Restoration, Revegetation, and the Importance of Genetic and Evolutionary Perspectives

Yan B. Linhart

Abstract—Sound biological principles must provide the framework of revegetation projects. Propagules of native species must be used, and these propagules must represent genetic material from sites that match the area to be revegetated as closely as possible. Such matching can be best achieved by using materials from nearby plants growing in nature or propagated in nearby nurseries. The closeness of matching will depend on the type of site to be revegetated. Within National Parks, whose mandate is to maintain the ecological and genetic integrity of the biota, plants or their progeny must come from nearby sites. At other locations, matching may not need to be so conservative. The primary reason for this cautious approach is that plant genomes show very precise adaptations to local conditions. Introduction of non-local materials may lead to failure of the revegetation project and endanger the long-term biological health of nearby populations.

The primary conclusions I wish to draw from the extensive scientific evidence available on these topics involve five recommendations.

1. *Whenever practicing restoration, use native species*. This is important primarily for ecological reasons. The world is already too full of introduced, "exotic" species that have run amok in their new environments and modified these environments so thoroughly as to render them unfit for many of the original, native species. The impacts of various introduced species on the grasslands of western North America provide excellent examples of these negative effects, and have been documented extensively (Baker 1978; Bock and others 1986; Joyce and others 1991; Mack 1981).

2. *The use of "native" species is not enough*. Just because two plants have the same Latin binomial does not make them "equal under the laws" of restoration and revegetation. For example, *Deschampsia caespitosa* grows in Colorado, Washington, and Germany. This does not mean that it can be moved with impunity among those locations.

3. *The best possible option is to use seeds or clones from nearby plants*. "Nearby" should be, if possible, about 100 m for herbs and 1 km for woody plants. In some revegetation projects, even these values may be too optimistic because significant genetic differentiation has been documented over shorter distances.

Yan B. Linhart is Professor of Biology, University of Colorado, Boulder, CO 80309-0334.

4. *If you wish to restore locale A, do not collect seeds or plants at A, grow them in a very different environment at locale B (50 km away across the Continental Divide), and return the progeny, after 4 generations to locale A.* Locale B may be so different in both physical and biotic features that it will create specific selective pressures that alter the original gene pools from locale A.

5. *Restoration methods are often species-specific, because different species have different life histories. These life histories must be taken into consideration when planning the work.* For example restoration with annual species, rhizomatous grasses, shrubs and coniferous trees all require somewhat different approaches.

The rest of this essay is devoted to providing evidence to back up these recommendations. The evidence is extensive: several hundred papers and several book-length treatments deal with these topics. I hope to convince readers with this evidence; consequently, this article is long. If the reader wants only the "bottom line," go directly to section IV "Management Applications" at the end. I would also like to hear opinions about what other research is needed to fine-tune these recommendations and develop others.

The organization will be as follows.

In "Life Histories of Plants," I will deal with a discussion of recommendation 5, "Life Histories," because it provides a convenient framework within which to think about plants.

In "The Genetic Structure of Plant Populations," recommendations 2 to 4 will be addressed in detail, as this is really what most of this essay is about, and various kinds of evidence for recommendations 2 to 5 are intermixed with each other in the context of genetic structure of plant species.

Recommendation 1, the importance of native species, will not be expanded primarily because it is self-evident and because of space constraints. It is self-evident in the context of extensive documentation of the negative impacts of the invasion of exotic species. Some of these species were introduced because they were thought to provide "quick fixes," often by virtue of their rapid growth or establishment in stressful ecological settings created as a result of severe human modification of native ecosystems. Some references to these introductions, and a discussion of the serious problems caused by these species, include annual grasses in the central valley of California (Baker 1978) and species of the genera *Bromus* (Mack 1981) and *Eragrostis* (Bock and others 1981). Incidentally, despite the problems caused by introduced species, there are still those who will argue that such species are not only acceptable, but often better than native species for revegetation. In this context, there is talk of a "New Range War" over the suitability of exotic species, and such species are said by some to be perfectly acceptable for revegetation, because they often resemble native species

morphologically, and because one should not base "acceptability of plants according to a foreign gene or two" (Anon. 1992).

Life Histories of Plants

The life history of plants used in revegetation and ecosystem restoration involves a variety of features which must be taken into account in order to be successful at reestablishing species and reconstructing communities. The list below is a compendium of the various features of a plant species' life history.

Stages of Life Span

Pollination—Stationary plants need mobile pollinators to ensure that gametes meet to produce seed. Native pollinators are needed for proper seed set in many native plants. In addition, breeding systems are relevant because species which are able to self-pollinate (self-compatible) will have very different genetic structures from species which are obligately cross-pollinated (self-incompatible).

Seed Dispersal—At this stage, seed dispersers are of paramount importance to plants, and both birds and mammals play important roles. Their behavior affects establishment and genetic structure of plant populations.

Germination—Most wild species have various dormancy mechanisms whose primary roles are to ensure that seeds germinate at the proper time and not all seeds germinate simultaneously, so that some are left in a "seed bank" for future years. These mechanisms are typically under genetic control, but respond to ecological cues such as day length, total rainfall and many others.

Stand Structure—As plants grow they are exposed to both intra-specific and inter-specific competition, a variety of soil conditions and other forms of landscape heterogeneity. Most plant species also need some species of mycorrhizal fungi to be healthy. The landscape is patchy, and plant populations reflect these patchy habitats with a patchy structure. All these factors create selection pressures that help shape genetic variability.

Maturation and Reproduction—As plants become larger, they are increasingly attractive to herbivores, parasites and seed eaters. All these species, in turn, generate selection.

Life Spans and Life Styles

Plants can be bryophytes, ferns, gymnosperms, or angiosperms, and can reproduce once (monocarpic or semelparous) or many times (polycarpic or iteroparous). If monocarpic, they are usually annual or biennial. If polycarpic they can live a few or many years. Plants can be herbaceous or woody, can have one or many trunks, and can have extensive vegetative spread by runners, rhizomes or other subterranean growth or have little or no such spread.

All these variables will affect revegetation strategies (annuals must set seed yearly or they will die out unless a seed bank is available in the soil) and genetic structuring (small annual plants can show genetic heterogeneity on scales of less than 10 m, whereas populations of tall trees are genetically substructured at scales of 100-1,000 m). Plants with extensive vegetative growth (many Poaceae, Cyperaceae, *Populus*) can be replanted with clonal material, genetically identical to their parents; in contrast, annuals, biennials, and most conifers must be regenerated from genetically heterogeneous seeds.

Ecological Settings

By "settings" I mean the sum total of physical and biotic features characterizing the niches of populations. These include both the total precipitation and its timing, soil conditions, light, above- and below-ground temperatures, pollinators, seed dispersers, herbivores, parasites, mycorrhizae, symbiotic bacteria, and other associated species.

These settings define the selective pressures encountered by various populations of a species, and contribute to the variable, genetically controlled features of these populations. For example, a given species, be it *Artemisia tridentata*, *Yucca glauca*, *Eriogonum niveum* or *Pinus ponderosa*, can grow on north-facing or south-facing slopes, in alkaline or neutral soils, or at sites differing in latitude by many hundreds of kilometers. At each site, it will encounter specific physical and biotic conditions that help shape its gene pool.

