
“How Local Is Local?”—A Review of Practical and Conceptual Issues in the Genetics of Restoration

John K. McKay,^{1,2,3} Caroline E. Christian,² Susan Harrison,⁴ and Kevin J. Rice^{1,2}

Abstract

In plant conservation, restoration (the augmentation or reestablishment of an extinct population or community) is a valuable tool to mitigate the loss of habitat. However, restoration efforts can result in the introduction of novel genes and genotypes into populations when plant materials used are not of local origin. This movement is potentially important because many plant species are subdivided into populations that are adapted to local environmental conditions. Here we focus on genetic concerns arising from ongoing restoration efforts, where often little is known

about “How local is local?” (i.e., the geographic or environmental scale over which plant species are adapted). We review the major issues regarding gene flow and local adaptation in the restoration of natural plant populations. Finally, we offer some practical, commonsense guidelines for the consideration of genetic structure when restoring natural plant populations.

Key words: ecotype, local adaptation, outbreeding depression, restoration, seed zones.

Introduction

Human activities are altering ecosystems at unprecedented rates and are having adverse effects on biodiversity worldwide (Vitousek et al. 1997; Raven 2002). These changes have led to increased interest in how to restore altered landscapes back to diverse systems that are rich in native species (Hobbs & Norton 1996; Dobson et al. 1997). Approaches to restoration range from the augmentation of populations with individuals from nearby sites to the creation of entirely novel species assemblages (Jones 2003). Although restoration is becoming a widespread practice, little is known about the extent to which practitioners should be concerned with the genetic composition of the plants used in restoration (Montalvo et al. 1997; Lesica & Allendorf 1999; Jones 2003). Some recent studies have argued that the augmentation of populations with nonlocal genotypes may actually do more harm than good (Keller et al. 2000; Edmands & Timmerman 2003; Hufford & Mazer 2003).

The genetic structure of species may affect restoration efforts in two major ways that remain mostly unexplored. First, the strength of local adaptation and the geographic scale over which local adaptation occurs raise concerns about how well novel genotypes will succeed in new environments. How will existing populations, adapted to local conditions, be affected by the introduction of these new

genes and genotypes? A tremendous amount of research has explored local adaptation and natural selection in natural plant populations (Stebbins 1950; Endler 1986; Linhart & Grant 1996; Geber & Griffin 2003). However, data exist for only a fraction of the species used in restoration, and even for these species, studies address only a subset of the populations within the species range. Thus, it remains unclear how general these findings are, nor is it clear how they can be used to guide restoration decisions. A second issue critical to the restoration process concerns the level of genetic diversity required to ensure the long-term success of restoration projects. Key questions include what level of starting genetic diversity is important in restoration and what levels of diversity should be maintained. Within-population genetic diversity may be needed to assure initial population establishment as well as long-term evolutionary potential of restored populations.

The motivation for this article is to better link research and theory of adaptation with practice in restoration. In California, for example, we know from studies in systematics, population biology, and phylogeography that species exhibit complex patterns of adaptation and gene flow among populations (Clausen & Heisey 1958; Knapp & Rice 1998; Montalvo & Ellstrand 2000; Calsbeek et al. 2003). We review the major issues regarding gene flow and local adaptation in the restoration and management of natural plant populations, including methods and motivations for examining patterns of genetic variation and gene flow within and among populations.

The Scale of Local Adaptation

The introduction of novel and potentially maladapted genotypes to restoration sites is a major genetic concern in

¹ Plant Sciences, University of California, Davis, Davis, CA 95616, U.S.A.

² Center for Population Biology, University of California, Davis, Davis, CA 95616, U.S.A.

³ Address correspondence to J. K. McKay, Plant Sciences, One Shields Avenue, University of California, Davis, Davis, CA 95616. email jkmckay@ucdavis.edu

⁴ Environmental Science and Policy, University of California, Davis, Davis, CA 95616, U.S.A.

restoration. Nonlocal genotypes might reduce the success of restoration projects if they are maladapted and/or negatively affect adjacent native populations adapted to local conditions through gene flow. Although many practitioners try to collect restoration material from local seed sources when possible, there is a pressing need for more information on the geographic and environmental scale of local adaptation. The field of restoration faces many practical limitations that must be considered to effectively bridge research and restoration practice. Organizations charged with restoring habitats often are severely constrained by funding, staff, and time. Although the use of locally collected plant material in restoration may be a conservative measure in the absence of much needed data on genetic patterns, in many restoration projects such an approach is logistically and economically unrealistic. Unless local adaptation is shown to be important, the above limitations often prevent the exclusive use of locally collected and propagated plant material in restoration projects. As a result, seed producers provide “local” material for only a handful of common plant species that are easy to propagate.

Genetic variation is a prerequisite for evolutionary change because in the absence of genetic variation, species and populations lack the ability to evolve. Genetic variation originates by the process of mutation and becomes organized by gene flow, recombination, random genetic drift, and natural selection. A growing concern in restoration recognizes that the preservation of adaptive genetic variation within and among populations ensures that evolutionary potential is maintained (Bradshaw 1984; McKay & Latta 2002). To help create guidelines for selecting genetic sources for restoration, we need to understand how adaptive variation is distributed within and among populations connected by varying degrees of gene flow. Ideally, this information will allow restorationists to maintain historic gene flow and local adaptation, while avoiding the loss of genetic variation.

