range show the strongest correlation with allozyme variation within populations (Table 5.3). With breeding system comparisons, a pattern emerges that contrasts with that for genetic variation among populations. For within population variation, the highest levels occur in mixed-mating, wind-pollinated species, and the lowest in selfing species. Endemic species tend to have the lowest levels of genetic variation within their populations. Narrow and regionally distributed species have intermediate levels, while widespread species, on average, have the highest levels of variation within populations. The widespread species, within their populations, have both a higher number of polymorphic loci and more alleles per locus, than the other categories of species.

Weaker correlations exist between other species features and within-population variation. Gymnosperms and angiosperm monocots have higher genetic variation within their populations, on average, than do dicots. Long-lived, woody, perennial species show more within-population variation than do short-lived perennials or

Table 5.2[1] Correlates with genetic variation among populations

Trait	Highest level	Lowest level
Breeding system	Selfing species	Outcrossing, wind-pollinated
Life form	Annual	Long-lived, woody perennial
Seed dispersal mechanism	Gravity dispersed	Gravity-attached
Successional status	Early	Late
Taxonomic status	Dicots	Gymnosperms
Regional distribution	Temperate	Boreal-temperate

[1] Traits are arranged in approximate order of their strength of correlation with genetic variation. Thus, breeding systems are very strongly correlated with genetic variation among populations, but regional distribution is not well associated.

Table 5.3[1] Correlates with genetic variation within populations

Trait	Highest level	Lowest level
Breeding system	Mixed-mating, wind-pollinated	Selfing species
Geographic range	Widespread	Endemic
Life form	Long-lived woody perennials	All others
Taxonomic status	Gymnosperms	Dicots
Seed dispersal mechanism	Attached	Explosive
Regional distribution	Boreal-temperate	Temperate, tropical
Successional status	Late	Early

[1] Traits are arranged in approximate order of their strength of correlation with genetic variation. Thus, breeding systems and geographic range are very strongly associated with genetic variation within populations, but successional status is only mildly related.

annuals. In a comparison of their regional distribution, boreal-temperate species are more genetically variable within their populations than temperate, temperate-tropical or tropical species. Seed dispersal mechanisms are also correlated with the level of within-population variation. Seeds dispersed by gravity, or in an explosive manner, exhibit the lowest levels of within-population variation, relative to all other mechanisms, including wind, ingestion, attached and gravity-attached dispersal. Species of a later successional status tend to have somewhat higher levels of within-population variation.

Another generalization regarding variation within populations comes from comparative studies of California conifers. Many of these species show a latitudinal pattern of within-population variability. Variability tends to be highest in the southern populations and decreases towards the north. Examples of species showing this pattern are Coulter pine (Pinus coulteri), giant sequoia (Sequoiadendron giganteum), Jeffrey pine (Pinus jeffreyi), western white pine (Pinus monticola), Douglas-fir (Pseudotsuga menziesii), and incense-cedar (Calocedrus decurrens).

Conclusions

The approximate nature of these correlations must be kept in mind. First, they are based on allozyme data only, and thus they may not reflect the broader basis of genetic variation. Second, although 'genetic variation' could be portrayed by numerous measurements (e.g., number of alleles per locus, percentage polymorphic loci) this summary has generalized the description of genetic variation. All genetic measurements would not always vary in the same way. Third, and most importantly, even where correlations of genetic variation with species features were strong on average, there are many departures from these relationships. In fact, the features analyzed accounted for only 24%, 47% and 28% of the genetic variation at the species, among-population and within-population levels, respectively. Thus, the trends reported here are broad generalizations, and individual species will often show significant, perhaps complete, departures from these trends. The risk of using indirect indicators of genetic variation in management decisions must be recognized.

Ideally, every species should have its own genetic study. However, this is probably unrealistic. In the absence of this direct genetic information, correlated features may provide some guidance about the genetic nature of the species. Some generalizations from this review are:

1. Long-lived, outcrossing, wind-pollinated species of the later stages of succession have higher levels of allozyme variation within populations and less among population variation than species with other combinations of traits.

2. Predominantly clonal species may maintain as much genetic diversity within their populations as sexually reproducing species.

3. Geographic range is the best predictor of levels of allozyme variation at the species and within population levels. It plays almost no role in the distribution of genetic variation among populations.

4. There seems to be a significant and positive relationship between genetic variation at the species and within-population levels, and within- and among-population levels. The species and among-population levels of genetic variation are not noticeably associated.

VI. GENETIC CONSERVATION METHODS

Introduction

In the broadest sense, genetic management serves to conserve: 1) specific genes or traits, 2) short-term ecological stability, and 3) long-term evolutionary flexibility. To realize these objectives it is important to consider genetic variation at all the levels where it is expressed - genes, gene complexes, individuals, populations, ecosystems or communities. Because genetic variation is complex and expressed in this hierarchy of organization, and because of the long-term nature of genetic conservation objectives, they are usually best achieved with a combination of methods.

At the extremes of a spectrum of approaches to genetic conservation are ex situ and in situ methods. These are sometimes referred to as static and dynamic approaches, respectively. They are similar in that they both involve sampling the species, and neither method is without risk. The basic distinctions between them are the level and type of risk accepted, the allowance for change in the genetic resource, and the location or situation in which the resource is maintained. The ex situ/static approach aims to preserve the germplasm (usually at the individual/genome level) in its present state and maintain its viability and genetic integrity over a long period. This involves removing the genetic resources of interest from their natural setting and maintaining them as individual plants, seeds or plant parts in storage facilities or a controlled garden environment.

Alternatively, the in situ/dynamic approach consists of maintaining the genetic variation of a species or population in its natural, ecological setting. This allows the genetic resource to continue to change in response to environmental influences but also leaves the resource vulnerable to erosion through catastrophic fires, climatic change, fragmentation, etc.

The most effective genetic conservation programs integrate elements from both approaches. This is a function of the complementary nature of the two basic approaches: a weakness in one is often a strength of the other (Table 6.1). A comparison of these two strategies will serve to emphasize their mutual dependence in the delivery of an adequate conservation function.

Ex situ/Static approach

Although now an important part of most genetic conservation programs, this approach has historically been used with rare, endangered or particularly valuable germplasm. It begins with sampling the genetic resource, collecting seeds and/or tissue samples from individuals that preferably span the range of genetic variation. There is no universal sampling scheme as this must take into account the extent and pattern of genetic variation within the species of interest, as well as the specific conservation goals. As the focus for this genetic conservation strategy is the individual, special attention is required in order to avoid the loss of rare alleles and the pattern of genetic architecture. Samples must be very large in order to capture the former and the latter requires more information than is generally available for most species.