Genetic Events

The primary factors that shape the genetic variability in a species are:

1. Breeding Systems—Whether a species is self-compatible or self-incompatible will dictate whether it can or cannot self pollinate. This in turn may determine how much dependence it will have upon natural pollinators. As will be seen below, various species, such as *Yucca glauca*, can be one or the other, depending upon the populations tested. Whether a species is self-compatible or not will also affect the patterns of genetic structuring within and among populations. Self-compatible species, especially those that are self pollinated, tend to show more localized genetic heterogeneity than do self-incompatible species.

2. Natural Selection—These processes shape the gene pools of most species more strongly than other evolutionary forces and will be discussed in detail below.

3. Genetic Drift—This describes what happens when populations are reduced, either by nature or by humans, to very small sizes. Much of the genetic variability is then lost by accident, and when this is coupled with the associated repeated matings between surviving relatives and self pollination, genetic erosion is even greater.

A practice which can lead to very serious loss of genetic variability in the context of revegetation involves the use of seeds from few parents which were sometimes propagated vegetatively themselves to establish nursery stock or seeding stock.

4. Gene Flow—Genetic exchange among individuals and populations can counteract the effects of selection, and genetic drift, prevent differentiation and maintain genetic integrity within a species.

The Genetic Structure of Plant Populations

Background

A species is more than just a Latin binomial name. As biologists and land managers, we have been taught that whenever we study a species, we must provide its Latin binomial. Having done so, we sometimes feel that we have described the species adequately. This perspective has many pitfalls. For example, at the scientific level, there is a tendency to believe that if you have characterized some few individuals, collected in one location, in terms of their physiology, ecology or genetics, you have characterized the whole species. At the practical level, there is a tendency to feel that if you need to replant a species in a given location, seeds carrying that same Latin binomial will be adequate whether they come from 10 m or 10,000 km away.

The primary objective of this section is to convince the reader that this simplistic perspective is incorrect and that, in fact, at all scales, from that of the species as a whole to that of the local population, there is a tremendous amount of genetic variability, organized or at least shaped, by a combination of all the forces that produce evolution—primarily selection, gene flow, breeding structure, and drift. The conclusion will be that every population is unique because it consists of a genome shaped by the interaction of the biological and physical features of its environment. This has very important implications for revegetation because it means that whenever possible, a very conservative approach must be taken, so that the most appropriate plants to use are those from nearby sources, and that the more pristine the conditions desired (inside a National Park) the more conservative one needs to be.

This section is organized to stress the fact that there are three important themes in discussions of genetic organization. First, there needs to be genetic variation in a species. Second, the variation is known to be shaped by the interplay between the homogenizing effects of gene flow and the opposing effects of selection. For this reason, the next two subsections will describe gene flow and other aspects of genetic recombination, and will be followed by a third section which describes selection and its impacts. In the concluding segment, I will address the consequences of the interplay between various evolutionary forces in the context of plant variation, evolution, and revegetation.

The literature associated with the various topics to be dealt with is truly vast, and growing daily. For example, several new book-length treatments of evolutionary ecology of plants have appeared within the last two years. Reviews of many topics are also plentiful. For this reason, such topics as large scale (many kilometers) geographic variation within species, gene flow, and phenotypic plasticity will not be discussed in detail beyond providing references to pertinent reviews. The major topic that has not been reviewed to date in the published literature is that of genetic differentiation between adjacent subpopulations or micro-differentiation. This will be discussed in most detail here because of its relevance to revegetation.

The information provided deals with plant species. Please note that it is equally valid for animal species, although the varying amounts of mobility, especially of birds, mammals and flying insects alter the details of some conclusions.

The tools used to study genetic variation have traditionally involved the analysis of morphological, physiological and breeding system variation in common gardens. Such gardens are very costly of funds and effort, and are not very suitable for large or long-lived species. Within the past 20 years, analyses of variation, gene flow and genetic structure have been aided tremendously thanks to biochemical techniques such as protein electrophoresis and various DNA-based molecular methods. There is concern in some places that much of this biochemical and molecular variation is neutral and therefore uninteresting. It is important to recognize that this is not so. Variation can be neutral and still be very useful and interesting, for instance, in studies of gene flow and population architecture. There is also concern that morphological, electrophoretic and DNA-based molecular variation show different patterns. This is true, and a "fact of life" (Bruce and Ayala 1979; Grant and others 1989). Consider the remarkable morphological and behavioral differences among humans, chimpanzees, gorillas, and orangutans. Yet biochemically, they are remarkably similar to one another. The contrast between the patterns at the biochemical, morphological and behavioral levels underscores some of the complexities of evolutionary dynamics and suggests that variation at all three levels needs to be studied if one wants to have a complete understanding of a species' genome.

Incidentally, the new molecular techniques are currently most useful in studies of systematic relationships among taxonomic entities from varieties on up. The techniques' relative complexity means that they are time-consuming, expensive, and therefore still difficult to apply to population-oriented questions such as patterns of within-species variability, gene flow and selection. Protein electropheresis is still the cheapest and best-developed methodology available for such work.

Genetic Variability

In order for species to survive and evolve, they must be genetically variable. Indeed one of the basic principles of evolutionary biology is that the rate of evolutionary change is proportional to the amount of genetic variability present in a species (Futuyma 1979).

Exact amounts of variation are difficult to measure in an absolute sense, because we cannot use the same methods for all plants and at all levels of biological organization from biochemistry to morphology. However, electrophoretic analyses allow us to make interspecific comparisons at the single gene level. There exist several reviews of this ever-growing literature (Brown 1979; Hamrick and Godt 1990; Hamrick and others 1979, 1991, 1992; Loveless and Hamrick 1984). These reviews have demonstrated the existence of very high levels of genetic variation (between 20 and 50% of loci sampled are commonly polymorphic) and significant correlations between the amount and distribution of genetic variability and various life history attributes of species. The number of species sampled as of 1992 was 448, representing 165 genera. Some of the major conclusions of these surveys are as follows:

1. In the overall analyses, geographic range alone accounted for the largest proportion of interspecific variation in genetic variability. As a result, species with large ranges are more variable than narrow endemics.

2. Woody, long-lived species are more genetically variable than short-lived ones.

3. Patterns of genetic organization within species are strongly influenced by the breeding system: for example, self-pollinated species had over 50% of their total genetic variability distributed among populations, while strongly outcrossed, wind-pollinated species had less than 10% of total variation among populations.

The final result must be interpreted with caution. It does mean that interpopulation differences tend to be more pronounced in self-pollinated than in outcrossed species. This is logical, since the essence of selfing is reduced gene flow and the associated recombination. It does not mean, however, that, since 90% of electrophoretically measured variation in certain species is within populations, one population is as good a seed source for revegetation as any other. This is because a small proportion of genes (meaning perhaps 500 out of a total genome of 5,000 genes) may be critical in terms of determining patterns of germination, or flowering time, root elongation, hardening off at the end of the growing season, or of other features critical to the well-being of a specific population in a specific site.

