

RESTORATION: DISNEYLAND OR A NATIVE ECOSYSTEM?

A Question of Genetics

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Let us be clear that we are unabashed fans of Disneyland. In our opinion, Disneyland is one of the finest things done for people by people. Among other things, it creates tangible fantasy and apparent reality, in ways that are pleasing to most of its visitors. But it is not reality; nor is it a natural ecosystem. Let us further assert that we believe the fantasy of a "Disneyland" to be better than the reality of another suburban parking lot. Similarly, if a truly native ecosystem cannot be restored, then we believe that the restoration of something biologically viable and sustainable is far preferable to the complete loss of that ecosystem.

What are some of the factors important for restoration that distinguish a "Disneyland" from a native ecosystem? One aspect that has been treated only superficially is the genetics of restoration. The genetic nature of introduced stock can profoundly influence the behavior of the individuals, which in turn may affect the dynamics of the entire community and disrupt or alter the course of co-evolution within the community. All of these effects are of great concern to the restorationist.

Most restorationists and ecological managers are aware in general of the consequences of using genetically inappropriate stock. They attempt to acquire material for restoration and re-introduction projects from within a reasonable distance from the project site—thirty to fifty miles, for example. But guidelines such as these are obviously rough ones that fail to consider the complex and irregular ways in which individual species vary genetically over the landscape. Some species vary gradually over large distances while others vary sharply over short distances. Within most species, many patterns can be found, depending on complex factors of the environment and history of the organisms. Each species has its own unique profile of genetic variation, which ideally would require a unique prescription for restoration.

Fortunately, there are some criteria which, though far from perfect, would be a big improvement over simple "collection radius" guidelines in many situations. In this article, we describe some of these guidelines and the experience behind them, and illustrate our hopes and concerns with examples drawn from our experience as forest geneticists.

The first is a restoration example in the loose sense that replanting or reseedling of trees after logging is a form of restoration. Before Redwood National Park was established in northern California, much of the land was owned and managed by timber companies. The exotic



Contamination of native stands of trees such as these Monterey Pines by foreign genes in wind blown pollen can occur over long distances. Photographs by William T. Follette unless otherwise noted.

species Monterey pine (*Pinus radiata*) had been planted in a few places. Other logged areas were aerially seeded, using seeds of coast redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), and Sitka spruce (*Picea sitchensis*). These species, though native to the



Local genetic variations of traits occur in white fir (*Abies concolor*) which are critical for the survival of trees, an important fact for the restorationist.

park, were introduced from exotic sources. The seeds were collected from forests as far away as Oregon and even Washington. The Sitka spruce and Douglas-fir seeds used in the aerial seeding had come from communities that did not include redwood as a component. Even the redwood seeds used were not native to the Park, and had not co-evolved with native trees there.

This raised some disturbing questions for the Park Service. Among the arguments for creation of the park had been its value as a large natural redwood forest that would be available for study. But were the planted areas, with their genetic hodge-podge of natives, near-but-not-quite natives and outright exotics, really "natural" forests? Did they pose a threat of ecological invasion or genetic contamination of the surrounding natural areas? Would they survive and be adapted to the new site? And could they be taken as representative examples of the natural forest for research purposes?

As it happened, a period of litigation followed the establishment of the park, during which time lawyers

advised the company foresters not to release information on the sources of the planted seed. Later, when this information became available, we urged park personnel to remove all seedlings of the species and age classes of the aerial seedlings in the seeded area in an attempt to eradicate the exotic material from the park.

In response, they agreed to remove some of the Monterey pines (*Pinus radiata*). This was an appropriate action since Monterey pine is not native to the park and should certainly be removed when found there. Unfortunately, however, from a genetic point of view it was the least threatening of the several species that had been introduced into the park. This is precisely because it is an exotic species, and can be distinguished easily from natives, and also because it would never contaminate existing gene pools by interbreeding with native populations.

We contacted the Sierra Club, a strong promoter of the idea that national parks should be natural ecosystems. Their spokesman opposed cutting the introduced redwood, Douglas-fir, and Sitka spruce in the seeded regions of the park on the grounds that the public would not understand. When we asked if a "Disneyland-type approximation to a native ecosystem" were acceptable, he replied that it was preferable to the Sierra Club supporting the cutting of native species within the park—whatever their sources.

Ultimately, park personnel left the interloping trees alone, rationalizing this management decision by noting that after a few millennia of recombination and selection, descendants of the introduced trees would have adapted to the site, and would function as natives. That is probably true. But a few thousand years is a long time. And of course the resulting "native" community would inevitably differ in unpredictable ways from the one it replaced.