Once collected, the genetic materials are placed in a situation where the viability and genetic composition are protected as much as possible. Conventional storage is with seeds or pollen. Progress has been made in developing appropriate long-term storage conditions for seeds and pollen of many plant species, but this is still a significant issue due to species variability. For example, seeds of pine species have germinated even after more than 50 years, but spruce (Abies), oak (Quercus), and many angiosperm species have relatively short-lived seeds. Seeds from many willow (Salix) species, for example, may store only a few weeks. According to Ledig (1989) approximately 200 of the 270 major tree species in the United States can be stored for extended periods of time. Poplar species generally have short-lived seeds but attention to this has resulted in protocols that can

Table 6.1 Advantages and disadvantages of two genetic conservation strategies

EX SITU APPROACH	IN SITU APPROACH
STRENGTHS	
Genetic resource is 'secure'	Opportunity for genetic resources to track environmental changes and remain adapted
Resources can be readily inventoried, compared and shared	Compatible with other natural resource objectives
Very space-conserving	May not involve much additional expense
Some methods (e.g., seed/pollen storage) are cheap and can store large numbers	Conserves genetic architecture as well
WEAKNESSES	
Vulnerable to human error, failure of technology and financial contingencies	Vulnerable to environmental extremes
Sensitive to sampling strategy	May be contaminated by exotic germplasm sources
Protocols for all species not available	Opportunities are limited; already defined areas.
Some techniques may be prone to (or even promote) mutations	Existing areas may not be complete or representative of species (i.e., Minimum viable population size and fragmentation concerns)
Some techniques are very expensive	
Vulnerable to undesirable selection pressures	
Genetic resource may be maladapted when re-introduced; Evolution frozen	

maintain seed viability for over five years. In summary, even though the goal is preservation of the status quo through sampling and provision of constant storage conditions, this strategy requires periodic attention. Even for the more 'storable' species, seeds or pollen must be monitored for viability, and germination/reproduction may occasionally be required to revitalize the seed supply.

The extent to which germplasm can be maintained in storage is species-specific and unknown for many native species. If seed viability is low, and thus frequent sexual propagation is required to replenish the collection, this will change the genetic composition over time. However, if the species is predominantly self-fertilizing, the propagation effect will be small. Periodic recollection from the natural stands, if not genetically impoverished, will refresh the collection.

Second, the loss in viability of the pollen or seeds that occurs in storage is unlikely to be random. The storage conditions act as a selection agent, and thus the viable gene pool in storage at any time has been altered from the original collection, if only slightly. Further, if tissue, rather than seeds or pollen, is the storage unit, then the continuous culture conditions can influence the genetic stability. Mutations arising in tissue culture are referred to as 'somaclonal variation' and may be a significant concern in the long-term storage for some plant species. A relatively new technique, somatic embryogenesis, may largely overcome this instability problem. Somatic embryos may be preserved in liquid nitrogen, which virtually guarantees that mutations do not occur. However, the caveat of these (tissue culture and somatic embryogenesis) technologies, as well as the more conventional storage of seeds and pollen, is that species-specific protocols are largely unavailable as yet due to the large investment required.

Ex situ collections may also be maintained in a living, whole-plant state in field gene banks such as arboreta, botanical gardens, or plantations. If the plants are allowed to regenerate naturally in these situations, then this allows some adaptation to occur. However, these whole-plant collections require well-considered spatial designs and intensive management to be successful. First, the samples would have to be quite large, well-chosen and appropriately positioned to achieve viable, healthy and desirable progeny, as well as to maintain proper genetic architecture. Second, care must be taken to prevent pollen contamination from native populations of the same species in the neighborhood. Third, the environment would need to be similar to that of the original collection to provide natural selection pressures that would result in adaptation of the progeny when recruited for restoration purposes. This is obviously more important for the shorter-lived than the longer-lived species. Again, this is unlikely if the collection spans a species' range or even several distinct populations. Finally, a high level of input is required to maintain the plants in a healthy and reproductively competent condition and protect them from threats due to weed competition, frost, drought, disease, insects or fire.

Other merits of the ex situ approach include the lower risk factor, with 'preserved' germplasm generally being at lower risk of erosion or extinction than in situ germplasm. Of course this is a broad generalization, as the risk entirely depends on the rate of decline of the stored pollen or seed, or the vulnerability of the whole-plant collection. Also, the nature of ex situ collections allows their composition to be more easily coordinated and shared with cooperating agencies.

In summary, the certainty, security and space-conserving nature of the ex situ approach makes it an attractive conservation strategy. However, its greatest weakness is that the 'preserved' germplasm has been removed from its adaptive landscape, does not evolve while in storage, and may be maladapted when returned to its (continually changing) native environment.

In situ/Dynamic Approach

With this conservation strategy the goal is not only to maintain the genetic resources of a particular species, but also its genetic architecture and supporting ecosystem. Maintaining the germplasm in its native environment allows continual evolution relative to changing environmental conditions. Thus, this approach compensates for the major weakness of an exclusively ex situ conservation strategy.

The risk with the in situ strategy is more influenced by environmental conditions than by financial or technical shortfalls. Although with this strategy the genetic resource can avail itself of natural pressures that lead to adaptation, the resource is also left vulnerable to changes that are too dramatic or occur too quickly to permit adaptation. Anthropogenic influences, in particular, may fall into this category. The atmospheric level of CO_2, for example, is expected to double during the next century. If this occurs, it will trigger changes in both biotic and abiotic elements of a species' range. If the species can keep pace then the in situ approach is not only highly effective, but ex situ collections may be obsolete. However, if the changes are overwhelming and populations decline, the ex situ collections may save some populations or even species from extinction.

The in situ approach also involves sampling, but in a different sense than the ex situ approach. Unless the species is represented only by a small relic population (in which case the entire area in which it exists might be preserved) a portion or samples of the species' range is normally selected for genetic conservation purposes. It is important to keep in mind that all areas in which a species exist, even if they are public domain, do not necessarily serve genetic conservation interests. All parks, for example, are not necessarily genetic reserves, this being a function of their use restrictions and management guidelines. Research Natural Areas and Botanical Areas, for example, are at present the only designated natural areas on federal lands where gene conservation is an identified goal, although a new designation, Genetic Conservation Areas, is being developed.

Effective in situ reserves must be selected with consideration of the spatial pattern of genetic variation. The scale of the area must be appropriate for the species or population of interest. If fragmented, the cluster of reserves must be sufficiently close to permit gene flow among them, or large enough for sufficient gene flow within. Even the land use of the area surrounding the reserve is key to its adequacy. This latter point, in particular, is a challenge in that species migration might be the only viable response to rapid climatic change, yet opportunities for gene migration are increasingly limited by urban development and agriculture.

Although in situ genetic reserves should be chosen for the purpose of genetic conservation, other resource uses of the same area are not necessarily incompatible with that goal. For example, plants can be removed or planted in such a way that natural genetic architectures are not significantly disrupted.