One result is worthy of specific mention in the context of species' management and protection. Endemic, therefore often rare, species are usually much less variable than more widely distributed ones.

Patterns of Recombination

Gene Flow—Gene flow can take place by pollen, seeds and other plant parts such as bulbils or other propagules. Studies of pollen and seed dispersal have been, and continue to be, very common. The two major reasons are that:

1. Gene flow is recognized as the primary homogenizing force of a species' genome. Gene exchange is what keeps a species together. For these reasons it is of basic scientific interest (Futuyma 1979).

2. Gene flow can involve the modification and dilution of a carefully selected and bred variety, it represents contamination.

3. Genes may "escape" from genetically engineered plants into nearby weeds with interesting, perhaps worrisome, consequences (Ellstrand and Hoffman 1990; Raybould and Gray 1994). For these reasons, it is of significant agronomic interest.

Recent reviews, providing genetic, ecological and evolutionary interpretations are available in Levin and Kerster (1974), Levin (1981, 1984), and Slatkin (1985). Pollen can be dispersed by wind, water, or animals. In most cases, the majority of the pollen dispersed travels a few meters. The rest can travel a few to many hundreds of meters. The shapes of the dispersal curves vary with pollination mode. Wind pollination generally produces so-called leptokurtic distributions. That means that, in comparison to a normal (bell-shaped) distribution, significantly larger than expected quantities travel short distances or very long distances, while smaller than expected amounts travel intermediate

distances. This same leptokurtic pattern is often observed in plants pollinated by relatively small- to medium-sized insects (honey bees). In contrast, larger insects such as bumble bees, hawk moths, bats and birds, can fly very long distances, providing the potential for more extensive pollen dispersal. Water pollination, or hydrophily, is very poorly studied. Studies of distances of water-mediated pollen dispersal are not reported but one can expect distances to be generally more extensive than in land plants, at least in moving water.

Most pollinators whose behavior has been studied in detail are primarily small bees and butterflies, and have short flight distances. Consequently the pollen they disperse does not travel very far, and provides the potential for mating between few individuals. These mating opportunities are described with Wright's (1978) neighborhood model. A neighborhood is defined as the area from which the potential parents of some individual in the center of the area can be drawn at random. A related perspective is that a neighborhood area encompasses all individuals that can mate at random within the area. Neighborhoods are calculated from known distances of pollen and seed dispersal. In herbaceous, insect-pollinated species, neighborhood areas (and numbers of individuals) have been reported as follows: *Primula vulgaris* 30 m^2 (175); *Viola rosstrata* 25 m^2 (167); *Phlox pilosa* 108 m^2 (1,409); *Liatris cylindracea* 63 m^2 (1,260); and *L. aspera* 38 m^2 (176). Within *L. aspera*, neighborhood size varied with plant density from 45 m^2 at 1 plant/m^2 to 363 m^2 at 11 plants/m^2. Note also that the two species of Liatris have very different neighborhood sizes (Levin 1986). For wind-dispersed forest trees, neighborhood sizes have also been estimated for a few species, sometimes from pollen dispersal data alone. Although the areas can be much higher than those noted above, in the hundreds of square meters, the numbers of individuals involved are generally comparable, tens to hundreds (Brunel and Rodolphe 1985; Levin 1981; Richards and Ibrahim 1978; Wright 1965). As noted above, species with large flowers, and pollinated by large, strong-flying animals (large Hymenoptera, Sphingidae, certain hummingbirds or bats) can be expected to have rather different population structures because of the long distances traveled by their pollinators (Emerson 1939; Linhart and Mendenhall 1977). For example, larger neighborhoods can be expected to have less inbreeding, and this appears to be true (Linhart and others 1987), although data are scarce.

Studies of seed dispersal are often anecdotal, poorly quantified, and hence difficult to be precise about (but see Williams 1994). This problem is further complicated by the fact that seed dispersal cannot be equated with plant establishment. Three general patterns of genetic relevance can, however, be stated fairly confidently:

1. Much seed dispersal is restricted to a few meters, especially in herbaceous species (Bannister 1965; Levin 1981).

2. Some establishment can occur over very long distances (Linhart 1988a; Linhart and Premoli 1994; Tomback and Linhart 1990).

3. The preponderance of short-distance dispersal means that plant populations often consist of groups of genetically related individuals living in close proximity to each other. These patterns of genetic substructuring have been identified in a variety of herbaceous and woody species (Brunel

and Rodolphe 1985; Hamrick and Allard 1972; Linhart 1989; Linhart and others 1981; Schaal 1975; Turner and others 1982; Wright 1943).

Breeding Systems—Plants are remarkably variable in their breeding systems. From the point of view of genetic recombination, this means that everything from a very conservative maintenance of specific genotypes to a complete genetic reshuffling every generation is possible. It must also be stressed that breeding systems are highly variable within taxa, so that patterns are seldom as clear as they seem. For example:

- Certain *Taraxacum* taxa are triploid, and thought to be strictly apomictic (asexually reproducing) and therefore rather genetically uniform. In fact, some triploid *Taraxacum* populations show sexual reproduction, and contain important amounts of genetic variation (Richards 1986).
- *Yucca* species are commonly perceived as being obligately associated with *Tegeticula* moths, needing these moths for pollination, as the plants are self-incompatible. Yet in Colorado, *Y. glauca* are self-compatible, and attract other insects that serve as potential pollinators (Dodd and Linhart 1994).
- Dioecy, because it requires the presence of individuals of separate sexes, is thought to be uncommon in colonizing species. Yet many island species are dioecious. A paradox? Not really, since many of these island species have "leaky dioecy"; they are able to circumvent the need for separate sexes under some circumstances (Cox 1989).

Variability in the breeding system, and the associated outcrossing rates, has been demonstrated in a wide variety of plant species, and is often affected by obvious landscape features such as elevation, exposure, and plant density, and may vary from year to year. In at least some cases, such variation can be observed between populations separated by distances of 100 m or less; under these circumstances it can be thought of as another suite of characters that are subject to the effects of selection (Antonovics 1968; Arroyo 1973; Baker 1966; Brown and others 1975; Cheliak and others 1985; Cuguen and others 1989; Ellstrand and Foster 1983; Ellstrand and others 1978; Ennos 1985; Ennos and Clegg 1982; Farris and Mitton 1984; Jain 1976; Lloyd 1965; Moore and Lewis 1965; Moran and Brown 1980; Neale and Adams 1985; Sander and Hamrick 1980; Wyatt 1984a,b, 1988). These interpopulation differences illustrate why the maxim "local seed sources are best" is important. Importing non-local populations may mean that plants with non-local, perhaps maladapted breeding systems, get established and disrupt locally-developed, specific features of genetic recombination.