Situations—and decisions—like this one disturb us. We see sensitivity here to the question of native species, but too little attention paid to the issue of genetic source of planting stock. And our own experience, together with a long tradition of experience with genetic variation and its ecological consequences among foresters and forest geneticists, make it clear that this can lead to problems. Similarly, forestry practice and forest genetics provide some clues that are likely to be useful to the restorationist for dealing with these problems. In this paper, we describe some of the potential consequences of using genetically inappropriate stock for restoration, and offer some recommendations to avoid problems and to restore genetically viable populations.

Forest Service experience

What insights can the forestry profession offer restoration science in the complex and critically important matter of genetic variation? Forestry has a long history of experience in one type of restoration, namely

planting or seeding to reestablish forests after logging, fire, or other catastrophic devastation. In the early 1700s, the Inspector General of the French Navy, H. L. Duhamel de Monceau, began planting Scots pine (*Pinus sylvestris*) in France, using seeds collected from both local and distant locations. He is credited with being the first to report that seeds of different geographic origins produced trees with substantially different survival and growth within the same plantations. Since then, research by foresters and forest geneticists has supported two points:

1. With few exceptions, species are genetically structured and, in most, the patterns of their genetic structure are hierarchical. By this we mean that the total genetic variation in a species is organized and can be described as variation among physiographic regions, variation among stands or populations within regions, variation among families (kinship groups) within stands, and variation among siblings within families.

2. The patterns of variation can often be understood to reflect adaptations of the trees to their unique environments in which ancestral populations have evolved.

It is important for restorationists to understand that each species they introduce will have such genetic patterning and specific adaptation. If they are to recreate native communities, the genetic structure should be replicated, for this will allow the greatest potential for the introductions to survive over the long time period. Knowledge of the hierarchical nature of variation allows the restorationist to select the genetically most appropriate material, even when collecting from within the restoration site.

Take the example of White Fir

We have studied the genetic structure of white fir (*Abies concolor*) in the western United States, and present it as an example of ecologically significant variation in a wide-ranging temperate-zone tree species. White fir grows in many kinds of environments, from moist, low-elevation sites in the Coast Ranges of California and Oregon to arid, high-elevation sites in the Great Basin and Rocky Mountains. Many aspects of the reproductive system of white fir affect the amount and pattern of its genetic variation, and most of these promote high levels of genetic variability.

In the course of our research during the last twenty years, we collected white fir seeds from throughout the species range, grew them in a nursery, and then planted the resulting equal-age seedlings together in a series of research plantations (called common gardens). Within each plantation, the trees were planted on an even grid-spacing, but trees from different sources were planted randomly with respect to one another. The phenotypes (appearance) of the trees varied greatly as they grew. The hierarchical nature of variation in white fir became obvious as the phenotypes in each plantation were statis-

tically analyzed. Families of white fir varied distinctly from other families that came from the same original populations. Populations within regions differed distinctly. And groups of populations clustered into distinct regional sets.

Indeed—and of special concern to restorationists—most of the variation we found that distinguished both major and minor geographic groups is in traits that contribute to the ability of the parent trees to survive, grow, and reproduce in the exact environments where the seeds originated. For example, differences in traits such as susceptibility to winter damage and water exchange in needles are associated with regional differences in climate that make the variations in these traits adaptive in their native populations. Within regions, correlated differences in some white fir traits occur over short distances in seed origin, especially noticeable when populations are sampled over steep elevational gradients. Since such repeated local patterns of variation occur for traits critical to the survival of the trees, for example, bud flushing date and date of growth cessation, the differences are likely to be maintained by strong selection in local environments.

To replicate the native genetic structure, a restorationist who is replanting white fir can use this information to determine where and how many plants to collect. For example, since there is great variability among trees within native white fir populations, seeds or shoots should be collected from many (versus few) trees. Since there is significant local variation among white fir populations from different elevations within regions, the seeds should be collected from an elevation similar to the planting site. And because there is distinct regional variation in white fir, the seeds should be collected from the same regional genetic unit that would include the restoration site. The important point here is that genetic structure does not necessarily correspond to geographic distance, and so the “collection radius” rule often is inaccurate.