In summary, in situ conservation provides a means by which to maintain genetic resources in a state that is compatible with the current environment. However, the gene pool remains at risk due to anthropogenic and potentially dramatic environmental fluctuations.

Conclusions

The best genetic conservation strategy involves well-considered integration of both ex situ and in situ approaches. Due to the complexity of threats to survival, every available tool should be engaged. Ex situ strategies alone are no longer considered sufficient even for highly domesticated crop species, where the current goal of gene resource managers is more ecologically oriented than that of earlier generations. In situ approaches are often considered too risk-laden to maintain without ex situ back-up. The implications of this integrated approach

to genetic conservation are two-fold. First, there is a requirement for much information - for appropriate location, design and maintenance of preserves, for sampling, for storage technologies, and for effective regeneration and restoration use of the genetic reserves. Second, successful integration depends on coordination among many land-holding agencies, and on long-term programmatic fiscal commitment.

VII. ANNOTATED BIBLIOGRAPHY OF GENETIC INFORMATION FOR CALIFORNIA PLANT SPECIES

INTRODUCTION

This section consists of an annotated bibliography of genetic information available for native plant species of California. References are included which are of most relevance to genetic conservation, principally studies of amount and/or structure of genetic variation. Taxonomic or systematic studies are not included unless they pertain to intraspecific genetic variation such as ecotype or sub-species delineations. The list is not comprehensive, but should provide a reference point for investigating a taxon of interest.

Due to the variability in amount of information available for various taxa, from many references for a species to little or no information for a whole genus or family, this bibliography is organized in general by family, and by genus within family. References within a genus are organized alphabetically by senior author. In cases where one family has two names (e.g., Compositae=Asteraceae; Gramineae=Poaceae) the name ending in 'aceae' is used.

FAMILY: ADIANTACEAE

Pellaea

Gastony, G.J. and L.D. Gottlieb. 1985. Genetic variation in the homosporous fern Pellaea andromedifolia. American Journal of Botany 72(2): 257-267.

This paper uses isozyme studies to examine genetic variability in 12 natural populations of Pellaea andromedifolia, a species with sexually and apogamously reproducing races restricted to California and Baja California Norte.

FAMILY: ASTERACEAE

Antennaria

Bayer, R.J. 1989. Patterns of isozyme variation in western North American Antennaria (Asteraceae: Inuleae) II. Diploid and polyploid species of section Alpinae. American Journal of Botany 76(5): 679-691.

This study includes one species native to California, Antennaria pulchella, and compares the pattern of genetic variation in six populations of this species with those of four other species in the genus.

Artemisia

Freeman, D.C., W.A. Turner, E.D. McArthur, and J.H. Graham. 1991. Characterization of a

FAMILY: CHENOPODIACEAE

Atriplex

Freas, K.E. and D.D. Murphy. 1991. The endangered Bakersfield Saltbush. Fremontia 19(2): 15-18.

This discussion paper describes the status of endangered Bakersfield Saltbush (Atriplex tularensis), including its last remaining population, recent conservation activities and a possible event of introgressive hybridization between A. tularensis and A. serenana.

Chenopodium

Crawford, D.J. and H.D. Wilson. 1977. Allozyme variation in Chenopodium fremontii. Systematic Botany 2(3): 180-190.

Genetic variation, as measured by allozyme variants, is discussed for 40 populations of C. fremontii, located throughout much of its range, including California. The three southern California populations are shown to differ from the others.

FAMILY: CUPRESSACEAE

Calocedrus

Harry, D.E. 1986. Inheritance and linkage of isozyme variants in incense-cedar. The Journal of Heredity 77: 261-266.

This investigation of isozyme variants in incense-cedar provides insight into the inheritance and linkage of isozymes encoded by 27 loci. The genetic interpretation of isozyme studies is also discussed.

Harry, D.E. 1983. Identification of a locus modifying the electrophoretic mobility of malate dehydrogenase isozymes in incense-cedar (Calocedrus decurrens), and its implications for population studies. Biochemical Genetics 21(5-6): 417-433.

This study focuses on the potential for misinterpretation of isozyme studies unless the genetic basis for the enzymes under study is known. Isozyme variation in incense-cedar is used as an example.

Chamaecyparis

Millar, C.I. and K.A. Marshall. 1991. Allozyme variation of Port-Orford-Cedar (Chamaecyparis lawsoniana): Implications for genetic conservation. Forest Science 37(4): 1060-1077.

Nine populations of Port-Orford-Cedar in northwestern California are sampled and analyzed for allozyme variation. Genetic variation is discussed relative to other California forest tree species and the current geographic distribution. The importance of genetic variation in this species and strategies for genetic conservation are presented.

Cupressus

Conkle, M.T. 1987. Electrophoretic analysis of variation in native Monterey cypress (Cupressus macrocarpa Hartw.). In Elias, T.S. and J. Nelson (eds). Conservation and Management of Rare and Endangered Plants. California Native Plant Society, pp 249-256.

Kafton, D.L. 1976. Isozyme variability and reproductive phenology of Monterey Cypress. Ph.D. dissertation, University of California at Berkeley.

Genetic variability in the two populations of Monterey cypress is investigated with isozyme analysis. The influence of selection and drift on these populations is discussed.

FAGACEAE

Quercus

Millar, C.I., D.L. Delany and L.A. Riggs. 1990. Genetic variation in California oaks. Fremontia 18(3): 20-21.

This brief paper summarizes the results of an isozyme study of three California oak species: valley oak, blue oak and coast live oak, and refers to additional studies that are required in order to have an adequate understanding of genetic variation in these and other oak species.

Scott, T.A. 1990. Conserving California's rarest white oak: the Engelmann oak. Fremontia 18(3): 26-29.

Although there is little genetic information available for this species (Quercus engelmannii), this paper summarizes its taxonomy and distribution, and describes the current approaches to its management and research.

FAMILY: LAMIACEAE

Agastache

Vogelmann, J.E. and G.J. Gastony. 1987. Electrophoretic enzyme analysis of North American and eastern Asian populations of Agastache Sect. Agastache (Labiatae). American Journal of Botany 74(3): 385-393.

Isozyme analysis is employed to asses genetic diversity and relationships within and among populations of the eight species of Agastache sect. Agastache. These species include two native to California, A. parvifolia and A. urticifolia.

FAMILY: LILIACEAE

Calochortus

Fiedler, P.L. 1985. Heavy metal accumulation and the nature of edaphic endemism in the genus Calochortus (Liliaceae). American Journal of Botany 72(11): 1712-1718.

Adaptation to ultramafic soils is investigated with controlled studies of five species of Calochortus, three of which are endemic to California.