Genetic Organization by Selection

Geographic Variation—The study of geographic variation in plants is really an analysis of the interplay between the four classes of events noted above. Selection obviously occupies a predominant role in the shaping of this variation, and I will assume so here. The earliest studies of morphological variation in plants were not motivated by evolutionary concerns but very pragmatic commercial and military

ones. The French Navy was especially concerned about having adequate supplies of timber for its ships. The Inspector General of the Navy was not an admiral but a well-known botanist, H. L. Duhamel de Monceau. He started to grow plantations of *Pinus sylvestris* for masts and oaks for hulls, from seeds collected in various parts of Europe. These studies demonstrated forcefully that trees from different geographic sources showed different morphologies (Langlet 1971). The results were so striking that they were used by Darwin (1872) to buttress his arguments about the reality of selection as an agent of evolutionary change. Geographic variation continued to be studied on a large scale by forest biologists who were interested in reforestation with proper material. Reviews are available in Langlet (1971), Libby and others (1969), Dorman (1974), and Stern and Roche (1974).

The best analyses of geographic variation in plants were initiated by Clausen, Keck, and Hiesey of the Carnegie Institution in California. They stand out because they were by far the largest, most complete analyses of morphological variation, and involved a variety of species such as *Achillea lanulosa*, *Potentilla glandulosa*, and several species of *Viola* and *Mimulus* (Clausen and Hiesey 1958; Hiesey and Milner 1965). Later, these studies were expanded to include physiological characters (Björkman 1968, Björkman and others 1969; Hiesey and Milner 1965). The most important lesson from all these studies is that every species studied shows significant levels of genetically based differentiation. The genome of species is not a fixed homogeneous entity, but a deeply fissured, rapidly changing assembly of shapes. Various features of the physical landscape provide good clues about the nature of genetic structure in a species. Differentiation as a function of distance is more dramatic along steep mountain slopes than in rolling hills. Abrupt differences in elevation, exposure (especially north vs. south faces) shifts in bedrock or soil characteristics, and water availability are all sources of selection-induced changes in this genome.

Differentiation usually involves large segments of the genome, because it involves many characteristics associated in some way with fitness and survival. For example, in *Potentilla glandulosa*, the following characters (and estimated numbers of loci involved) showed significant differentiation between populations from different localities: winter dormancy (3); seed weight (6); seed color (4); petal length (4); width (2); color (1); pubescence (5); anthocyanin levels (4); flowering time (many); stem length (many); and leaf length (many) (Clausen and Hiesey 1958).

In early studies of geographic variation, one major focus of the analyses was whether the variation showed a clinal (continuous) pattern or an ecotypic (discontinuous) one. The same results were sometimes interpreted as clinal or ecotypic by different groups of researchers. This dichotomy of views reflects the fact that, for taxonomically inclined botanists, ecotypes were far easier to interpret and deal with than clines. That is because, being discrete entities, ecotypes could be considered as hierarchies of classification, below varieties in order of importance. Clines however were "messy" from this perspective. Detailed analyses of variation now show that, within the same species, some characters can vary gradually, others discontinuously, depending on gene flow, intensity of selection, number of

genes involved, or terrain configuration; the controversy is not useful and has died down (Langlet 1971).

Another general conclusion is that most species studied are very variable and extensively differentiated on a geographic scale, whether it be at the morphological (Clausen and Hiesey 1958; Libby and others 1969), electrophoretic (Guries and Ledig 1982; Hiebert and Hamrick 1983; Li and Adams 1989; Loukas and others 1983; Lundkvist 1979; Plessas and Strauss 1986; Yeh and El Kassaby 1980; Yeh and Layton 1979; Yeh and O'Malley 1980; Yeh and others 1985), or physiological (Björkman 1981; Denno and McClure 1983; Hiesey and Milner 1965; Mooney and Dunn 1970) levels.

Exceptions to this pattern of extensive differentiation do exist. They tend to involve species with little genetic variability, species that live in aquatic environments, and those with large amounts of phenotypic plasticity. These exceptions will be dealt with in more detail in a subsequent section.

Microgeographic Differentiation—This section will focus on genetic differentiation on a small scale: tens to hundreds of meters. The primary concern will be a review of the studies that have analyzed differentiation either between adjacent sub-populations occupying contrasting habitats or within populations exposed to diversifying selection. These studies have dealt with herbaceous species, whose populations can show genetic heterogeneity on a scale of tens of meters or less, and with larger woody species which generally show such heterogeneity on a scale of 100 to 300 m. Species for which genetic differentiation has been demonstrated on scales of 300 m or less are listed in table 1.

In general, physical components of the environment (moisture, soil conditions, exposure) vary spatially either in a gradient, or abruptly. Consequently, they produce differentiation between adjacent populations. Conversely, biotic components (competition, herbivory, parasitism) vary much more dynamically, because the elements providing the selection (competitors, herbivores, and parasites) can move about within a given area (plant competitors or parasites can move about via seed or spores, from one generation to the next). Consequently, they usually produce differentiation within populations.

Agents of Selection

Toxic Soils—These human-induced patterns of genetic differentiation are worth mentioning because they may be relevant in the context of revegetation of old mines and other toxic habitats. Mining activities, especially for toxic metals such as copper, zinc, lead and tin have produced large tailings of refuse, consisting of soils mixed with high concentrations of these metals. Many of these mines have been abandoned, and the heaps have been colonized. Studies of the evolution of this tolerance are abundant, and among the most detailed, complete, and elegant in evolutionary biology. Some of the most important results are as follows.

- Selection has been very intense. As a result, metal tolerant "races" have evolved very rapidly, within hundreds of years or less (Antonovics and others 1971;

Bradshaw 1976; Gibson and Pollard 1988; Jain and Bradshaw 1966; Shaw 1990).

- Selection can produce differentiation on a scale of 10 m or less. Boundaries of mine heaps are very abrupt, and plants on either side of a boundary, 1 to 2 m apart, can be very different.

- Adaptation to heavy metals evolves at some cost: individuals that are metal-tolerant are generally competitively inferior to individuals that grow on adjacent, non-metalliferous soils, when grown on this latter soil type (Antonovics and others 1971; Bradshaw 1976; Hickey and McNeilly 1975). The same pattern appears to be true in plants that are tolerant of serpentine soils (Kruckeberg 1954), and may be a generally applicable conclusion.

- Evolution of metal tolerance has occurred in a wide variety of plant species with many different life histories and characterized by different (wind and insect) pollination systems and life spans. Most are herbaceous, but tolerance has evolved in at least one tree (Betula) (Bronn and Wilkins 1985). The species include *Armeria maritima* (Lefebvre 1989), *Agrostis tenuis* (McNeilly 1968), *Anthoxanthum odoratum* (Antonovics and others 1971), *Agrostis stolonifera* (Wu and others 1975), *Arrhenatherum elatius* (Ducousso and others 1990), *Silene cucubalus* (Verkleij and others 1985), *Mimulus guttatus* (Allen and Shepard 1971), the legume *Lotus purshianus* and its symbiont *Rhizobium loti* (Wu and Lin 1990), and a variety of mosses and other bryophytes. In many bryophytes evolution has not necessarily occurred with the speed documented for angiosperms, nor has the existence of adjacent metal-tolerant and intolerant populations been demonstrated (Shaw 1987a,b, 1990; Shaw and others 1987).

