



GENETIC EROSION
GENETIC EROSION
GENETIC EROSION

No longer just an agricultural issue

Deborah L Rogers |

ABSTRACT

Genetic considerations pertaining to planting projects usually emphasize locally adapted source material. However, the amount of genetic diversity in the plant materials is important as well. Genetic erosion is the loss of genetic diversity—often magnified or accelerated by human activities. In native plant populations, genetic erosion results from habitat loss and fragmentation, but it also can result from a narrow genetic base in the original collections or by practices that reduce genetic diversity. Although species-specific guidelines are not available, managers can minimize the risk of genetic erosion by being familiar with the biology of the affected species (including breeding system, mode of reproduction, and pattern of genetic diversity). Narrowly based genetic collections should be avoided, providers of plant materials for revegetation projects should offer information on their collection methods, and nursery managers should endeavor to minimize diversity losses at all stages of nursery culture.

KEY WORDS

genetic diversity, reforestation, restoration, revegetation, source materials, natural areas, conservation

NOMENCLATURE

USDA NRCS (2004)

The loss of biological diversity has been measured traditionally by frequency of species extinctions. However, not only does genetic diversity underlie species diversity, being concomitantly lost with species extinctions, but also genetic diversity has been recognized in its own right as one of three levels of biological diversity recommended for conservation by the World Conservation Union (IUCN) (McNeely and others 1990). There is urgency associated with the current rate of species loss. In fact, the term “sixth extinction” has been coined to convey the serious scale of the problem, and to equate it in magnitude to the previous 5 mass extinctions that are known from the geological record. Species currently are being lost at a rate that far exceeds the origin of new species, and, unlike the previous mass extinctions, this is primarily the result of human activities (Frankham and others 2004). Similarly, the seriousness of recent and ongoing losses of genetic diversity—in particular, locally adapted gene complexes—has been recognized with the term “secret extinctions” (Ledig 1991). As suggested by this term, however, it is difficult to sense the urgency of taking measures to mitigate genetic losses, as such losses are often cryptic.

In many instances, the genetic resource may be severely degraded without an immediate loss in census number. For example, there are few tree species in Canada or the US that are so diminished in presence that they have been federally listed as “endangered” or “threatened.” There is serious concern about genetic erosion in forest tree species, however, as expressed at a 1995 international workshop on the status of temperate North American forest genetic resources (Rogers and Ledig 1996). In general, genetic erosion is loss of genetic diversity within a species. It can represent the loss of entire populations genetically differentiated from others, the loss or change in frequency of specific alleles (that is, different forms of a gene) within populations or over the species as a whole, or the loss of allele combinations.

The first well-publicized use of the term “genetic erosion” was in reference to the loss of the primitive races and varieties of cultivated plants as they were gradually replaced in agriculture with newer and more productive crop varieties. Genetic erosion was a topic of discussion in the international agricultural community in the mid-1900s and received prominence with the twin catastrophic outbreaks in 1970 of southern corn-leaf blight in the US and of coffee rust in Brazil. These events illuminated the consequences of genetic erosion, stimulated international discussions, and provided a major focus at the United Nations Conference on Human Environment in Stockholm in 1972. The lesson was that “genetic uniformity is the basis of vulnerability to epidemics and, more generally, to biotic and abiotic stresses” (Scarascia-Mugnazza and Perrino 2002). Concerns about genetic erosion resulted in the initiation of a global network of gene banks to

Figure 1. Management practices have affected genetic diversity in Mead's milkweed (*Asclepias meadii*), a threatened species. Photo by Jessie M Harris

conserve agriculturally important genetic resources. In the agricultural sphere, there is ongoing concern and attention at all levels, including the Food and Agriculture Organization of the United Nations. “Genetic erosion, or the steady loss of genetic diversity in on-farm agriculture, is perhaps the key ‘pressure’ on the sustainable management of domesticated plant genetic resources” (Brown and Brubaker 2002).