FAMILY: LIMNANTHACEAE

Limnanthes

Kesseli, R. and S.K. Jain. 1984. An ecological genetic study of gynodioecy in Limnanthes Douglasii (Limnanthaceae). American Journal of Botany 71(6): 775-786.

Male sterility is investigated in two populations of this species and discussed in relation to fitness, including is affect on inbreeding depression.

FAMILY: ONAGRACEAE

Sytsma, K.J. and L.D. Gottlieb. 1986. Chloroplast DNA evidence for the origin of the genus Heterogaura from a species of Clarkia (Onagraceae). Proceedings of the National Academy of Science 83: 5554-5557.

The analysis of chloroplast DNA has provided evidence that the monotypic genus Heterogaura is closely related to a species of Clarkia. The paper compares morphological and biochemical evidence as it pertains to discerning genetic relationships.

Clarkia

Allen, G.A., V.S. Ford, and L.D. Gottlieb. 1990. A new subspecies of Clarkia concinna (Onagraceae) from Marin County, California. Madroño 37(4): 305-310.

A third and new subspecies of Clarkia concinna is described, based on nursery studies of samples from five populations of the three subspecies. The new subspecies designation is based on floral characteristics, pollen viability of the subspecies and their hybrids and chromosome counts.

Gottlieb, L.D. and N.F. Weeden. 1979. Gene duplication and phylogeny in Clarkia. Evolution 33(4): 1024-1039.

Electrophoretic variation in one particular enzyme was explored in 30 species of Clarkia. The number of gene loci coding for this enzyme was used to infer the phylogenetic relationship of these species.

Gottlieb, L.D. and V.S. Ford. 1988. Genetic studies of the pattern of floral pigmentation in Clarkia gracilis. Heredity 60: 237-246.

A genetic analysis of petal size and floral pigmentation patterns in Clarkia gracilis was conducted by constructing three generations of hybrids between two interfertile subspecies. Pigmentation was shown to be governed by a single gene. This inheritance pattern is discussed relative to the role of natural selection (especially pollinator preference) in this and other Clarkia species.

Holsinger, K.E. and L.D. Gottlieb. 1988. Isozyme variability in the tetraploid Clarkia gracilis (Onagraceae) and its diploid relatives. Systematic Botany 13(1): 1-6.

Genetic variation at the electrophoretic level is compared among populations of four subspecies of the tetraploid Clarkia gracilis and three diploid Clarkia species. The genetic relationship among these subspecies and species are discussed, as is the most likely evolutionary origin of the tetraploid subspecies.

Soltis, P.S. and W.L. Bloom. 1986. Genetic variation and estimates of gene flow in Clarkia speciosa subsp. Polyantha (Onagraceae). American Journal of Botany 73(12): 1677-1682.

This study uses isozyme variation to discuss genetic diversity within the subspecies Polyantha - a disjunct subspecies occurring in the foothills of the California Sierra Nevada. Results are discussed in relation to its putative hybridization and introgression with the closely-related C. nitens.

Vasek, F.C. 1977. Phenotypic variation and adaptation in Clarkia section Phaeostoma. Systematic Botany 2(4): 251-279.

Progenies from nine populations of six species of Clarkia are compared using morphological and developmental traits as assessed in a common-garden study. Variation within and among populations and species are discussed relative to breeding system and habitat.

FAMILY: PINACEAE

Critchfield, W.B. 1984. Impact of the Pleistocene on the genetic structure of North American conifers. In Lanner, R.M. (ed). Proceedings of the Eighth North American Forest Biology Workshop, July 30-August 1, 1984, Logan, Utah. Utah State University Press, pp 70-117.

True to its title, this is an extremely informative paper on Pleistocene impacts on genetic variation, with the coniferous species logically organized under the sub-headings of "reduced variation", redistribution of variation: transitory races", and "increased variation".

Abies (Firs)

Bonnicksen, T.M. 1972. White fir (Abies concolor Gord. and Glend.) Lindl.) -- A bibliography with abstracts. Unpublished manuscript, Department of Forestry, University of California at Berkeley, 98 pp.

This bibliography contains 426 references on white fir, with abstracts, including 12 which are genetic in nature.

Hamrick, J.L. 1976. Variation and selection in western montane species. II. Variation within and between populations of white fir on an elevational transect. Theoretical and Applied Genetics 47: 27-34.

This paper reports the results of a common-garden nursery study which measured the distribution of genetic variation for 13 morphological characteristics within and among four populations of white fir from an elevational transect of the central Sierra Nevada.

Hamrick, J.L. and W.J. Libby. 1972. Variation and selection in western U.S. montane species. I. White fir. Silvae Genetica 21(1-2): 29-35.

This reference reports on ecotypic and clinal patterns of genetic variation in white fir across its natural range, based on common-garden studies. Morphological and phenological characteristics were used to assess genetic variation relative to geographic location and elevation of seed source. Evolutionary relationships with grand fir are also discussed.

Libby, W.J., K. Isik, and J.P. King. 1980. Variation in flushing time among white fir population samples. Annales Forestales 8(6): 123-138.

With observations taken from common-garden plantations of white fir in the central Sierra Nevada, significant genetic variation in spring flushing time is demonstrated between geographic regions, among populations within regions, and among families within populations.

Sturgeon, K.B. and J.B. Mitton. 1980. Cone color polymorphism associated with elevation in white fir, Abies concolor, in southern Colorado. American Journal of Botany 67(7): 1040-1045.

The adaptive value of differing cone colors in white fir from various elevations is discussed.

Pinus (Pines)

Conkle, M.T. 1977. Knobcone pine self compatibility and isozyme inheritance. Ph.D. dissertation, University of California, Berkeley, California.

This study examines the differences between selfed and outcrossed families of knobcone pine in terms of production of sound seed and early height growth of seedlings. The inheritance of certain isozyme variants is investigated.

Critchfield, W.B. 1956. Morphological and physiological variation in Pinus contorta Dougl. Ph.D. dissertation, University of California, Berkeley, 230 pp.

This work, a cornerstone study in intraspecific variation of lodgepole pine, reveals differences in leaf and cone characteristics throughout the species' range. Genetic and environmental differences are discriminated between in nursery studies of seedling differences. All results are discussed in relation to genetic variation within and among populations.

Critchfield, W.B. 1957. Geographic variation in Pinus contorta. Maria Moors Cabot Foundation publication No. 3, Harvard University, Cambridge, Mass. 118 pp.

This study of lodgepole pine is primarily based on field sampling across the species' range. As such, it does not clearly distinguish between genetic and environmental sources of variation. However, it presents a comprehensive picture of ecogeographic variation in the species, and is supplemented with some data from common-garden studies.

Crowley, J.J. 1977. An analysis of nine year growth data on the California coastal closed-cone pines. B.S. thesis, University of California at Berkeley.