Herbicides—Just as insects have evolved resistance to insecticides, and rodents have evolved resistance to rodenticides, so have plants evolved resistance to herbicides. These are typically weedy plants, such as *Convolvulus arvensis*, *Tripleurospermum inodorum*, *Daucus carota*, *Echinocloa crusgalli*, *Senecio vulgaris* and *Amaranthus retroflexus*. Resistance has been found to most important herbicides, including, 2,4-D, Atrazine and Simazine. Such resistance is becoming a problem, as resistant populations of *S. vulgaris* occupy hundreds of thousands of acres in the Western United States, and resistant *A. retroflexus* are found in Washington, Maryland, Pennsylvania, Ontario and Nova Scotia (Holliday and Putwain 1977, 1980; Lebaron and Gessel 1982). These results are worrisome, as they suggest that the use of herbicides in the context of revegetation manipulations is probably counterproductive.

Nursery Conditions—The rearing of plants in greenhouses, nurseries or well-fertilized fields or fish in hatcheries and of other animals in "captive" domesticated conditions, where food and shelter are easy to obtain, and where natural conditions never prevail have led to adaptation by these populations to their domesticated situations (Davies and Snaydon 1975; Schontz and Schontz 1975; Briggs and Walters 1984). Such genetic changes have led to problems whenever these species are planted or released in the wild. After even a few generations of leading a comfortable, protected lifestyle, the species in question have clearly become

Table 1—Examples of species for which significant genetic differentiation among adjacent subpopulations has been demonstrated. For annual and herbaceous perennial species, the scale of differentiation is usually 5 to 20 m. For forest trees, the scale is usually 100 to 300 m. Only one reference is cited, but more than one is available for most species.

ANNUALS

Graminae
 Hordeum spontaneum (Nevo and others 1986)
 Avena barbata (Hamrick and Allard 1972)
 Poa annua (Law and others 1977)

Polemoniaceae
 Linanthus parryae (Epling and Dobzhansky 1942)

Balsaminaceae
 Impatiens pallida (Schemske 1984)
 I. capensis (Schmitt and Gamble 1990)

Compositae
 Galinsoga ciliata (Shontz and Shontz 1972)
 Lasthenia fremontii (Linhart 1976)

Limnanthaceae
 Limnanthes floccosa (Arroyo 1973)

Lobeliaceae
 Downingia concolor (Linhart 1976)

Onagraceae
 Boisduvalia glabella (Linhart 1976)

Scrophulariaceae
 Veronica peregrina (Linhart 1988b)

HERBACEOUS PERENNIALS

Graminae
 A*nthoxanthum odoratum* (Grant and Antonovics 1978)
 Agrostis tenuis (McNeilly 1968)
 A. stolonifera (Aston and Bradshaw 1966)
 Arrhenatherum elatius (Ducousso and others 1990)

Plantaginaceae
 Plantago lanceolata (Gregor and Lang 1950)
 P. major (Warwick and Briggs 1980b)

Compositae
 Liatris cylindracea (Schaal 1978)
 Taraxacum officinale (Solbrig and Simpson 1974)
 Bellis perennis (Warwick and Briggs 1980a)
 Achillea millefolium (Warwick and Briggs 1980c)
 A. borealis (Kruckeberg 1954), *Lysimachia volkensii*
  (Agnew 1968)

Leguminosae
 Trifolium repens (Turkington and Aarrsen, 1984)
 T. hirtum (Jain and Martin 1979)
 Lotus alpinus (Urbanska 1984)
 L. purshianus (Wu and Lin 1990)

Ranunculaceae
 Ranunculus montanus (Dickenman 1982)

Labiateae
 Prunella vulgaris (Warwick and Briggs 1979)

Rosaceae
 Potentilla erecta (Watson 1969)
 Dryas octopetala, (McGraw and Antonovics 1983)

Caryophyllaceae
 Silene cucubalus (Verkleij and others 1989)
 Armeria maritina (Lefebvre and Vernet 1989)

Scrophulariaceae
 Mimulus guttatus (Allen and Sheppard 1971)

Viscaceae
 Arceuthobium vaginatum (Linhart and others 1994)
 A. americanum (Linhart and others 1994)
 Viscum album (Paine 1950)
 Phoradendron tomentosum (Clay and others 1985)

FOREST TREES

Pinaceae
 Pinus ponderosa (Mitton and others 1977)
 P. sylvestris (Gullberg and others 1982)
 Pseudotsuga menziesii (Herman and Lavender 1968)
 Picea abies (Tigerstedt 1973)
 P. engelmannii (Grant and Mitton 1977)
 Abies lasiocarpa (Grant and Mitton 1977)

Cupressaceae
 Cryptomeria japonica (Sakai and Park 1971)

Myrtaceae
 Eucalyptus urnigera (Thomas and Barber 1974)

genetically modified. As a result, they may do poorly and die off in large numbers following planting in nature. This "nursery effect" has been of concern to a number of people involved in revegetation, but needs some serious scrutiny to develop potential solutions to the problem (Kitzmiller 1993).

Maritime Exposure—Plants growing on cliffs, dunes and other seaside habitats are exposed to extremes of light, wind, salt deposition, wave action and other difficult conditions, and were the object of study of some of the earlier investigations of intra-specific differentiation by Turesson (1922, 1930). On a finer scale, Gregor (1946, and his collaborators, Gregor and Lang 1950) were the first to demonstrate genetic differentiation between populations separated by a few meters. Seaside *Plantago* were more tolerant of high winds and salt spray, and generally markedly more prostrate than *Plantago* in adjacent meadows.

Moisture, Temperature, Elevation—These factors are often interrelated. Several studies of differentiation have been done in habitats that contrast in one or more of these features. Inevitably, associated features are known to, or can be expected to, contribute to the differentiation observed. In these cases, the effects of single factors cannot be isolated, or, when several factors are involved, they cannot be ranked in terms of their relative importance. For example, genetic differentiation has been demonstrated between trees in forests and their conspecifics growing nearby as shrubby "Krummholtz" at tree line (Grant and Mitton 1977). Differences between these habitats include temperature extremes, snow accumulation, insolation, competition and herbivory on seedlings, wind and probably soil factors such as fertility and mycorrhizae. We cannot determine which of these factors is most important in producing the genetic differences observed. Nonetheless, we can at least conclude that, in *Abies lasiocarpa* and *Picea engelmanii* there are significant genetic differences associated with growth morphology, detectable at the scale of 100 to 200 m. On a similar scale, there is significant genetic differentiation in *Pinus ponderosa* occupying north and south-facing slopes in the Colorado Rocky Mountains (Mitton and others 1977), and in *Pseudotsuga menziesii* where roots of plants from south-facing slopes show genetically based greater growth rates than those from north-facing slopes with more plentiful water supplies (Herman and Lavender 1968). This observation led these authors to suggest that "aspect races" have evolved in Douglas-fir. Similar results have also been reported in *Pseudotsuga menziesii* (Campbell 1979), *Pinus sylvestris* (Gullberg and others 1982), and several species of *Eucalyptus* (Barber 1965; Barber and Jackson 1957).