There is a rich history of ecological genetics in plants (Stebbins 1950), and the sessile nature of plants makes them particularly amenable for field experimentation. However, when traits are measured in the wild, care is needed to avoid the confounding effects of environmental variation versus heritable genetic variation. To separate these two components of trait variation, ecological genetic data should be collected using reciprocal transplant and common garden approaches that include field plantings, greenhouse trials, and growth chamber screenings (McKay & Latta 2002). Using these approaches, many traits have been studied including morphological, physiological, and life history components of fitness (reviewed in Arntz & Delph 2001; Mazer & LeBuhn 1999). The field of plant ecological genetics has provided overwhelming support that many native plant populations are locally adapted over a variety of spatial scales (Endler 1986; Linhart & Grant 1996).

Although the primary conclusion from most of this experimental work is that local adaptation is widespread,

it is important to realize not all populations are locally adapted. There exists convincing evidence for maladaptation (reviewed in Crespi 2000), where local genotypes express phenotypes that are not optimum for current local conditions. Conversely, the success of some invasive species demonstrates that nonlocal genotypes may possess the ability to grow and compete in novel environments without significant genetic differentiation. For example, in introduced populations of Fountain grass (*Pennisetum setaceum*), Williams et al. (1995) found no evidence for local adaptation across a steep environmental gradient. Instead, this invasive species has broad environmental tolerance because of phenotypic plasticity. The likelihood of local adaptation is addressed further below (in Adaptation vs. Gene Flow and the Potential for “Genetic Pollution”).

Evolutionary Potential—Genetic Variation within Populations

Responsible practitioners try to collect material broadly from many individual plants across a collection site in order to maintain genetic variation in plant populations used in restoration projects. In addition, federal and state agencies now recognize the importance of genetic structure and evolutionary potential in the restoration and long-term management of plant populations (National Park Service 1993; California Department of Parks and Recreation 1994; USDA Forest Service 1994). To achieve this goal, seed collections should be made from a minimum number of individuals at a site and at a minimum number of sites (Knapp & Rice 1994). These efforts help to maintain adaptive genetic variation found within native plant populations. Although maintaining evolutionary potential is often a concern, inbreeding depression appears to be the primary impetus for maintaining genetic variation in restored populations.

When populations become small, either by population reduction or founder events, the likelihood of inbreeding increases and genetic variation is lost due to genetic drift. Often, decisions to move individuals between populations are motivated by the perceived danger of inbreeding depression in small populations (Ralls & Ballou 1983). Inbreeding depression—lower fitness among inbred individuals—is well documented for both outcrossing and selfing plant species and should indeed be a concern in restoration. Empirical studies support the theoretical prediction that rapid inbreeding decreases fitness (Ralls & Ballou 1983) and can result in further decreases in genetic variation through extinction of inbred lines (Newman & Pilson 1997; Saccheri et al. 1998). However, many exceptions exist in the literature and levels of genetic variation within and among plant populations vary greatly among taxa (Byers & Waller 1999). In populations experiencing lower levels of inbreeding over longer-time scales, “purging” of deleterious recessive alleles by selection becomes more likely, and smaller reductions in genetic variation

occur (Byers & Waller 1999; Hedrick & Kalinowski 2000). Naturally low levels of genetic variation in a species may reflect historically small population sizes and may not be a problem that needs to be mitigated. Many rare species lack the genetic diversity found in their more widespread relatives (Hamrick & Godt 1996). However, for many species used in restoration, inbreeding depression should clearly be a concern, particularly in historically outcrossing species (Ralls & Ballou 1983).

Although maintaining genetic variation is necessary for allowing populations to adapt to future stress, aiming to increase genetic variation may not always be a proper management goal. Not all evolution is adaptive, and simply managing for high genetic variance will not necessarily be the best strategy for sustaining plant species. Lande and Shannon (1996) examined how genetic variation can increase or decrease the risk of extinction, depending on the amount and pattern of environmental change. In unpredictable or unchanging environments, excessive additive genetic variance will result in individuals deviating too much from the optimal phenotype. The existence of suboptimal phenotypes that lower the mean fitness of the population is referred to as genetic load. In contrast, higher amounts of additive genetic variance in highly variable, yet predictable, environments will allow the population to track the varying selection pressures of the environment. Thus, depending on the degree of local adaptation and environmental heterogeneity, increasing within-population genetic variation may result in increased or decreased fitness.

Adaptation versus Gene Flow and the Potential for "Genetic Pollution"

Genetic contamination is a serious concern in restoration given that small, isolated populations of plant species are most vulnerable to the translocation of distant, potentially maladapted genetic material (Hufford & Mazer 2003; Rice & Emery 2003). Those concerned with genetic contamination (e.g., California Crop Improvement Association) recommend the use of locally collected stock from a reputable nursery or seed supplier who can identify the geographic source of their plant materials. Fundamental to these concerns is the need for a greater understanding of the importance of the genetic variation that exists within species.

In relating this aspect of restoration to ecological genetics, it is clear that there are actually two primary concerns. The first is whether the restoration project will succeed or fail. The second concern is whether restored populations will be the "same" as original populations. To address the first concern, the survival and reproduction of planted populations are monitored for some specified time interval. Whether they are optimally adapted to the local habitat is not considered. That is, if they establish a self-sustaining population, it can be considered a restoration success, even if the genetic variation of the new

population differs markedly from that of the original (extirpated) population. The second concern involves a more ambitious goal of maintaining the natural genetic structure of the species, as well as ensuring population survival and reproduction.