Studies of genetic variation have been conducted for many temperate-zone tree species with generally similar results. Trees are among the most variable organisms known. (A few tree species have very low genetic diversity, but these are interesting exceptions.) Time and again, common-garden tests have shown that the patterns of detected variation for at least some of the traits studied reflect adaptations to variations in the environments within a species range, and are hierarchical, with local variations superimposed on regional patterns.

Lack of understanding can lead to failure

The failure to understand and take into account these variations and their patterns can have several undesirable consequences for the restorationist. One consequence—certainly not the worst for the health of the

native community—is that introduced stock may die soon after planting in the restored site. This commonly occurs if the introduced stock comes from an environment that poorly matches the restored site. In common-garden studies, stock from regions far from the plantation site often does not survive. For example, in a range-wide test of ponderosa pine (*Pinus ponderosa*) planted in Colorado, frost damage killed seedlings of California and Oregon origins in the first year, while seedlings from local sources survived. Similarly, in a study of lodgepole pine (*Pinus contorta*) at an interior British Columbia nursery, seedlings of coastal origin died, whereas local stock had a high survival rate. In forestry operations, there is often a demand for large quantities of seeds following major fires. Before the significance of genetic variation was understood, seeds from any readily available trees were collected and planted. Many of the resulting plantations failed soon after planting due to the inability of the introduced seedlings to cope with the environmental conditions of the new site.

If introduced stock survives the early years, another common consequence is delayed death. This is especially likely with long-lived organisms such as trees, which must face not only normal seasonal fluctuations but also cyclic or episodic events such as droughts, unusually low temperatures, or pest epidemics. Populations that evolved on or near a planting site generally contain the combination of genes that allows them to survive these extreme events peculiar to the site, whereas trees from populations that evolved in other regions, lacking such tested evolutionary advantages, may succumb.

In the early years of common-garden testing of trees, initial rapid height growth by a few non-local populations led to the planting of stock from these apparently superior populations on a wide variety of sites. In many cases, the resulting stands were devastated in ensuing years by infrequent events that are nonetheless characteristic of the site. For example, in common-garden studies of Douglas-fir, trees from coastal sources planted in the interior of the range were killed during infrequent episodes of low temperatures, while trees from local sources survived. Conversely, trees from interior sources planted on coastal sites gradually died over several decades as a result of endemic needle diseases that did not seriously affect trees from nearby coastal sources.

If rapid or delayed plantation failure does not occur, non-native stock may nevertheless grow much more poorly than stock from locally adapted populations. The forestry literature abounds with examples of this nature. Local loblolly pines (*Pinus taeda*) grew 400 percent faster than loblolly pines of non-local origin in one major study reported by Zobel and Talbert in 1984 in the southeastern United States. In another study in western Oregon reported by Silen in 1978, Douglas-firs from the intermountain portion of the range grew at only fourteen percent the rate

of Douglas-firs from local origins. In a study of thirty-year-old ponderosa pines (*P. ponderosa*), Squillace and Silen reported in 1962 that average stem volumes of trees of certain non-local sources were only two percent the average stem volumes of trees of local sources.

These are examples of mistakes that usually become evident within a few years or at most a few decades. But in cases where the introduced stock not only survives but grows relatively well, there may still be serious problems. If the introduced stock all came from few closely related parents, then interbreeding among the stock will bring about high levels of inbred offspring in following generations. In many species of plants and animals, including most of the temperate-zone conifers that have been studied, increasing levels of inbreeding result in poor health and vigor. The likelihood of this occurring is greater if the restored site is isolated from native individuals of the same species, precluding outbreeding with native stock. Unfortunately, this is most likely to occur in just those fragmented landscapes where restoration projects are most often carried out.

Mixing non-local and local populations⁷⁷

An even more serious consequence can be genetic contamination when non-local populations are used to restore sites that are near areas with native populations, or if a remnant population of natives still exists on the restored site. At sexual maturity, the introduced stock is likely to interbreed with natives, passing non-native genes or gene complexes on to the offspring of native individuals. In this way, wild areas surrounding the restored sites may be contaminated, and the genetic composition of native populations irreversibly altered.

The leakage of foreign genes into wild populations can occur, at least in wind-pollinated forest trees, over a distance of many kilometers from the site of introduction. We have observed this situation in two native stands of Monterey pine. The entire native distribution of this commercially valuable species is limited to two Mexican islands and three mainland sites in California, two of which (Cambria and Monterey) are urbanized. Monterey pine has been widely planted as an ornamental, on private lands and for highway landscaping. At Cambria and Monterey, the planted pines intermix with or are adjacent to the native stands. Much of the planting stock came from suppliers in New Zealand and was derived from plantation trees of the New Zealand landrace, which originated as introductions from the native California populations several generations ago. Thus, the identity of these landscape trees is not only uncertain, but much of the stock has gone through several generations of interbreeding and selection in southern hemisphere environments before being reintroduced to its native site.