The term “genetic erosion” is now more generally applied to loss of genetic diversity, including the loss of diversity in native plant species. But just as the term “climate change” is more commonly understood to represent an *accelerated* change in climate patterns, which reflects human influences rather than simply natural cycles, “genetic erosion” is more often used in the context of human-driven or -related losses in genetic diversity that are faster in rate or larger in scale than would be expected under natural processes alone. Here, we will focus on the anthropogenically related loss of genetic diversity in native plant populations within a restoration context.

ARTICLE CONTEXT AND OBJECTIVES

There is a diverse array of objectives associated with natural areas management including maintaining diversity and ecosystem functioning in natural areas, revegetating after fires or harvests, rehabilitating mine sites or other degraded areas, improving habitat for wildlife, restoring threatened or degraded populations, and providing access and infrastructure for recreation and other activities. The context for this article is natural areas conservation and restoration. If one’s objectives differ from maintaining or recreating natural types and levels of genetic diversity in native plant populations, then the discussion and recommendations provided here are not entirely relevant. Furthermore, if the objectives include rehabilitation of degraded sites, then the environment may no longer be completely natural, and the relationship with natural patterns of genetic diversity will have been altered. In those cases, what is “genetically appropriate” for the sites, at least in the short term, is less clear. Indeed, even the use of non-native species may be appropriate, at least as a nurse crop to help restore soil stability or quality.

Within the topic of genetic erosion in natural plant communities, one could address maintaining genetic diversity within the populations, re-introducing appropriate levels of genetic diversity in projects involving planting or seeding of native plant species, or monitoring plant populations to detect decreases in genetic diversity—each a broad topic in its own right. Here, we focus on explaining the importance of genetic diversity and the problems associated with genetic erosion in native plant populations and on suggesting some means to maintain genetic diversity within the context of restoration efforts.

Throughout this brief review of genetic erosion and its consequences, it is important to remember the dynamic nature of

genetic diversity. Genetic diversity is always changing—over space and time. Spatially, it sometimes reflects patterns in the environment (such as elevation, soil moisture gradients, or climatic patterns), suggesting adaptation of plants to their conditions. But whether the genetic diversity is adaptive or not, it is constantly in motion over the landscape, moving through pollen and seeds and other propagules and being lost through mortality—random and selective. The general arena in which much of reproductive activity and genetic movement occurs is called the “population”—which, for many plant species, is a “virtual entity” and difficult to identify in the field. Genetic diversity also changes over time as a result of random factors. Whether a particular seed—with its inherent genetic diversity—germinates and survives depends, to some extent, not only on its suitability for its environment but also the fortuity of being in the right place at the right time. And whether it passes on its genetic heritage to the next generation depends not only on its reproductive output but also on chance events that influence its mating and survival of its progeny. With each generation, genes are reshuffled and recombined, to greater or lesser extents depending on the breeding system of the species. The longevity and life form of the species (for example, annual, perennial, long-lived woody species), the ploidy level (for example, diploid or tetraploid), the mode of reproduction (for example, asexual, sexual, or some combination; dioecious or monoecious), and the breeding system (for example, outbreeding, inbreeding, or various combinations) all weigh heavily in determining the movement of genes and the natural amounts of genetic diversity. It is against this dynamic landscape of genetic change, and within the important context of individual species’ biology, that we consider the issue of genetic erosion.

HOW CAN GENETIC DIVERSITY BE LOST AND WHY IS IT A PROBLEM?

Genetic diversity is lost in much the same manner as species become extinct. Habitat loss and habitat fragmentation can reduce the size of plant populations (Figure 2). If the habitat and not just the plants are removed (such as in land conversion), and there is no subsequent regeneration from seedbanks or previously collected seeds, then loss of genetic diversity can occur immediately, assuming that there is some diversity in the removed plants that is not contained elsewhere. The link between habitat fragmentation and loss of genetic diversity has been well established, both theoretically and empirically, particularly in forest tree species (for example, Templeton and others 1990; Ledig 1992).