The interaction between gene flow and selection determines the balance between within- and among-population adaptive variation. Although gene flow is a fundamental process in theoretical population genetics, empirical estimation of gene flow in natural plant populations is in its infancy. With the advent of molecular markers, it is now possible to directly and indirectly estimate levels of gene flow (see Neigel 1997, for a review of these methods). Molecular markers can be used as direct measures of gene flow when diagnostic markers or distinct genotypes exist among populations (Ellstrand et al. 1989; Devlin & Ellstrand 1990; Rannala & Mountain 1997). Estimating current levels of gene flow using highly variable markers can potentially address concerns about the potential danger of genetic contamination (i.e., loss of local adaptation caused by gene flow from translocation). More typically, markers are used to measure how genetic variation is partitioned within and among populations due to historical processes, using parameters like F_{st} (Wright 1951). By assuming equilibrium states, these parameters provide an estimate of historical levels of gene flow. From a restoration perspective, studies of marker variation can be used to estimate historic levels of connectivity and, in turn, practitioners can use this information to determine the relative importance of maintaining these levels by moving individuals or maintaining and restoring connecting habitats. By combining several powerful new methods for estimating gene flow, including nonequilibrium approaches (e.g., Rannala & Mountain 1997) and coalescent-based approaches (e.g., Beerli & Felsenstein 2001), it is now possible to get estimates of both current and historical gene flow.

The conditions for local adaptation are a function of the relative strength of selection and gene flow (Endler 1973; Slatkin 1985). In theory, gene flow can either prevent or promote adaptation, but few data exist on which of these effects is more common (Slatkin 1985; Lenormand 2002). The phenomenon where increased gene flow between populations constrains or "swamps" adaptive differentiation is referred to as migration load. There are a number of cases where gene flow among populations appears to be swamping local adaptation (King & Lawson 1995; others reviewed in Storer 1999). On the other hand, many studies demonstrate local adaptation and population divergence even in the face of substantial historical gene flow, implying very strong local selection pressures. Examples of adaptation to heavy-metal soils in mine tailings where selection maintains a cline in several traits despite substantial gene flow are those most familiar to plant ecologists (e.g., Antonovics & Bradshaw 1970). Another striking example is the well-documented adaptive cline in Scots pine along a latitudinal gradient in Scandinavia

(Eriksson et al. 1980; Mikola 1982; Hurme 1999; Davis & Shaw 2001) in spite of very high gene flow among populations (Gullberg et al. 1985; Hurme 1999).

Conversely, studies in other species have found that convergent selection acts to constrain population divergence in some adaptive traits, despite divergence at neutral marker loci (Waldmann & Andersson 1998; Petit et al. 2001; McKay & Latta 2002). The latter presumably reflects a low level of gene flow. Differences among traits in the degree of divergence among sites are also of interest to conservation and restoration ecologists because this may reflect the strength of selection on different traits (Antonovics & Bradshaw 1970; McKay & Latta 2002). Because restoration projects involving translocations could largely alter the historical levels of gene flow (Storfer 1999), these questions are increasingly relevant.

One of the major challenges in restoring plant populations is striking a balance between avoiding inbreeding depression, while at the same time preventing outbreeding depression. Outbreeding depression can be the expression of migration load or "genetic pollution" resulting from crossing among populations adapted to different environments. Unfortunately, a large number of restoration studies promoting the translocation of genetic material are apparently unconcerned with the potentially negative effects that human-caused gene flow could have on locally adapted populations (Storfer 1999). Ignoring local adaptation could undermine both the success of restoration efforts and the long-term viability of populations (Templeton 1986). A greater understanding of the spatial patterns of adaptive variation is needed to facilitate translocation decisions and to ensure that populations have the ability to respond to rapid climate change.

Outbreeding depression can result from two main mechanisms (Fenster & Galloway 2000). The first is related to local adaptation. As discussed above, crosses among ecologically divergent populations may result in individuals expressing intermediate phenotypes that are not favored locally. This can reduce the viability of the population by increasing the proportion of maladapted individuals. Second, outbreeding depression can result from the breakdown of associations among loci, or more accurately, linkage disequilibrium among alleles at different loci (Fenster et al. 1997). This is because the phenotypic expression of a particular allele will often depend on the alleles at other loci (Whitlock et al. 1995). Certain loci across the genome interact (i.e., epistasis) to produce a functionally integrated phenotype, a phenomenon referred to as "coadapted gene complexes." Even if two populations are phenotypically similar and experience identical selection pressures, crosses among these populations may produce unfit hybrids because of the breakdown of these gene complexes.

To date, there are few studies that specifically test for the contribution of epistasis to outbreeding depression, so it is not yet possible to make general conclusions. Keller et al. (2000) found that local adaptation was the main

cause of outbreeding depression but found evidence for coadapted gene complexes manifested as a reduction in fitness in subsequent generations (i.e., F₂ generation plants). Fenster and Galloway (2000) found evidence for epistasis in the form of increased fitness in outbred individuals (a phenomenon known as heterosis) but found little evidence for outbreeding depression resulting from the breakdown of linkage disequilibrium among loci. Finally, a study of a marine copepod by Edmands (1999) provides convincing evidence for this mechanism of outbreeding depression.