What effects these New Zealand landrace trees will have after cross-breeding with native individuals in the Monterey and Cambria populations is largely unknown, but a situation such as this is clearly a cause for concern. This is especially critical since interbreeding of native and non-native stock within an important native population can occur within a fairly short time, making it difficult or impossible to distinguish introduced from native individuals. When this happens, removal of the exotic genes is practically impossible, and the native gene pool is irreversibly contaminated.

Detection may be difficult even during the first generation, before interbreeding has occurred. Recently, for example, we studied genetic variation in twelve groves in the Monterey population of Monterey pine. Only after genetic analysis of the entire species and careful reexamination of the sampled site, did it become apparent that one of these groves was composed of planted, non-native trees.

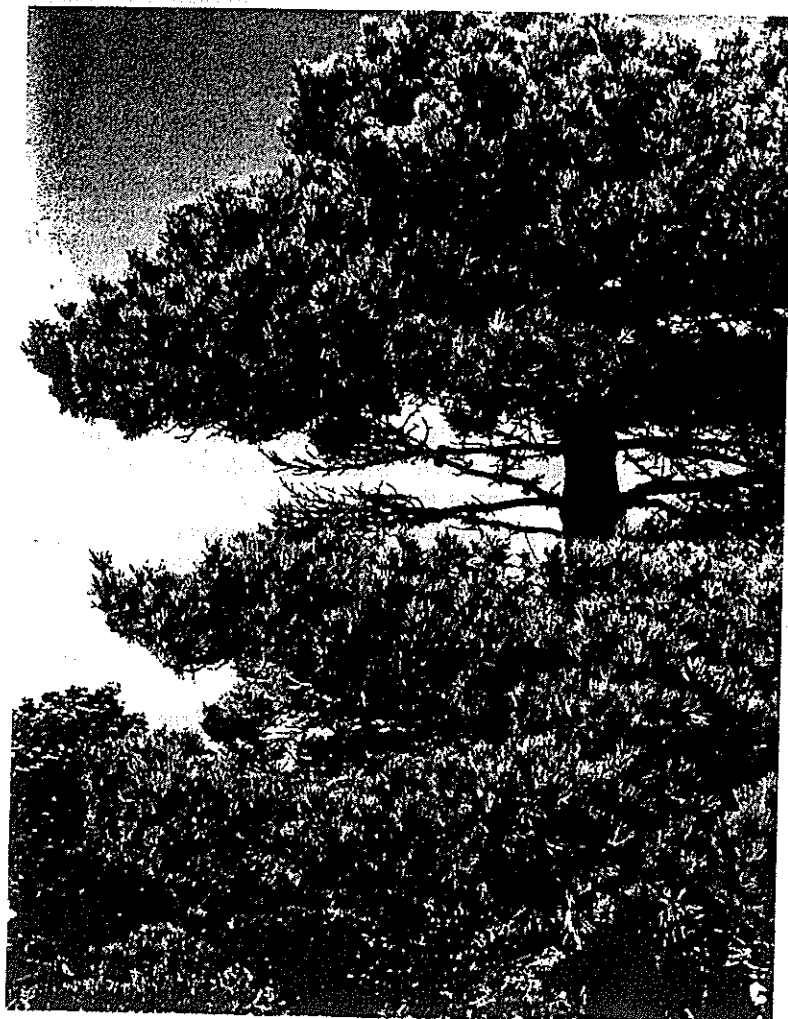
Another example comes from a recent study we conducted on a related species, bishop pine (*Pinus muricata*). In northern California, two distinct races of bishop pine overlap in a genetically and ecologically unusual zone that overlaps for only 1.3 miles. A large recreational community has been built that completely includes this zone. In the mid-1960s, large quantities of bishop pine seeds of unknown origin were aerially sown

over much of this development. The introduced stock thrived, and now it is not only difficult to distinguish these from native trees, but the introduced trees are contributing significantly to the pollen cloud. By 1982, substantial percentages of the seeds from even the older native trees contained non-native genes. As a result, this unusual and interesting site is rapidly losing its value for genetic and evolutionary studies.