Genetic variation in populations of radiata and bishop pine is measured with ninth year morphological data (height, diameter, branch angle, needle length, etc.) from two common-garden studies situated in northern California.

Furnier, G.R. and W.T. Adams. 1986. Mating system in natural populations of Jeffrey Pine. American Journal of Botany 73(7): 1002-1008.

The genetic variation within and among five populations of Jeffrey pine in southern Oregon and California is compared using isozyme analysis.

Furnier, G.R. and W.T. Adams. 1986. Geographic patterns of allozyme variation in Jeffrey pine. American Journal of Botany 73(7): 1009-1015.

The genetic structure of seven Jeffrey pine populations restricted to ultramafic soils in southern Oregon and California is compared with that of seven populations occurring on a broader range of soils in the rest of the Sierra Nevada range. Genetic adaptation to ultramafic soils is discussed.

Grant, M.C., Y.B. Linhart, and R.K. Monson. 1989. Experimental studies of ponderosa pine. II. Quantitative genetics of morphological traits. American Journal of Botany 76(7): 1033-1040.

Seedlings from crosses involving California parents and intervarietal crosses of ponderosa pine, growing in a common-garden situation, are studied and compared on a morphological basis. The patterns of differentiation are discussed in relation to the known ecological distinctions between the habitats of the two varieties.

Guinon, M., J.V. Hood, and W.J. Libby. 1982. A clonal study of intraspecific variability in radiata pine. II. Growth and form. Australian Forest Research 12:191-201.

The extent to which genetic differences account for variability in growth and form of three populations of radiata pine growing in a common-garden study are reported.

Hamrick, J.L., H.M. Blanton, and K.J. Hamrick. 1989. Genetic structure of geographically marginal populations of ponderosa pine. American Journal of Botany 76(11): 1559-1568.

Although the populations sampled in this study are all located in Colorado, the results speak to the general distribution of genetic variation within and among populations of ponderosa pine (based on allozyme variation), and relates this variation to the pattern of seedling recruitment in these stands.

Harry, D.E., J.L. Jenkinson, and B.B. Kinloch. 1983. Early growth of sugar pine from an elevational transect. Forest Science 29(3): 660-669.

Genetic variation in sugar pine associated with seed source elevation is studied in a nursery trial. The study is structured to allow discussion of genetic variation relative to stands, families within stands and elevation of source.

Hood, J.V. and W.J. Libby. 1980. A clonal study of intraspecific variability in radiata pine. I. Cold and animal damage. Australian Forest Research (10): 9-20.

This study examines the genetic differences in susceptibility to cold and animal damage of young radiata pine at the population and clonal levels. Comparisons between rooted cuttings and seedlings with respect to these traits are made.

Knowles, P. and M.C. Grant. 1981. Genetic patterns associated with growth variability in Ponderosa pine. American Journal of Botany 68(7): 942-946.

Heterozygosity in populations of ponderosa pine is measured with isozyme variants in pollen samples, and discussed in relation to growth variability as measured by annual ring widths.

Ledig, F.T. and M.T. Conkle. 1983. Gene diversity and genetic structure in a narrow endemic Torrey pine (Pinus Torreyana Parry ex Carr.). Evolution 37(1): 79-85.

An allozyme study is used to measure amount and structure of genetic variation in Torrey pine. The possible course of events leading to the two extant populations of this species, and consequences for genetic conservation strategies, are discussed.

Libby, W.J. 1990. Genetic conservation of radiata pine and coast redwood. Forest Ecology and Management 35: 109-120.

This paper presents details of the history of collections of radiata pine for research and genetic conservation purposes, and discusses factors and efforts involved in establishing in situ reserves.

Libby, W.J., M.H. Bannister, and Y.B. Linhart. 1968. The pines of Cedros and Guadalupe Islands. Journal of Forestry: 846-852.

Observations are presented on cone, needle and growth characteristics of in situ pine trees on the Cedros and Guadalupe Islands. The relationship of these pines to mainland bishop, Monterey and island pine is speculated and reference is made to planned common-garden studies to further elucidate these relationships.

Linhart, Y.B., B. Burr, and M.T. Conkle. 19?. The closed-cone pines of the Northern Channel Islands. Source? pp 151-177.

In situ descriptions, including needle and cone characteristics, are made of the populations of closed-cone pines Santa Cruz and Santa Rosa Islands. Variation within these populations is used to discuss their relationship with mainland radiata pine and bishop pine in an attempt to clarify their taxonomic status.

Linhart, Y.B., M.C. Grant, and P. Montazer. 1989. Experimental studies in ponderosa pine. I. Relationship between variation in proteins and morphology. American Journal of Botany 76(7): 1024-1032.

Families of ponderosa pine resulting from crosses among some California populations, and crosses between these and individuals from a Rocky Mountain source, are studied. Variation among allozymes is compared with morphological observations from seedling studies. The relationship of these two levels of genetic variation is discussed.

Millar, C.I. 1986. The Californian closed cone pines (Subsection Oocarpae Little and Critchfield): A taxonomic history and review. Taxon 35(4): 657-670.

This paper reviews the taxonomic history and currently available genetic information for knobcone pine, bishop pine and Monterey pine, both in terms of intraspecific patterns of variation and their relationships to each other and other species of the subsection Oocarpae. .

Millar, C.I., S.H. Strauss, M.T. Conkle, and R.D. Westfall. 1988. Allozyme differentiation and biosystematics of the Californian closed-cone pines (Pinus subsect. Oocarpae). Systematic Botany 13(3): 351-370.

This allozyme study reveals patterns of genetic variation among populations of three species of the closed-cone pines: Pinus radiata, P. muricata, and P. attenuata. The allozyme variation among the three species is discussed with respect to their probable evolutionary relationships with each other, and with other species of the subsection Oocarpae.

Miller, J.T. and F.B. Knowles. 1988. Introduced forest trees in New Zealand: Recognition, role and seed source. 5. Pinus attenuata Lemmon - Knobcone pine. Forest Research Institute Bulletin No. 124, Ministry of Forestry, Rotorua, New Zealand.

Although the context of this report is the performance and commercial usefulness of knobcone pine in New Zealand, it also includes more general information on genetic variation related to geographic source and basic biology of the species.

Monson, R.K. and M.C. Grant. 1989. Experimental studies of ponderosa pine. III. Differences in photosynthesis, stomatal conductance, and water-use efficiency between two genetic lines. American Journal of Botany 76(7): 1041-1047.

The progeny of ponderosa pine parents from two contrasting habitats (coastal vs. interior, continental) are examined for certain physiological differences in a greenhouse situation. The results are discussed in relation to parental adaptation to their respective environments.