In herbaceous species, the observed differentiation is on a smaller scale. For example, *Avena barbata* is an annual plant in California introduced primarily in the past 100 years. It shows significant genetic differentiation both in allozyme patterns and in morphology, between cool, mesic northern California, and the hot, xeric southern parts of the state. When the variation was analyzed on the scale of a single hillside, genetic differentiation was also demonstrated between locations 5 to 50 m apart. The pattern was consistent with the large-scale, state-wide analyses. Genotypes characteristic of the mesic sections of the state were also most common in the mesic sections of the hillside bottom. Conversely, the genotypes and allele frequencies characteristic of southern California were also found in the xeric

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hilltop (Hamrick and Allard 1972; Hamrick and Holden 1979). Note that, as in the *P. ponderosa* results discussed above, large-scale patterns and small-scale patterns are consistent with each other, providing stronger evidence that selection is involved in the differentiation observed. Given the recent arrival of *A. barbata* in California, differentiation has obviously occurred in less than 100 generations.

Gradients of environmental variability can span very small distances, no more than 10 m, and still create genetic differentiation over these distances. For example, small depressions that fill with water seasonally, and then dry out, provide microhabitats that vary from one another in many characteristics, including moisture availability, soil pH, temperatures, soil aeration and vegetation composition. Such depressions, called vernal pools, are important sites of endemism of the California flora; their existence is threatened because of agricultural activities (Jain and Moyle 1984). Several species have been studied in these pools, especially along the microgradients found along pool sides. Differentiation associated with environmental heterogeneity has been demonstrated in *Limnathes* spp. (Arroyo 1973; Jain and Moyle 1984) and in *Downingia concolor*, *Boisduvalia glabella*, *Lasthenia fremontii* and *Veronica peregrina* (Linhart 1976). *V. peregrina* was studied in most detail, and there was demonstrable differentiation between plants occupying the central, moist to water-logged, densely populated sections of pools and plants occupying the drier periphery, where *Veronica* are few (intra-specific competition is minimal) but where taller grasses are common (interspecific competition is severe). The differentiation involved a combination of responses to water-logging (Linhart and Baker 1973), phenology, reproductive output, plant size, seed size and seed number (Linhart 1974, 1976, 1988b), and electrophoretic variability (Keeler 1978). Plants at the center and periphery had adapted to the different moisture regimes and especially to the competition regimes prevalent in their original habitats. The larger, fast-germinating seed of center plants provided a significant early advantage in intra-specific competition. Periphery plants flowered later and grew taller, providing an advantage in inter-specific competition. Gene flow via seed was potentially important, in that, within a vernal pool that was plowed yearly, but retained its general physical and biological features, center-periphery differences in *Veronica* sub-populations were much less pronounced than in an undisturbed population.

Soils—Whenever edaphic conditions are somewhat extreme in terms of pH, mineral contents, or other features, they can be expected to generate selection pressures of the sort documented in the section dealing with mine tailings above. Among the best examples of such soils are serpentine-derived ones, which, among other features, have high levels of magnesium and low levels of calcium. Such conditions can lead to the formation of strongly differentiated populations, as in *Achillea borealis* (Kruckeberg 1954). These unusual soils are especially interesting in the long run, because they form sites for potential endemism. For example, there are serpentine-associated endemic species in Zimbabwe, New Caledonia (where 2 families, over 30 genera and 900 species are restricted to serpentine outcrops), Yugoslavia, and California. There are also edaphic endemics on other unusual soil formations. *Astragalus phoenix* is restricted to calcareous alkaline soils in Nevada.

Hudsonia montana is restricted to quartzite ledges in Burke County, N.C. These endemics also illustrate another reason why the study of genetic differentiation can be important: it can provide clues to the formation of new species via selection, and perhaps random events, coupled with barriers to gene flow.

Less extreme variation in soil conditions is more common in nature than are serpentine outcrops. Differentiation associated with such variable soil conditions has also been documented. In the Swiss Alps, variation in frequencies of acyanogenic and cyanogenic morphs of *Lotus alpinus* (Urbanska 1984) and *Ranunculus montanus* (Dickenman 1982) was demonstrated in adjacent populations occupying soils characterized as with "acidic silicate" or "carbonate."

Competition—Plants may compete with one another for light, water, nutrients, space and other features of their "living space." Therefore, competition can involve many different kinds of competitive interactions. For example, intra-specific and interspecific competition differ from each other, and *Veronica peregrina* sub-populations exposed to these two regimes showed adaptive differentiation in seed size, timing of germination, growth rate, branching patterns and overall plant size as a result (Linhart 1988b). In addition, interspecific competition involves competitive interactions with many species. *Trifolium* repens in competition with *Lolium*, *Agrostis*, *Phleum* and *Dactylis* showed differentiation in response to being associated with these four species (Turkington and Aarssen 1984).

Herbivory, Predation, Parasitism—All these factors have demonstrable selective effects upon plants. What is especially important is to understand how these factors act in concert to affect evolutionary change in plants. In the juvenile part of its life, a plant is likely to be chewed by caterpillars, rasped by mollusks, clipped by beetle larvae, invaded by fungal mycelia, colonized by bacteria, or play host to viral infection. With the onset of maturity, a plant can, in addition, be mined, drilled, defoliated, grazed, shredded and uprooted. If it reaches sexual maturity, its flowers, fruits, and seeds may be robbed, eaten, parasitized, or otherwise harmed. This is but a small sample of the possible fates which a plant may experience due to its position in the natural food web of the community in which it grows.

Ford (1942) and Haldane (1949) were among the first biologists to suggest that diseases and parasites play a significant role in evolution. The Ford-Haldane perspective has been largely validated for various animals. For plants, the important roles of fungi and arthropods (Denno and McClure 1983; Fritz and Simms 1992) in shaping evolutionary change have also been demonstrated.

Parasites and disease organisms are of particular interest to students of evolution because the modes of selection they are capable of exerting on their potential hosts differ from the selective patterns often exerted by physical components of the environment. Whereas temperature and soil moisture, salinity and heavy metal status exert directional selection which then generate evolutionary change, parasitism and disease are often apt to create various forms of diversifying selection. One reason for this is that, very often, rare biochemical genotypes of the host plant, because they possess novel or at least uncommon defenses in the

form of secondary compounds, are less likely to suffer harmful attack (Haldane 1949). Among the evolutionary consequences of this type of selection are the maintenance (preservation) of large numbers of alleles at particular loci, and the possibility of selection favoring mechanisms which generate genetic change, such as intragenic recombination and mutation. Furthermore, the various allelic combinations at one or more loci which may bestow a resistance to certain parasites may simultaneously render the host susceptible to attack by other parasites.

One evolutionary consequence of this selection pattern is the maintenance of variability via diversifying selection, since alternative genotypes at a given locus or loci will be favored under different conditions. Diversifying selection can also operate if one allele or genotype is selected against by the dependent species but is selected for in the absence of the dependent species because it is associated with a higher growth rate, reproductive output, or some other component of total fitness (Denno and McClure 1983; Linhart 1989, 1991).