In the absence of interactions between genes, gene flow among locally adapted populations should only present a short-term decrease in fitness because nonlocal alleles cause an increase in the migration load (Bradshaw 1984). Mean population fitness should then recover as maladaptive alleles are removed by selection and the locally adapted alleles increase in frequency. Although there has been debate over the importance of epistatic interactions in maintaining fitness in natural populations (Whitlock et al. 1995), a better understanding of the importance of coadapted gene complexes is crucial for assessing the long-term impacts of translocations often done in restoration.

Molecular Data in Restoration

The increasing use of molecular genetics in conservation suggests that some discussion of the use (and misuse) of this emerging technology might be instructive. The use of molecular marker techniques for assessing genetic relationships among populations and patterns of gene flow has exploded in the past 20 years (Avice 1998), and molecular techniques have been increasingly useful in identifying areas of specific concern to conservationists. For example, recent studies along the west coast of the United States have shown distinct patterns of genetic differentiation among plant populations that were previously considered panmictic or nearly panmictic (Soltis et al. 1991; Brown et al. 1997; Rodriguez-Robles et al. 1999; Riddle et al. 2000). Conversely, molecular data can also reveal that there is little differentiation among populations that were previously considered diverged based on morphology (Schneider et al. 1999), particularly when morphological differences among populations are measured in the field and may represent largely phenotypic plasticity (Coyne & Orr 2004). Combining molecular studies of large-scale patterns with ecological studies of local adaptation provides the kind of hierarchical analysis of genetic structure that can inform conservation and restoration efforts.

Molecular markers are neutral or nearly neutral to natural selection and therefore overall patterns of diversity at markers should primarily reflect past gene flow and genetic drift (including mutation accumulation; Hedrick 1999). These are certainly interesting parameters to estimate. However, simply studying the patterns of variation in molecular markers in plant species will not lead to an

understanding of the species' adaptive potential, the critical information often needed for restoration decisions. Although preserving genetic diversity in molecular markers is an approach that has been suggested (Vrijenhoek 1994), there is no theoretical basis for assuming that the population with the highest level of genetic diversity in molecular markers will be the best genetic source for restoration (Turelli & Ginzburg 1983; Cheverud et al. 1994; Savolainen & Hedrick 1995; Britten 1996; Lynch 1996; Storfer 1996; David 1998; Parker et al. 1999; McKay et al. 2001). For populations with small effective sizes, rare alleles may be deleterious, so a strategy that simply seeks to maximize allelic diversity may even be counterproductive. Overall, these studies suggest that the use of neutral markers is not an effective method for defining scales of local adaptation. This is because among-population differentiation in ecological traits will be more influenced by selection, whereas neutral markers will reflect historical gene flow and genetic drift (reviewed in McKay & Latta 2002).

Summary

A major genetic concern of restoration practitioners is, "How local is local?" Practitioners have a tendency to assume that local adaptation is almost ubiquitous at most spatial scales. Ecological genetics studies generally support the idea that local adaptation, especially across larger geographic or climatic gradients, is the norm. There are also many scientific studies indicating that local adaptation can occur (to varying degrees) at small spatial scales. However, there is also evidence that gene flow, seed banks and, perhaps most importantly, temporal fluctuations in selection can reduce the probability of highly localized ecotypes.

An important issue for restoration strategies is whether genetic variation within populations is more or less of a concern than local adaptation. Genetic diversity within populations represents the raw material for future adaptation (Davis & Shaw 2001) and reduces the potential danger of inbreeding depression. This "mix or match" dilemma was reviewed by Lesica and Allendorf (1999). Unfortunately, there is no obvious answer from scientific theory and empirical studies. For example, theoreticians recognize that the rate of evolutionary change in response to selection depends on heritable genetic variation within populations and so genetic variation within populations is critical in adaptation. However, there is also a large body of theory that focuses on negative aspects of genetic variation when many genotypes are far from the selective optimum (i.e., the "genetic load" is large).

Concern about the potential for "genetic pollution" to negatively impact restoration success by introducing highly maladapted genotypes into a restoration site has been raised in the literature (Storfer 1999; Hufford & Mazer 2003; Rice & Emery 2003). This phenomenon represents a very high gene flow of genotypes that are highly

maladapted to the local conditions (i.e., high genetic load). This combination of extremely high gene flow and highly maladapted genotypes is analogous to the dynamics within hybrid zones between species (Barton & Hewitt 1989; Coyne & Orr 2004).

As we pointed out earlier, there are really two issues involved in genetic pollution concerns. The first is that the introduction of nonlocal genotypes will create a large genetic load that causes the restoration to fail. The second concern is that the introduction of nonlocal genotypes will, over the short term, swamp out locally adapted genotypes in the resident population. Thus, the "genetic memory" of past, perhaps infrequent, selective events will be lost. This suggests that a practical strategy might be one of "coarse selective tuning" where restored populations are composed of mixtures of genotypes from climatically local populations. Ideally, without large epistatic effects, this strategy would prevent the formation of large genetic loads because highly maladapted genotypes would not be included in the mix, but there would still be sufficient genetic variation within the restored population for further adaptive "fine-tuning."

Recommendations

Our review of the literature indicates that we have a long way to go before we understand "How local is local?" for most plant species. However, there are some recommendations that can be gleaned from ecological genetics that may provide useful guidelines for genetic restoration. The ideas below are intuitive and represent commonsense approaches that are already practiced by some restorationists.