Moran, G.F., J.C. Bell, and K.G. Eldridge. 1988. The genetic structure and the conservation of the five natural populations of Pinus radiata. Canadian Journal of Forest Research 18: 506-514.

Allozyme variation is used to discuss genetic variation among and within populations of radiata pine. Implications for the development of in situ conservation strategies are discussed.

Old, K.M., W.J. Libby, and J.H. Russell. 1985. Patterns of susceptibility to western gall rust in Pinus radiata. In Barrows-Broaddus and H.R. Powers (eds), Proceedings of the Rusts of Hard Pines Working Party Conference, University of Georgia, Athens, Georgia, U.S.A., pp 285-305.

This study examines variability in susceptibility to western gall rust of native populations, inter-population crosses and repatriate (from New Zealand and Australia) families of radiata pine. The heritability of susceptibility to this disease is estimated and implications for breeding for resistance are discussed. Differences in susceptibility between seedlings and rooted cuttings are explored.

Old, K.M., W.J. Libby, J.H. Russell, and K.G. Eldridge. 1986. Genetic variability in susceptibility of Pinus radiata to western gall rust. Silvae Genetica 35(4): 145-149.

Differences in susceptibility to western gall rust among the five native populations of radiata pine are reported, based on a common-garden study. The heritability of resistance to this fungus and implications for breeding strategy are also discussed.

Park, Y.S. and D.P. Fowler. 1983. Inbreeding depression and genetic variances estimated from self- and cross-pollinated families of Pinus radiata. Silvae Genetica 32(3-4): 89-96.

Plessas, J.E. and S.H. Strauss. 1986. Allozyme differentiation among populations, stands, and cohorts in Monterey pine. Canadian Journal of Forest Research 16: 1155-1164.

The genetic architecture of the three mainland populations of Monterey pine is explored using allozyme differences.

Schuster, W.S., D.L. Allies, and J.B. Mitton. 1989. Gene flow in limber pine: Evidence from pollination phenology and genetic differentiation along an elevational transect. American Journal of Botany 76(9): 1395-1403.

Although the populations in this study are all located in Colorado, the study speaks to level of gene flow in general among populations of limber pine, and discusses the relative contribution of pollen flow and seed dispersal to gene flow.

Strauss, S.H. 1985. The relation of heterozygosity to growth rate and stability among inbred and crossbred knobcone pine (Pinus attenuata Lemm.). Ph.D. dissertation, University of California, Berkeley, California.

This study examines how inbreeding, crossbreeding and climatic variability affect heterosis (i.e., hybrid vigor) in knobcone pine. The relationship with heterozygosity is measured by allozymes.

Strauss, S.H. 1986. Heterosis at allozyme loci under inbreeding and crossbreeding in Pinus attenuata. Genetics 113: 115-134.

The relationship between heterosis or hybrid vigor, based on vegetative growth and cone production, and heterozygosity is explored for both inbred and crossbred families of knobcone pine.

Strauss, S.H. 1987. Heterozygosity and developmental stability under inbreeding and crossbreeding in Pinus attenuata . Evolution 41(2): 331-339.

The relationship between heterozygosity and growth stability in knobcone pine is explored. Results from allozyme analysis of seeds from self- and interpopulation cross-pollinations are compared.

Strauss, S.H. and M.T. Conkle. 1986. Segregation, linkage, and diversity of allozymes in knobcone pine. Theoretical and Applied Genetics 72: 483-493.

The main theme of this paper is inheritance and linkage in allozymes in knobcone pine, but there is also some valuable information presented on genetic variation within populations from a rangewide sample of this species.

Strauss, S.H. and W.J. Libby. 1987. Allozyme heterosis in radiata pine is poorly explained by overdominance. The American Naturalist 130(6): 879-890.

The relationship between heterozygosity (based on allozyme variation) and rate of growth in radiata pine is studied to determine whether there is a consistent explanation for heterosis.

Wang, Chi-Wu. 1977. Genetics of ponderosa pine. USDA Forest Service Research Paper No. WO-34.

This paper is a summary of information available at time of publication regarding the evolution, taxonomy and geographically related genetic variation, based on progeny and provenance tests, in ponderosa pine.

Wells, O.O. 1964. Geographic variation in ponderosa pine. I. The ecotypes and their distribution. Silvae Genetica 13(4): 89-103.

This study explores genetic variability in ponderosa pine relative to geographic source. Genetic variation is measured with seed and seedling characteristics in a nursery study located outside the natural range of the species.
This paper also provides a review of previous work on the genetics of ponderosa pine, including provenance and crossability studies.

Wheeler, N.C. and R.P. Guries. 1982. Population structure, genic diversity, and morphological variation in Pinus contorta Dougl. Canadian Journal of Forest Research 12: 595-606.

The patterns of intraspecific genetic variation in lodgepole pine suggested by allozyme analysis and morphological variation are compared and contrasted.

White, E.E. 1990. Chloroplast DNA in Pinus monticola. 2. Survey of within-species variability and detection of heteroplasmic individuals. Theoretical and Applied Genetics 79: 251-255.

Intraspecific genetic variation of western white pine is explored via analysis of chloroplast (cp) DNA . Differences among populations in cpDNA variants, and the mode of inheritance of cpDNA are discussed. Implications for breeding for resistance to white pine blister rust are noted.

Wilcox, M.D. 1983. Inbreeding depression and genetic variances estimated from self- and cross-pollinated families of Pinus radiata. Silvae Genetica 32(3-4):89-96.

The effects of inbreeding on radiata pine are measured relative to growth rate, stem form, branching habit and needle retention. Estimates of the type of genetic control (i.e., additive, non-additive, etc.) for these traits are provided.

FAMILY: POACEAE

McNaughton, S.J. 1970. Structure and function in California grasslands. In Connell, J.H., D.B. Mertz and W.W. Murdoch (eds.) Readings in Ecology and Ecological Genetics, Harper and Row, New York, pp 342-352.

The study reported discusses the effects of soil type and exposure upon composition, diversity, biomass, productivity and stability in California's annual grasslands. Although many ecological in content, adaptations are discussed.

Stebbins, G.L., Jr. and R.M. Love. 1941. A cytological study of California forage grasses. American Journal of Botany 28: 371-383.

This paper is a preliminary cytological survey of numerous grass species characteristic of the valley and foothill ranges of California. The variation in chromosome numbers, both among and within the sampled populations, is presented. Speculation as to the selective advantage of polyploidy is included.

Calamagrostis

MacDonald, S.E. and V.J. Lieffers. 1991. Population variation, outcrossing, and colonization of disturbed areas by Calamagrostis Canadensis: Evidence from allozyme analysis. American Journal of Botany 78(8): 1123-1129.