Plants can serve as hosts to a wide variety of disease organisms, parasites, herbivores, commensals, symbionts and other life styles. For the sake of simplicity these species in the aggregate are referred to as dependent species. The number of dependent species that can be associated with a species of host plant is often large: more than 200 insect species have been identified for several tree species (Furniss and Carolin 1977). In addition, a plant species is usually susceptible to viral, bacterial and fungal diseases, plant parasites and mammalian herbivores, although not all these dependent species will be active simultaneously. Neither is it likely that every dependent species has a unique suite of physiological and behavioral characteristics, and can thereby generate a unique set of selection pressures. Nevertheless, variation in the direction of selection can be expected. These differences engender what is referred to as species-specific host selection. The life-forms for which species-specific host selection has been documented include algae, herbaceous plants, and forest trees. In some cases, preference by dependent species, or susceptibility by a host, has not been related to precise features of the host phenotype. However, in some cases, a class of compounds has a deterrent effect upon one herbivore, but stimulates feeding by another herbivore species. In other cases, variability in morphology is associated with resistance to some and susceptibility to other dependent species (Linhart 1989, 1991).

Comments on Patterns of Differentiation

Selection Over Time—Such selection is important in two contexts. The great majority of studies documenting rapid evolutionary change have involved comparisons of spatially adjacent groups. In some cases, analyses of populations residing on mine soils or fertilized plots of known date of origin, the rate of change can be given a time frame. In most cases, the time frame is imprecise or unknown. However, such a time frame is important to know, because it gives us information about rates of evolution.

Many plants live long periods of time. As a result, populations often consist of cohorts of different ages, established under different conditions, and therefore subject to different selection pressures. This also provides the opportunity for genetic differentiation among such cohorts. This means that such age-structured populations can consist of groups occupying the same site but having very different genetic constitutions despite the fact that the younger plants are descended from the older plants on the site, and are therefore genetically closely related to these older plants. The theoretical consequences of this possibility have been explored by Charlesworth (1980), and there is evidence for such temporal differentiation in both herbaceous (Gray 1987) and woody species (Beckman and Mitton 1984; Linhart and Davis 1991).

Spatial Scale of Differentiation—This scale depends primarily on two sets of factors. One has to do with the relationship between the intensity of selection, whose effect is to disrupt a gene pool, and the extent of gene flow, whose effect is to homogenize the gene pool, thereby counteracting the impact of selection. The finest scale of differentiation, 10 m or less, has been found in situations with extremely strong selection pressures, either human-related, such as mining (Antonovics and others 1971; Shaw 1990), or natural such as those on the sides of temporary pools (Linhart 1988b). However, even in these situations, gene flow has been documented as reducing the extent of differentiation. All these cases involve annual or short-lived perennial plants of small stature.

The second factor has to do with plant size. Forest trees, because of their stature, typically have much more extensive gene flow than do herbs. In addition, they tend to be primarily outcrossing, and therefore have a more open breeding system. For these reasons, the selection-associated differentiation documented to date between adjacent sub-populations is usually on a minimum scale of 100 to 300 m (Grant and Mitton 1977; Herman and Lavender 1967; Mitton and others 1977). However, strong differentiation on a scale of 10 to 50 m can be found, usually as a result of very localized seed dispersal, generating the existence of family groups (Brunel and Rodolphe 1985; Linhart 1989; Linhart and others 1981).

Life History and Systematic Position—Microgeographic differentiation has been demonstrated in bryophytes (Shaw 1990), in coniferous trees (Grant and Mitton 1977; Moran and Adams 1989; Tigerstedt 1973), and among angiosperms, in plants of all life forms including annuals, herbaceous perennials and forest trees (table 1). Among herbs, there is evidence of differentiation among species with the potential for extensive vegetative propagation, such as *Mimulus guttatus* (Allen and Sheppard 1971), *Agrostis stolonifera* (Aston and Bradshaw 1966), and *Trifolium repens* (Turkington and Aarssen 1984). Breeding systems vary among all the species. Both self-pollinated and outcrossed species are clearly capable of having significantly differentiated sub-populations adjacent to one another, especially if selection is intense enough. However, as a general rule, it is clear that self-pollinated species are likely to show more inter-population differentiation than primarily outcrossed ones.

Exceptions—Although most land plants studied show a significant amount of genetic heterogeneity, both on a large and a small scale, in association with environmental heterogeneity, there are some notable exceptions to this

pattern. The exceptions typically involve species that tend to possess little genetic variability to begin with. For this reason, it is not too surprising that there is little observable differentiation. For example, *Pinus resinosa*, although it occupies an extensive geographic range in eastern North America, has remarkably little morphological or electrophoretic variation (Fowler and Morris 1977). The same is true for *Pinus torreyana*, a California endemic (Ledig and Conkle 1983). Both species are thought to have undergone significant reductions in population size and associated genetic bottlenecks in the past. Despite this low genetic variability, however, there is evidence of some geographic variation in morphological characters in both species.

Aquatic species present especially intriguing exceptions. Most aquatic angiosperms have remarkably little genetic variability compared to land plants. They also have much less pronounced geographic differentiation, and what there is of it, is on a very large scale: populations form northern Europe are differentiated from those of southern Europe and the Middle East, for example (Triest 1991). The same is true for at least certain marsh plants such as *Spartina maritima*, *S. alterniflora*, and their presumed hybrid *S. angelica* (Thompson and others 1991). Reasons for these low amounts of variation are debated. The relatively more environmentally buffered conditions available to water-dwelling species are involved, as are the large amounts of phenotypic plasticity that are commonly found in these species. This plasticity is itself a trait, or more precisely a suite of traits, open to selection and evolutionary change (Bradshaw 1965; Thompson 1991).

One other class of exceptions involves studies that failed to find differentiation under conditions where it might be expected, such as in strongly contrasting habitats. These studies, very few in number, involve situations where sampling was inadequate and therefore differences between sub-populations were not statistically significant. For example, if sampling involves 3 to 5 individuals per location, differentiation is unlikely to be detected.

Management Applications

Biological Synthesis

Most plant species have a good deal of genetic variation. This variability is shaped, reasonably predictably, primarily by the interplay of gene flow, selection and random effects. The first two of these factors are most predictable: gene flow is a homogenizing force, and "dilutes" the effects of selection. In specific cases, however, especially those involving restricted seed dispersal, groups of seeds will lead to the simultaneous establishment of groups of genetically related individuals, i.e., family groups. A population will then consist of patches of family groups.

Selection is predictable in that, whenever a population, or stand, of a species spans some environmental gradient (a mountain side) or is exposed to severe biological interactions (competition or herbivory), adaptation to the conditions observed is likely to have occurred. Adaptive differentiation is evident in most species studied. Microgeographic differentiation has been documented in at least 50 species (table 1) and this is probably a very conservative figure.

The list includes species which, by virtue of extensive cloning, can theoretically cover many square meter or hectares of area. In clonal species, there are often 10 or more clones per square meter, also allowing for differentiation. Random events, in the form of establishment following long distance dispersal of one or a few popagules, or large-scale mortality of all but a few individuals, are unpredictable, but their general effect is also likely to contribute to the highly patchy nature of genetic structure.