- (1) *Collect locally if at all possible:* The farther apart the restoration site is from the site where the source plant material was collected, the greater the chance the genetic "integrity" of the restored population will be compromised. This results, in part, from maladaptation to the site because usually sites farther apart are more likely to be environmentally different than sites close together. In addition to differences in selective regimes among widely separated sites, rates of dispersal/gene flow between these sites are likely to be less than those between sites close together. As a result of this reduced gene flow, two things may happen. First, the capacity of gene flow to swamp selection and prevent the formation of locally adapted populations is reduced. Second, the potential for genetic drift to form genetically distinct populations is greatly increased. However, because the intensity of selection gradients and the rate of gene flow can vary widely, it is impossible (and counterproductive) to prescribe a standard geographic distance as a scale for local adaptation (e.g., a "50-km rule").
- (2) *Match climatic and environmental conditions between collection and restoration sites:* Although a bit more difficult to obtain than geographic distance, a much more useful gauge of the potential scale of adaptation

is the environmental “distance” between the restoration site and the source collection site. Elevation and composite indexes of easily obtained climatic variables for a site are much more likely to describe selective differences between sites than geographic distance. Information on climatic zones can often be obtained from sources in the popular press. For tree species, much effort has gone into delineating these so-called seed zones (Buck et al. 1970; Randall 1996; Randall & Berrang 2002). For other species, garden climate zones such as those found in the *Western Garden Book* (Brenzel 2001) are probably excellent indicators of climatically distinct selection regimes and could be used as guides for developing seed collection zones. Within a single climatic zone, there may also be strong but localized selection gradients in the edaphic environment, such as drought, serpentine soil. Ecotypic divergence and even speciation are commonly observed across such gradients in California (Stebbins 1952; Kruckeberg 1986). Although we generally lack an understanding of which particular traits confer adaptation to particular environments, collection efforts aimed at simply sampling genetic variation across major ecological gradients within the species’ range may help to preserve the adaptive potential of species (McKay & Latta 2002). This approach can be substantially improved by sampling within the framework of historical gene flow, where clines are likely to contain a great deal of allelic variation (McKay & Latta 2002). This “gene conservation” approach may be more appropriate for many species of concern, where experimental ecological genetic studies are impractical.

Finally, the idea of using more widely available “coarsely adapted” genetic mixtures that contain genetic variation necessary for further adaptive fine-tuning is a practical approach that may increase the feasibility and economic viability of genetic restoration (Lesica & Allendorf 1999; Rice & Emery 2003).

- (3) *Determine the breeding systems of restoration species:* Measuring gene flow has been and will continue to be difficult, but molecular marker technology is becoming more and more powerful and accessible for estimating the measuring patterns and rates of this somewhat underappreciated evolutionary force. At a within-population level, the breeding system of a plant species can be an important determinant of the rates of gene flow expected for a species. In general, inbreeding species are thought to experience lower rates of gene flow than outcrossing species. In species where molecular data are not available, traditional measurements of floral morphology and simple experiments can provide some estimates of breeding system. Flower showiness, observations on pollinator visitations, and pollen to ovule ratios (Cruden 1977) can give rough estimates as to the degree of outcrossing. Simple flower bagging experiments can be used to
- test whether a species is self-compatible and thus more likely to have a higher level of inbreeding. For highly selfing species, inbreeding depression and gene flow with local populations are less likely but instead populations are more likely to be differentiated and exhibit little within-population variation for future adaptation. In contrast, for highly outcrossing species that are regularly receiving gene flow, local adaptation and coadapted gene complexes are less likely but instead inbreeding depression and allele effects become concerns in restoration.
- (4) *Determine the ploidy systems of restoration species:* Differences in ploidy levels within species are another concern for some of the species used in restoration. Although the results of mixing ploidy levels are varied and beyond the scope of this article and have been reviewed elsewhere (Ramsey & Schemske 1998; Petit et al. 1999; Husband & Sabara 2004), care should be taken to avoid introducing genotypes with ploidy levels different from those of the native populations. Plant keys, such as the Jepson Manual (Hickman 1993 and <http://ucjeps.berkeley.edu/jepman.html>), provide chromosome counts for many species. This can be supplemented by searching the cytogenetics literature to look for evidence of ploidy variation in the species of concern. If ploidy races are known to exist in a species, these races can often be categorized by morphological differences in pollen, guard cell, and even flower size (Johanson & von Bothmer 1994). In addition, flow cytometry can be a relatively easy way to look for ploidy differences and can often be outsourced to universities and private companies.
- (5) *Minimize “unconscious” selection during seed increases:* In many restoration projects, because of logistic constraints or small resident population sizes at the site, it is impossible to obtain enough seed for the project. As a result, it is a common practice to collect what seed is available at the site and then provide this seed to a local grower for a “seed increase.” Typically, these seed increase operations are conducted under agronomic conditions that, although artificial and unnatural for native plants, are assumed to not alter the genetic composition between the initial seed collection and the seed produced from the field plantings. Unfortunately, there is little evidence to support this assumption of no selection, and in fact, recent research suggests that harvesting patterns and local pathogens can cause large genetic shifts within a single generation in these seed-increase operations (Rice & Knapp, unpublished data). To reduce the potential for unconscious selection to occur during seed increase, it is important to harvest from the entire planted population and it is advisable to harvest from the planted populations as often as possible. It is very important to conduct the seed-increase operation as close as possible (in an environmental distance sense)

to the source of the initial seed collection. This will increase the probability that the population undergoing seed increase will be adapted to the local climate and pathogens.