Using allozyme analysis, four populations of this grass species ('bluejoint') from different habitat types (i.e., mature forest, intermediate aged forest, forest cutblock and wetland) are examined for relative levels of genetic variation. The nature of colonization in the four areas (i.e., by sexual or asexual means) are also discussed.

FAMILY: POLEMONIACEAE

Eriastrum

Patterson, R. and B.D. Tanowitz. 1989. Evolutionary and geographic trends in adaptive wood anatomy in Eriastrum densifolium (Polemoniaceae). American Journal of Botany 76(5): 706-713.

Stem and leaf samples taken from in situ populations of Eriastrum densifolium across most of its geographic and elevational range are compared on an anatomical basis. The variation seen is compared with the current subspecies designations and discussed in relation to water use efficiency in different habitats. Genetic and environmental sources of variation are not distinguished in this study.

Ipomopsis

Wolf, P.G., P.S. Soltis, and D.G. Soltis. 1991. Genetic relationships and patterns of allozymic divergence in the Ipomopsis aggregata complex and related species (Polemoniaceae). American Journal of Botany 78(4): 515-526.

Patterns of genetic variation based on allozyme data from 60 populations from three species of the Ipomopsis aggregata complex (I. aggregata, I. tenuituba, and I. arizonica) are discussed. Allozyme diversity, within and among populations, is discussed relative to morphological differences and taxonomic classification.

FAMILY: POLYGONACEAE

Dedeckera

Wiens, D., D.I. Davern and C.L. Calvin. 1988. Exceptionally low seed set in Dedeckera eurekensis: Is there a genetic component of extinction? In Hall, C.A., Jr. and V. Doyle-Jones (eds.). Proceedings of the Mary DeDecker Symposium: Plant Biology of Eastern California, University of California White Mountain Research Station, Los Angeles, California, pp 19-29.

Reasons for exceptionally low observed seed set in this monotypic genus are explored. At the time of publication, seedlings for this species, which has a highly restricted geographic distribution, were unknown. The opposing pressures of fitness/heterozygosity and low reproductive success/genetic load are discussed.

FAMILY: PORTULACACEAE

Claytonia

Miller, J.M. 1976. Variation in populations of Claytonia perfoliata (Portulacaceae). Systematic Botany 1(1): 20-34.

Chromosome number and morphological characteristics of greenhouse-grown seedlings from 102 populations of C. perfoliata (Miners' lettuce) are compared, and related to habitat and probable patterns of gene flow.

FAMILY: RANUNCULACEAE

Ranunculus

Eaton, L.C. 1971. Population variability in the Ranunculus occidentalis complex. Ph.D. dissertation, Stanford University, Palo Alto, California.

Common-garden studies are used to reveal the genetic variation among populations of the species which are included in this complex. The observed pattern of variation is compared with ecogeographic variables.

FAMILY: ROSACEAE

Fragaria

Hancock, J.F. and R.S. Bringhurst. 1981. Evolution in California populations of diploid and octoploic Fragaria (Rosaceae): A comparison. American Journal of Botany 68(1): 1-5.

Genetic differentiation, physiological homeostasis and heterozygosity are contrasted in three strawberry species: Fragaria chiloensis, F. virginiana and F. vesca, based on greenhouse studies of samples from 27 natural populations in California.

FAMILY: SALICACEAE

Salix (Willows)

Brunsfeld, S.J., D.E. Soltis, and P.S. Soltis. 1991. Patterns of genetic variation in Salix section Longifoliae (Salicaceae). American Journal of Botany 78(6): 855-869.

The genus Salix is notorious for its taxonomic difficulty due to a number of reasons, including abundant hybridization and high levels of genetic diversity within species. This study uses allozyme data to discuss genetic variability within and among 48 populations of willow (including seven in California). Allozyme patterns are compared and contrasted with traditional taxonomic groupings.

FAMILY: SCROPHULARIACEAE

Mimulus

Searcy, K.B. and D.L. Mulcahy. 1985. Pollen selection and gametophytic expression of metal tolerance in Silene dioica (Caryophyllaceae) and Mimulus guttatus (Scrophulariaceae). American Journal of Botany 72(11): 1700-1706.

This paper explores one type of adaptive response - via pollen selection - to the presence of elevated concentrations of heavy metals in the soil. The response of the common monkeyflower, native to California, is compared with that of Silene dioica.

FAMILY: TAXACEAE (Yew)

Taxus

Scher, S. 1991. Conserving the Pacific Yew. Fremontia 19(4): 15-18.

This discussion paper describes the natural distribution of Pacific yew (Taxus brevifolia), together with forest management impacts and conservation strategies for this species.

FAMILY: TAXODIACEAE (Redwood)

Sequoia (Coast redwood)

Hall, G.D. 1985. Leaf monoterpenes of Coast Redwood (Sequoia sempervirens) [D. Don] Endl.). Ph.D. dissertation, University of California at Santa Cruz.

This dissertation explores several aspects of foliage monoterpenes in coast redwood, those of genetic consequence being: 1) within-tree (i.e., within clone) variation and 2) geographic variation.

W.J. Libby, B.G. McCutchan, and C.I. Millar. 1981. Inbreeding depression in selfs of redwood. Silvae Genetica 30(1): 15-25.

The products of selfed and related outcrossed families of coast redwood are compared with respect to cone abortion, number of seed per cone, germination success and seedling growth under both benign and stressed conditions. The results are discussed relative to the polyploid nature of the genome, and implications for breeding are offered.

W.J. Libby. 1990. Genetic conservation of radiata pine and coast redwood. Forest Ecology and Management 35: 109-120.

This paper briefly describes a genetic conservation collection of coast redwood.

Millar, C.I., J.M. Dunlap, and N.K. Walker. 1985. Analysis of growth and specific gravity in a 20-year-old provenance test of Sequoia sempervirens. California Agricultural Experiment Station Report No. 59, University of California, Berkeley, California.

Characteristics including survival, growth traits and wood specific gravity are used to measure genetic variation within and among ten populations of coast redwoods, growing in common-garden studies in three locations in California.

Sequoiadendron

Du, W. 1985. Genetic variation among giant sequoia (Sequoiadendron giganteum (Lindl.) Buchh.) populations planted in Moscow, Idaho. M.S. thesis, University of Idaho, Moscow, Idaho.

Genetic variation among five populations of giant sequoia is discussed based on differences in height growth, cold damage, branch angle and crown form of rooted cuttings growing in a common-garden study located in Moscow, Idaho.

Fins, L. and W.J. Libby. 1982. Population variation in Sequoiadendron: Seed and seedling studies, vegetative propagation, and isozyme variation. Silvae Genetica 31(4): 102-110.

Genetic variation within and among 35 natural populations of giant sequoia is described relative to isozyme variability. Isozyme heterozygosity is discussed in relation to probable level of gene flow among groves.