In these examples, the only way to eliminate the introduced stock would have been to cut all individuals of the appropriate age class in the suspected area before they began to reproduce. In each case, it is now too late.

Guidelines for restorationists

For the practicing restorationist, of course, the question is how to minimize the risks involved in bringing together artificial assemblages of populations. During the past several decades, foresters have used their knowledge of genetic variation in operational practice to develop guidelines for this purpose that are likely to be useful to the restorationist. These generally involve rough guidelines for the movement of seeds backed up by common-garden tests and other (biochemical or molecular) studies of genetic diversity. The results make it possible to establish fairly well-defined



Two distinct races of Bishop pine (*Pinus muricata*) overlap in Northern California but are being genetically polluted by pollen from trees introduced to landscape a residential development. Male cones of the Bishop pine (shown above) produce clouds of pollen which blanket large areas.

"seed zones." Within each zone, trees are regarded as having similar genetic adaptations to the environment of the zone. For example, these tests might indicate the variation in elevation that might be allowed for transfer of a particular species: it may be 400 yards for one, 200 yards for another. As techniques in analyzing genetic variation advance, seed-transfer guidelines become more sophisticated, and the resolution of prescribed seed transfer within zones becomes finer, sometimes calling for a reduction in allowable transfer distance, sometimes allowing an increase.

Of course, detailed guidelines such as these are based on exhaustive studies of a handful of economically important species. Genetic information is lacking for many of the non-commercial species that are of concern to the restorationist, and transfer guidelines are nonexistent. To aid in planning of restoration and reintroduction projects, we offer the following general recommendations:

1. Do not buy planting stock unless absolutely necessary—collect it yourself, ideally on or near the restoration site. Keep in mind, however, that since significant variation may occur over a short distance, geographic distance alone is an unreliable guide, and must be supplemented by a qualitative matching of site conditions, taking into account factors such as elevation, slope, aspect, soils, drainages, frost dates, and the like. If this conservative approach is followed meticulously, a reasonable genetic matching may be achieved, even without information on genetic variation within the species involved.

2. When forced to collect off the site, then collect from adjacent wildlands of similar topography and vegetation. Keep in mind that distance alone is only a rough index of the risk of genetic incompatibility, and that distinct races may develop and persist within distances as short as a few meters in some instances. Be alert for abrupt variations in edaphic conditions, slope, exposure, elevation, microclimate, and floristic composition that might favor evolution of genetic differences.

3. Similarly, when forced to collect from more distant sites, find out all you can about genetic variation in the species or taxonomic group you are working with. Some species have a surprising amount of information that would be helpful. This is especially so for species in taxonomic groups that contain economically important species. Use this information to determine which distant regions are likely to provide similarly adapted stock for the restoration site. When genetic information is lacking, try to match the collection sites with the restoration site by picking sites similar in soils, elevation, vegetation, and ecology.

When information about a particular species or its taxonomic group is lacking, there are a few clues that may reflect the genetic structure of the species. Plants that are outbreeding, have widely dispersed pollen and seeds, or are long-lived tend to have a lot of genetic

variation among individuals and are likely to suffer inbreeding depression. When these species occur in large continuous populations, they may vary gradually over geographic distance in adaptive rates, although abrupt gradients may evolve when ecotones are sharp. By contrast, plants that are inbreeding do not disperse seeds or pollen widely, are annuals or short-lived, and grow in small disjunct populations may contain little variation within populations, but distinct variation among populations. Early successional species on average vary less than late successional species; angiosperms on average vary less than gymnosperms. Note that these generalizations are frequently broken for specific species and situations.

4. When collecting your own stock, it is almost always better to expend energy collecting from many than from just a few parents. The reason for this is that individuals within populations of many species vary among one another, and this variability buffers the population against environmental vicissitudes. A restoration site containing genetically diverse, adapted individuals runs a lower risk of developing inbreeding depression, or falling victim to pathogens or severe climatic conditions than a genetically homogeneous population.

For example, for a typically variable conifer species such as white fir, a minimum of twenty-five parent trees should be used to provide seeds to restore a relatively homogeneous site. The seed-collection trees should be spaced at 100 yards apart, to reduce the chance of collecting from close relatives. An attempt should be made to collect the same amount of genetic material from each parent. The number of parents and the distance separating them decreases as the within-population variation in native stands decreases. A species with no or little variation within populations (e.g., *Pinus torreyana*, or *P. resinosa*) could be adequately represented by collecting from only a few individuals within a population.