In closing, it might be instructive to point out that the science of ecological genetics and the practice of restoration would benefit greatly by increased collaboration between practitioners and researchers. It is not that difficult to make a restoration project into an experiment in ecological genetics. It primarily involves documentation of (1) where plant material comes from; (2) where it is planted in the site; and (3) how it performs (survival, growth, reproduction, etc.). In a very real sense, the thousands of restoration projects that are currently being conducted across the world could be transformed, with relatively little modification, into thousands of experiments in local adaptation.

Acknowledgments

We thank John N. Thompson and two anonymous reviewers for helpful comments on this manuscript. This study was funded by a planning grant from the Packard Foundation.

LITERATURE CITED

- Antonovics, J., and A. D. Bradshaw. 1970. Evolution in closely adjacent plant populations. VII. Clinal patterns at a mine boundary. *Heredity* **25**:349–362.
- Arntz, A. M., and L. F. Delph. 2001. Pattern and process: evidence for the evolution of photosynthetic traits in natural populations. *Oecologia* **127**:455–467.
- Avice, J. C. 1998. The history and purview of phylogeography: a personal reflection. *Molecular Ecology* **7**:371–379.
- Barton, N. H., and G. M. Hewitt. 1989. Adaptation, speciation and hybrid zones. *Nature* **341**:497–503.
- Beerli, P., and J. Felsenstein. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in *n* subpopulations by using a coalescent approach. *Proceedings of the National Academy of Sciences U.S.A.* **98**:4563–4568.
- Bradshaw, A. D. 1984. Ecological significance of genetic variation between populations. Pages 213–228 in R. J. S. Dirzo, editor. *Perspectives on plants population ecology*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Brenzel, K. N. 2001. *Western garden book*. 7th edition. Sunset Publishing, Menlo Park, California.
- Britten, H. 1996. Meta-analyses of the association between multilocus heterozygosity and fitness. *Evolution* **50**:2158–2164.
- Brown, J. M., J. H. Leebens-Mack, J. N. Thompson, O. Pellmyr, and R. G. Harrison. 1997. Phylogeography and host association in a pollinating seed parasite *Greya politella* (Lepidoptera: Prodoxidae). *Molecular Ecology* **6**:215–224.
- Buck, J. M., R. S. Adams, J. Cone, M. T. Conkle, W. J. Libby, C. J. Eden, and M. J. Knight. 1970. *California tree seed zones*. U.S. Forest Service, San Francisco, California.
- Byers, D. L., and D. M. Waller. 1999. Do plant populations purge their genetic load? Effects of population size and mating history on inbreeding depression. *Annual Review of Ecology and Systematics* **30**:479–513.
- California Department of Parks and Recreation. 1994. *Statement of Policy II.4 Preservation of vegetative entities*. Sacramento, CA.
- Calsbeek, R., J. N. Thompson, and J. E. Richardson. 2003. Patterns of molecular evolution and diversification in a biodiversity hotspot: the California Floristic Province. *Molecular Ecology* **12**:1021–1029.
- Cheverud, J., E. Routman, and C. Jaquish. 1994. Quantitative and molecular genetic variation in captive cotton-top tamarins (*Saguinus oedipus*). *Conservation Biology* **8**:95–105.
- Clausen, J., and W. M. Hiesey. 1958. Experimental studies on the nature of species. IV. Genetic structure of ecological races. Carnegie Institution of Washington Publication 615, Washington, D.C.
- Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Crespi, B. J. 2000. The evolution of maladaptation. *Heredity* **84**:623–629.
- Cruden, R. W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in plants. *Evolution* **31**:32–46.
- David, P. 1998. Heterozygosity-fitness correlations: new perspectives on old problems. *Heredity* **80**:531–537.
- Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to quaternary climate change. *Science* **292**:673–679.
- Devlin, B., and N. C. Ellstrand. 1990. The development and application of a refined method for estimating gene flow from angiosperm paternity analysis. *Evolution* **44**:248–259.
- Dobson, A. P., A. D. Bradshaw, and A. J. M. Baker. 1997. Hopes for the future: restoration ecology and conservation biology. *Science* **277**:515–522.
- Edmunds, S. 1999. Heterosis and outbreeding depression in interpopulation crosses spanning a wide range of divergence. *Evolution* **53**:1757–1768.
- Edmunds, S., and C. C. Timmerman. 2003. Modeling factors affecting the severity of outbreeding depression. *Conservation Biology* **17**:883–892.
- Ellstrand, N. C., B. Devlin, and D. L. Marshall. 1989. Gene flow by pollen into small populations: data from experimental and natural stands of wild radish. *Proceedings of the National Academy of Sciences U.S.A.* **86**:9044–9047.
- Endler, J. A. 1986. *Natural selection in the wild*. Monographs in Population Biology 21. Princeton University Press, Princeton, New Jersey.
- Eriksson, G., S. Andersson, V. Eiche, J. Ifver, and A. Persson. 1980. Severity index and transfer effects on survival and volume production of *Pinus sylvestris* in northern Sweden. *Studia Forestalia Suecica* **156**:1–32.
- Fenster, C. B., and L. F. Galloway. 2000. Population differentiation in an annual legume: genetic architecture. *Evolution* **54**:1157–1172.
- Fenster, C. B., L. F. Galloway, and L. Chao. 1997. Epistasis and its consequences for the evolution of natural populations. *Trends in Ecology and Evolution* **12**:282–286.
- Geber, M. A., and L. R. Griffen. 2003. Inheritance and natural selection on functional traits. *International Journal of Plant Science* **164**:S21–S42.
- Gullberg, U., R. Yazdani, D. Rudin, and N. Ryman. 1985. Allozyme variation in Scots pine (*Pinus sylvestris* L.) in Sweden. *Silvae Genetica* **34**:193–201.
- Hamrick, J. L., and M. J. W. Godt. 1996. Conservation genetics of endemic plant species. Pages 287–291 in J. C. Avice and J. L. Hamrick, editors. *Conservation genetics: case histories from nature*. Chapman and Hall, New York.
- Hedrick, P. W. 1999. Perspective: highly variable loci and their interpretation in evolution and conservation. *Evolution* **53**:313–318.
- Hedrick, P. W., and S. T. Kalinowski. 2000. Inbreeding depression in conservation biology. *Annual Review of Ecology and Systematics* **30**:139–162.
- Hickman, J. C., editor. 1993. *The Jepson Manual*. University of California Press, Berkeley.
- Hobbs, R. J., and D. A. Norton. 1996. Towards a conceptual framework for restoration ecology. *Restoration Ecology* **4**:93–110.