Libby, W.J. 1986. Genetic variation and early performance of giant sequoia in plantations. In Weatherspoon, C.P., Y.R. Iwamoto, and D.D. Piirto (Technical Coordinators), Proceedings of the Workshop on Management of Giant Sequoia. May 24-25, 1985, Reedley, California.

This is a brief review of then available genetic information on Sierra redwood (i.e., giant sequoia), summarizing the results from allozyme studies and common-garden studies. Included also are some recommendations for planting giant sequoia.

Mahalovich, M.F. 1985. A genetic architecture study of giant sequoia: Early growth characteristics. M.S. thesis, University of California, Berkeley, California.

This study measures genetic variation based on common-garden comparisons of early growth of rooted cuttings sampled from 21 giant sequoia groves.

FAMILY: VISCACEAE

Arceuthobium

Nickrent, D.L. and T.L. Butler. 1990. Allozyme relationships of Arceuthobium campylopodum and allies in California. Biochemical Systematics and Ecology 18(4): 253-265.

Allozyme electrophoresis is used to examine genetic variation among populations of the dwarf mistletoes parasitic on several west coast pine species. Genetic variation within and among populations is discussed, and this information is compared with the two putative taxa in this group.

Nickrent, D.L. and A.L. Stell. 1990. Electrophoretic evidence for genetic differentiation in two host races of hemlock dwarf mistletoe (Arceuthobium tsugense). Biochemical Systematics and Ecology 18(4): 267-280.

Genetic variation (as measured by allozyme variation) within and among populations of several putative geographic and host-related races of the hemlock dwarf mistletoe is discussed. The natural, primary hosts of this species are western hemlock, mountain hemlock and shore pine.

GLOSSARY

Allele - one of several distinguishable forms of a gene.

Biodiversity - is a general term used to refer to species, habitat, and genetic diversity, inclusively.

Critical-link species - are those species that play a vital role in ecosystem function regardless of their biomass, place in a food web, or possible role as a keystone species.

Endemism - an endemic species is one which is restricted to a specific locality or habitat.

Fitness - this refers to the combined effects of individual viability and fertility. It is a relative term and very much related to selection pressures. Although conventionally it is a characteristic of the individual organism, allele fitness and population fitness are also discussed.

Gamete - a mature germ-line cell. Colloquially, a cell containing one parent's contribution to its (sexually produced) offspring.

Heritability - a quantitative estimate of the degree to which phenotypic differences for a trait are inherited among individuals in a population.

Heterozygosity - the degree to which an individual has non-identical alleles at chromosomal loci.

Homologous - chromosomes that pair with each other at meiosis or chromosome pairs, each chromosome of which was derived from a different parent.

Homozygosity - the degree to which an individual has identical alleles at chromosomal loci.

Inbreeding - mating between relatives. Inbreeding increases the homozygosity in a population, and affects all genes.

Keystone species - a strongly interacting species, whose addition or removal (to an ecosystem) causes marked changes in community structure and function.

Locus/Loci - the position on a chromosome occupied by a gene (or set of alternative alleles).

Monoecy - The condition of having both sexes of flowers on the same plant, as opposed to dioecy in which male and female flowers reside on different plants.

Phenotype - the manifested attributes of an organism, the joint product of its genes and their environment. A gene may be said to have phenotypic expression in, for example, flower color.

Ploidy - the number of sets of chromosomes possessed by an individual. Usually, each parent contributes one set of chromosomes (1n) to the progeny, so each individual has two sets and is called diploid (2n).

Polymorphism - literally, a polymorphic gene is a gene which has more than one allelic form. However, technically, the definition also embodies the concept of frequency. Thus, a polymorphic gene, technically speaking, is a gene for which the most common allele has a frequency of less than 0.95 (some prefer a less stringent cutoff of 0.99). Polymorphism is also a term used to describe the proportion of genes that are polymorphic by the above criterion, for an individual, population or species.

Population - a group of individuals of the same species living within a sufficiently restricted geographical area that any member can potentially mate with any other member.

Quantitative traits - these are characteristics which exhibit a gradation in the phenotype, and are thus described with a measurement as opposed to a simple presence/absence designation. These traits are controlled by more than one genetic locus. Examples of quantitative traits are stem height, seed weight and leaf width.

Somatic - pertaining to the non-germ cells, tissue or protoplasm. (Colloquially, the 'body cells', as opposed to gametes.)

Species - a group of actually or potentially interbreeding populations that are reproductively isolated from all other kinds of organisms. However, with plants in particular, this criterion of reproductive isolation frequently breaks down, as some populations of a species may have reproductive barriers between them, and interspecific hybridization is not uncommon (e.g., oaks, willows). Thus, evolutionary history is used to guide demarcations. Species are dynamic units: the concensus is that speciation is still occurring. Also, the species unit is used for conceptual convenience and organizational purposes, but is more a paradigm than a biological reality. Thus, there are many 'species concepts' including the 'ecological species', 'recognition concept of a species' and even an economic model. For more information on the definition of a species, see the Further Reading section for Chapter II.

Species richness - the number of species per unit area.

Transcription - the process in which DNA serves as a template for the production of a complementary RNA strand.

Vascular - a vascular plant is one which has a well-developed vascular system consisting of specialized cells that function to transport water, dissolved minerals and other substances throughout the plant body (Ornduff, 1974).

Viability - this refers to the probability that an individual survives from fertilization to reproductive age.

FURTHER READING

I. Introduction

Callicott, J.B. 1990. Whither conservation ethics? Cons. Bio. 4(1): 15-20.

Karr, J.R. 1990. Biological integrity and the goal of environmental legislation: Lessons for Conservation Biology. Cons. Bio. 4(3): 244-250.

Lande, R. 1988. Genetics and demography in biological conservation. Science 241: 1455-1460.

Murphy, D.D. 1989. Conservation and confusion: Wrong species, wrong scale, wrong conclusions. Cons. Bio. 3(1):82-84.

Noss, R.F. 1990. Can we maintain biological and ecological integrity? Cons. Bio. 4(3): 241-243.

Raven, P.H. 1990. The politics of preserving biodiversity. BioScience 40: 769-774.

Westman, W.E. 1990. Managing for biodiversity: Unresolved science and policy questions. BioScience 40(1): 26-33.

Wilson, E.O. (ed.) 1988. Biodiversity. National Academy Press, Washington, D.C. 521 pp.

II. Genetic variation: its nature and significance

Brown, A.H.D. 1990. Genetic characterization of plant mating systems. In Brown, A.H.D., M.T. Clegg, A.L. Kahler and B.S. Weir, eds. Plant Population Genetics, Breeding and Genetic Resources, Sinauer Associates Inc., Massachusetts, pp 145-162.

California Department of Food and Agriculture. 1986. California Agriculture Statistical Review. 1985.

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