5. When it is impossible to collect and grow plants yourself, try to find a nursery that maintains good records of the origins of their stock. Use these records to match stock as closely as possible, following the guidelines suggested above. State and federal agencies (State Department of Forestry or U.S.D.A. Forest Service) or native plant societies can lead you to sources. If your local nursery provides stock for wildland restoration and does not maintain records of plant origins, impress the manager with the importance of doing so. Location of plant origin is as important as knowing how many parents contributed to the nursery stock.

If you must use nursery stock, and the origins of the stock are all unknown, then the best advice is to keep the numbers high and buy from several different nurseries. By so doing, you hopefully include some genetic variation that may be adaptive, if not native, to the restoration site.



An example for potential gene contamination exists in this view of the Cambrian Monterey pine. On left is a planted row of Monterey pine of unknown origin; at right is a native stand. Photograph by the author.

6. It may be useful to give nature a chance first. For example, following the 1977 Marble Cone fire in California, there was a flurry of restoration planning, which focused on reestablishing the groves of rare bristlecone fir (*Abies bracteata*) in the burned area. Plantations of bristlecone fir growing in Tilden Park in Berkeley have long served as the major donor for seeds for landscaping plantings of this species. However, the original native source of the firs in Tilden Park was one of the few groves not in the burned area; clearly these seeds would be inappropriate for regenerating the burned groves. In the midst of the ensuing arguments, it became apparent that many of the bristlecone firs in the burned regions had survived the fire, and that natural regeneration would be sufficient to assure the continuance of most or all of the burned groves. As a result, most of the bristlecone fir populations survived, even though the Marble Cone fire was unnaturally intense due to the massive buildup of fuel loads following years of fire protection. In this case, then, the best course for restoration was one of no human intervention.

Similar situations are encountered in other communities. Jordan reports that degraded prairies in the Midwest,

for example, often include a suppressed flora, which will recover under proper management, reducing or even eliminating the need to introduce stock from outside.

7. Another strategy, especially useful when native populations are not available and when none of the alternatives about matching distant sites are available, is to deliberately build a new landrace (naturalized strain of individuals having a non-local origin) for the site. The first step is to plant a mixture of individuals from several donor populations to create a broad genetic base. Individuals that survive may interbreed, creating novel genetic variation for selection to act upon. In succeeding generations, a collection of individuals that is increasingly adapted to the restored site should evolve. This happens frequently in forestry when exotic species are introduced for commercial plantations.

Keep records, however minimal

So much for advice. It is our impression that restorationists probably have as much to teach population geneticists as they have to learn from them. This is

especially true when it comes to understanding the ecology of particular areas and the many native species that the restorationist works with commonly, but which may escape the attention of academic researchers.

Almost any project that entails the introduction of species from another habitat will yield information about genetic variation and its ecological significance. The problem is that constraints on time and planning often limit the practicing restorationist's ability to set up projects as controlled experiments and to gather data in a systematic, statistically replicated way. Nevertheless, the research value of almost any project can be enhanced by maintaining even minimal records. Especially critical are:

- Maps of restored sites, indicating identities, including place of origin, age, and date of planting, of all planted individuals. If this is impossible for individuals, indicate at least the place of origin for each introduced species. This will allow future analysis of genetic adaptedness of the introduced stock.
- Records of the survival and performance of planted stock at appropriate intervals (for example, at one, three, five, ten, twenty, fifty, and 100 years after introduction). Whenever possible, compare the growth to similar-aged native individuals of the same species living in the same or adjacent areas.

-Comments on the ecological behavior of the introduced stock—whether it is more or less aggressive than local stock, response of other native species, behavior during periods of severe climatic events (droughts, freezes, etc.).

What we have offered here is, of course, only a brief summary of some of the issues related to the movement and introduction of species that are of concern to ecological restorationists. This is a complex subject with a long history. Those interested in delving more deeply into the literature on this subject may find the references listed below useful starting points.

In addition, a number of agencies and organizations have responded to the rapid increase in interest in restoration in recent years by developing guidelines for the consideration of genetic factors in restoration projects. The National Park Service is developing a set of guidelines that, among other things, will require the use of local stock in restoration projects in national parks. The California Department of Parks and Recreation is developing similar policies. The U.S. Forest Service recommends the use of seed zones and seed transfer guidelines based on genetic structure for reforesting logged areas. We applaud these efforts as signs of the growing awareness of the importance of genetic factors in restoration, and hope this paper will contribute to the continuing effort to restore truly native ecosystems.

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