- Hufford, K. M., and S. J. Mazer. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecology and Evolution* **18**:147–155.
- Hurme, P. 1999. Genetic basis of adaptation: bud-set date and frost hardness variation in Scots pine. Acta Univ. Oul. A339. University Oulu Press, Oulu, Finland.
- Husband, B. C., and H. A. Sabara. 2004. Reproductive isolation between autotetraploids and their diploid progenitors in fireweed, *Chamerion angustifolium* (Onagraceae). *New Phytologist* **161**:703–713.
- Johansen, B., and R. von Bothmer. 1994. Pollen size in *Hordeum* L. correlation between size, ploidy level, and breeding system. *Sexual Plant Reproduction* **7**:259–263.
- Jones, T. A. 2003. The restoration gene pool concept: beyond the native versus non-native debate. *Restoration Ecology* **7**:42–50.
- Keller, M., J. Kollmann, and P. J. Edwards. 2000. Genetic introgression from distant provenances reduces fitness in local weed populations. *Journal of Applied Ecology* **37**:647–659.
- King, R. B., and R. Lawson. 1995. Color-pattern variation in Lake Erie water snakes: the role of gene flow. *Evolution* **49**:885–896.
- Knapp, E. E., and K. J. Rice. 1994. Starting from seed: genetic issues in using native grasses for restoration. *Restoration and Management Notes* **12**:40–45.
- Knapp, E. E., and K. J. Rice. 1998. Comparisons of isozymes and quantitative traits for evaluating patterns of genetic variation in purple needlegrass (*Nassella pulchra*). *Conservation Biology* **12**:1031–1041.
- Kruckeberg, A. R. 1986. An essay: the stimulus of unusual geologies for plant speciation. *Systematic Botany* **11**:455–463.
- Lande, R., and S. Shannon. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution* **50**:434–437.
- Lenormand, T. 2002. Gene flow and the limits to natural selection. *Trends in Ecology and Evolution* **17**:183–189.
- Lesica, P., and F. W. Allendorf. 1999. Ecological genetics and the restoration of plant communities: mix or match? *Restoration Ecology* **7**:42–50.
- Linhart, Y. B., and M. C. Grant. 1996. Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics* **27**:237–277.
- Lynch, M. 1996. A quantitative-genetic perspective on conservation issues. Pages 471–499 in J. C. Avise and J. L. Hamrick, editors. *Conservation genetics: case histories from nature*. Chapman and Hall, New York.
- Mazer, S. J., and G. LeBuhn. 1999. Genetic variation in life-history traits: heritability estimates within and genetic differentiation among populations. Pages 85–170 in T. O. Vuorisalo and P. K. Mutikainen, editors. *Life history evolution in plants*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- McKay, J. K., J. G. Bishop, J.-Z. Lin, A. Sala, J. H. Richards, and T. Mitchell-Olds. 2001. Local adaptation across a climatic gradient despite small effective population size in the rare Sapphire Rockcress. *Proceedings of the Royal Society London B* **268**:1715–1721.
- McKay, J. K., and R. G. Latta. 2002. Adaptive population divergence: markers, QTL and traits. *Trends in Ecology and Evolution* **17**:285–291.
- Mikola, J. 1982. Bud-set phenology as an indicator of climatic adaptation of Scots pine in Finland. *Silva Fennica* **16**:178–184.
- Montalvo, A. M., and N. C. Ellstrand. 2000. Transplantation of the shrub *Lotus scoparius*: testing the home-site advantage hypothesis. *Conservation Biology* **14**:1034–1045.
- Montalvo, A. M., S. L. Williams, K. J. Rice, S. L. Buchmann, C. Cory, S. N. Handel, G. P. Nabhan, R. Primack, and R. H. Robichaux. 1997. Restoration biology: a population biology perspective. *Restoration Ecology* **5**:277–290.
- National Park Service. 1993. Western Region Directive #WR-094 and guidelines for revegetation in disturbed areas. San Francisco, CA.
- Neigel, J. E. 1997. A comparison of alternative strategies for estimating gene flow from genetic markers. *Annual Review of Ecology and Systematics* **28**:105–128.
- Newman, D., and D. Pilson. 1997. Increased probability of extinction due to decreased genetic effective population size: experimental populations of *Clarkia pulchella*. *Evolution* **51**:354–362.
- Parker, K. M., R. J. Sheffer, and P. W. Hedrick. 1999. Molecular variation and evolutionarily significant units in the endangered gila topminnow. *Conservation Biology* **13**:108–116.
- Petit, C., F. Bretagnolle, and F. Felber. 1999. Evolutionary consequences of diploid-polyploid hybrid zones in wild species. *Trends in Ecology and Evolution* **14**:306–311.
- Petit, C., H. Freville, A. Mignot, B. Colas, M. Riba, E. Imbert, S. Hurtrez-Bousses, M. Virevaire, and I. Olivieri. 2001. Gene flow and local adaptation in two endemic plant species. *Biological Conservation* **100**:21–34.
- Ralls, K., and J. Ballou. 1983. Extinction lessons from zoos. Pages 164–184 in C. M. Shonewald-Cox, S. M. Chambers, B. MacBryde, and L. Thomas, editors. *Genetics and Conservation*. Benjamin/Cummings, Menlo Park, California.
- Ramsey, J., and D. W. Schemske. 1998. Pathways, mechanisms and rates of polyploidy formation in flowering plants. *Annual Review of Ecology and Systematics* **29**:467–4501.
- Randall, W. K. 1996. Forest tree seed zones for western Oregon. Oregon Department of Forestry, Salem, Oregon.
- Randall, W. K., and P. Berrang. 2002. Washington tree seed transfer zones. Washington Department of Natural Resources, Olympia, Washington, D.C.
- Rannala, B., and J. L. Mountain. 1997. Detecting immigration using multi-locus genotypes. *Proceedings of the National Academy of Sciences U.S.A.* **94**:9197–9201.
- Raven, P. H. 2002. Science, sustainability, and the human prospect. *Science* **297**:954–958.
- Rice, K. J., and N. C. Emery. 2003. Managing microevolution: restoration in the face of global change. *Frontiers in Ecology and the Environment* **9**:469–478.
- Riddle, B. R., D. J. Hafner, L. F. Alexander, and J. R. Jaeger. 2000. Cryptic vicariance in the historical assembly of a Baja California Peninsular Desert biota. *Proceedings of the National Academy of Sciences U.S.A.* **97**:14438–14443.
- Rodriguez-Robles, J., D. F. DeNardo, and R. Staub. 1999. Phylogeography of the California mountain kingsnake, *Lampropeltis zonata* (Colubridae). *Molecular Ecology* **8**:1923–1934.
- Saccheri, I., M. Kuussaari, M. Kankare, P. Vikman, W. Fortelius, and I. Hanski. 1998. Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**:491–494.
- Savolainen, O., and P. Hedrick. 1995. Heterozygosity and fitness: no association in Scots pine. *Genetics* **140**:755–766.
- Schneider, C. J., T. B. Smith, B. Larison, and C. Moritz. 1999. A test of alternative models of diversification in tropical rainforests: ecological gradients vs. rainforest refugia. *Proceedings of the National Academy of Sciences U.S.A.* **96**:13869–13873.
- Slatkin, M. 1985. Gene flow in natural populations. *Annual Review of Ecology and Systematics* **16**:393–430.
- Soltis, D. E., P. S. Soltis, T. G. Collier, and M. L. Edgerton. 1991. Chloroplast DNA variation within and among genera of the *Heuchera* group (Saxifragaceae): evidence for chloroplast transfer and paralogy. *American Journal of Botany* **78**:1091–1111.
- Stebbins, G. L. 1950. Variation and evolution in plants. Columbia University Press, New York.
- Stebbins, G. L. 1952. Aridity as a stimulus to plant evolution. *American Naturalist* **86**:33–44.
- Storfer, A. 1996. Quantitative genetics: a promising approach for the assessment of genetic variation in endangered species. *Trends in Ecology and Evolution* **11**:343–348.