Considering all the factors together, there emerges the following perspective: In any ecosystem (or whatever other term is deemed suitable) the individuals of a single species are often grouped into assemblages that differ from one another very strongly. Some of the differences, usually due to selection, are predictable. For example, individuals on north-facing slopes will be characterized by certain features, those on south-facing slopes, by other features. At the local population level (a single hillside or a small valley) there may also be significant genetic differentiation if a strong environmental gradient is crossed. For example, plants along a streamside are likely to be genetically differentiated from their conspecifics on a nearby hillside. Superimposed on this selection-maintained heterogeneity is the patchiness produced by localized gene flow, especially seed dispersal. The end result is an extremely small-scale mosaic of genetic variation. This has been recognized for some time as being one of the important "consequences of being a plant" (Bradshaw 1972; Harper 1977; Levin 1978).

Selection-induced genetic differentiation is not only evident at the morphological and physiological levels. It also concerns other crucially important components of the life cycle. These include the mating system, the propensity to decrease or increase outcrossing and therefore gene exchange among individuals and populations. Such flexibility in the mating system in response to selection is common and indicates that plants can adjust some very basic features of their life history to a given environment. Even more fundamental a feature of life history is life span: in *Poa annua*, certain populations are annual, while other nearby ones are perennial (Law and others 1977). We tend to think of life spans as species characteristics, but they can also reflect adaptations to specific local conditions.

Adaptation to local conditions can involve varying amounts of the genome, depending, presumably, on the complexity of the environmental conditions generating selection. At one extreme, tolerance of heavy metals or herbicides can involve one or a few loci. However, even under these conditions, other loci seem to be affected, through epistatic interactions or modifier effects. That is a logical conclusion drawn from observations that plants tolerant of toxic levels of metals in soils are also poor competitors against non-tolerant plants in normal soils (Antonovics and others 1971; Kruckeberg 1954; Shaw 1990). At the other extreme, plants adapted, both morphologically and by a modified mating system, to specific situations including specific nursery conditions, have probably undergone changes at dozens of loci, or more.

If local adaptation is so precise, and so important, one may expect that disruption of such adaptation would have seriously negative effects. Such disruption can occur by mating between plants that are from very different environments. That is because such mating may be expected

to break up the integrated gene complexes that allowed adaptation to a specific locale. That prediction is, in fact, being borne out, and "outbreeding depression" as it is now called is known in several herbaceous species (*Ipomopsis aggregata*, *Delphinium nelsonii*, *Impatiens capensis*) where there is evidence that progeny of plants produced by wide outcrossing between parents separated by about 100 to 200 m in some cases, and as little as 15 to 20 m in others, are poorly adapted to the environment of either parent: they either die off in higher frequencies, or grow more slowly than progeny of crosses between parents 1 to 5 m apart (Schmitt and Gamble 1990) and may be more susceptible to insects and diseases (Whitham 1988).

In conclusion, there appears to be genetic variability where you look for it. Environmental heterogeneity is a good predictor of local genetic variability. Marked differences in exposure, soil conditions, or community structure will be associated with local genetic differentiation in most plants spanning such environmental patchiness. Exceptions seem to involve mostly species that have little variation, such as most aquatic species, those that underwent serious population bottlenecks in the past, or those species which, for a variety of reasons have high levels of phenotypic plasticity.

Practical Applications

Individuals and populations tend to be highly adapted to local environmental conditions. If sampling of a species' gene pool is to be representative of a specific area, such as a National Park, seeds from a few (or many) individuals from one population only will be inadequate. Actual sampling schemes will depend on how the samples are to be used. If severe disturbance occurs, and revegetation must be done, the very best option is to use seeds or plant parts adjacent to the disturbance, and to encourage natural regrowth and regeneration.

If there is revegetation to be done, the very worst option is to use seeds from very far away, even if the seeds come from a "similar" environment because if the non-native plants grow to reproduce, they will introduce new alleles and therefore new features (growth form, flowering phenology, breeding system) into the local populations of the same species. These alleles can have negative effects:

- Local adaptedness of the native populations may be diluted by this gene flow, creating possible problems of diebacks or unexpected poor health in local populations (Schmitt and Gamble 1990). This is difficult to document. However, some European forest biologists think that the large-scale diebacks observed in many native European forests are in part due to the large-scale unplanned and unrecorded moving about of seed sources of many species in the 18th and early 19th centuries. Pollution is undoubtedly a major contributing factor, but poorly adapted offspring of hybrids between very different parental stock may be important as well.
- A related problem is that hybrids between very dissimilar parents may actually be poorly adapted to local herbivores and parasites. As a result, zones of contact between local and non-local plants may become foci of herbivore, parasite and disease activity. This is somewhat speculative, but it is based on studies

demonstrating that hybrids between species are indeed more heavily parasitized than is either parent in zones of overlap (Whitham 1989). This has been demonstrated in oaks (*Quercus* spp.), poplars (*Populus* spp.), and in intervarietal hybrids of mice (*Mus*).

- A breakdown of adaptedness at the level of life history (spring-flowering annual versus fall-flowering biennial) is also possible as a result of hybridization. The Mountain Ibex of the Tatra Mountains in Czechoslovakia (*Capra ibex ibex*) was killed off by overhunting. It was successfully reintroduced from nearby Austria. Some years later, to enlarge the herd, *Capra ibex aegarus* from Turkey and *C. ibex nubiana* from Sinai were also brought in. The hybrids were fertile; unfortunately, they rutted in early fall rather than winter, as *C. ibex ibex* do. The kids of the hybrids were born in February, died of exposure, and the whole population went extinct shortly thereafter (Greig 1979).

Seeds or other plant materials for revegetation are often needed in large numbers, and for that reason are likely to come from nurseries. Nursery-grown stock are often exposed, perhaps for several generations, to nursery environments which include regular watering, fertilization and perhaps soil modifications, superimposed on local conditions. Given the heterogeneity of the landscapes of western North America, nursery grown stock from maritime West Coast environments, or even western, mesic Colorado may not be suitable for arid Utah, Nevada or eastern Colorado sites.

Species with small geographic ranges, endemics, which are often rare, tend to have less genetic variability than widespread species and are therefore somewhat vulnerable to abrupt environmental changes. They are worthy of special nurturing and protection in the contexts discussed here.

Different agencies will need to adapt the findings reported to their own specific missions and goals. For example, the National Park Service should be among the most "conservative" of the agencies, because one of its stated goals is to protect the genetic integrity of plants and animals within our National Parks. For this reason, a genetic and evolutionary perspective is needed to recognize that one of the attributes of every species is its genetic heritage, shaped by the local environments. This genetic heritage needs protection as well. Conversely, revegetation of seriously disturbed sites outside of parks, such as the Nevada Test Site and other sites where all native biota was essentially eradicated, need not be as conservative. At least some native plants should be started to prepare a base for the new biological communities that will, one hopes, get established there in the future.

Acknowledgments

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