- Storfer, A. 1999. Gene flow and endangered species translocations: a topic revisited. *Biological Conservation* **87**:173–180.
- Templeton, A. R. 1986. Coadaptation and outbreeding depression. Pages 105–116 in M. Soule, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Turelli, M., and L. R. Ginzburg. 1983. Should individual fitness increase with heterozygosity? *Genetics* **104**:191–209.
- USDA Forest Service. 1994. Use of native vegetative materials on National Forests. US Forest Service Pacific Southwest Region. San Francisco, CA.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**: 494–499.
- Vrijenhoek, R. C. 1994. Genetic diversity and fitness in small populations. Pages 37–53 in V. Loeschke, J. Tomiuk, and S. K. Jain, editors. *Conservation genetics*. Birkhauser, Basel, Switzerland.
- Waldman, P., and S. Andersson. 1998. Comparison of quantitative genetic variation and allozyme diversity within and between populations of *Scabiosa canescens* and *S columbaria*. *Heredity* **81**:79–86.
- Whitlock, M. C., P. C. Phillips, F. B.-G. Moore, and S. J. Tonsor. 1995. Multiple fitness peaks and epistasis. *Annual Review of Ecology and Systematics* **26**:601–629.
- Williams, D. G., R. N. Mack, and R. A. Black. 1995. Ecophysiology of introduced *Pennisetum setaceum* on Hawaii: the role of phenotypic plasticity. *Ecology* **76**:1569–1580.
- Wright, S. 1951. The genetical structure of populations. *Annals of Eugenics* **15**:323–354.