But even if genetic diversity is not lost immediately, it is often reduced gradually in the resulting smaller populations (for example, Lacy 1987). This loss is presumably the result of genetic drift, a random process, which can result in inbreeding. When plants reproduce (for simplicity, let us consider a sexually reproducing



Photos by Adina Merenlander

Figure 2. Genetic erosion often results when native vegetation is removed or fragmented by development, as shown here in Lake County, California. *Left:* Vineyard development. *Right:* Native vegetation fragmentation on Mt Konockti.

diploid species), the seeds that result do not necessarily contain all of the genetic diversity from the parental generation because they represent only a sample of that diversity. The genes from some potential parent plants may not be represented in the seeds because of random factors such as phenological differences, distance from other plants, weather patterns that influence pollen dispersal, random mortality of plants, random abortion of embryos, and others. In particular, alleles that are rare in a plant population may not persist into the next generation so that the next generation represents a “sample” of the genetic diversity in the parental population. Therefore, rare alleles, present in only a few individuals, may by chance, not be passed to the next generation.

The relationship between population size and loss of genetic diversity has been well established and quantified, with Wright’s (1931) work being seminal. Generally, smaller populations tend to lose genetic variation by genetic drift much more quickly than larger populations. And the shorter the generation length (that is, time to reproductive maturity), the more rapid the diversity loss in absolute time (for example, Frankham and others 2004). There is considerable theory and empirical research on the relationship between population size and genetic diversity. A review of that literature is beyond the scope of this paper but see, for example, Falk and Holsinger (1991) and Ellstrand and Elam (1993). This relationship has also been examined at the species level, and various reviews have found restricted or rare species generally less genetically diverse than more common plant species (for example, Karron 1987, 1991; Hamrick and Godt 1990; Gitzendanner and Soltis 2000; Cole 2003). It is important to note, however, that there may be different processes underlying the relationship between genetic diversity and size in populations versus species.

Genetic drift has a second consequence that negatively impacts genetic diversity. Simply put, smaller populations are more likely to have higher rates of inbreeding. Again, considering a sexually reproducing diploid species that is mainly an

outbreeder, mating among relatives (inbreeding) is more likely in smaller populations. And the process is cumulative, so that over time matings between unrelated individuals become impossible (for example, Frankham and others 2004). Inbreeding also occurs in larger populations, but it occurs less frequently and its impacts take longer to manifest. An increase in the level of inbreeding (in plants that are mainly outbreeders in nature) has profound consequences for the population. This increases the level of homozygosity in the population (that is, in an individual [diploid] plant, there are 2 copies of the same allele rather than 2 different alleles for a given locus). In general, increased homozygosity also leads to reduced reproduction and survival (that is, lower reproductive fitness) and ultimately to increased risk of extinction. This cascade of events that results from increased inbreeding is termed “inbreeding depression.”

Plant populations that are less genetically diverse may be more susceptible to pathogens (for example, Schmid 1994) or other environmental stresses. Natural selection acts on genetic diversity; the more fit individuals survive and reproduce. Loss of genetic diversity reduces the ability of the plant population to genetically respond to a changing environment over time, reduces evolutionary potential, and lowers reproductive fitness. In fact, one of the basic tenets of evolutionary biology is that the rate of evolutionary change is proportional to the amount of genetic variability in a species (Futuyma 1979).

Some loss of genetic diversity is natural. Genetic diversity is a dynamic entity, changing over time. Natural selection removes some genetic diversity (at least at the population, if not the species, level). But too rapid a loss, or losses that aren’t associated with natural processes such as natural selection, can cause problems in a conservation or restoration context.

In addition to habitat loss and fragmentation, other less obvious influences can also cause genetic erosion. For example, there

is the potential to inadvertently reduce genetic diversity through planting or reseedling activities associated with restoration, rehabilitation, or reforestation, particularly in large-scale projects. In such projects, the genetically appropriate decision is often framed as “planting local”—which is a proxy for planting or seeding with a genetic source that is locally adapted. However, using genetically appropriate planting materials is not only a matter of using the correct source but also of how the source was sampled. That is, “genetically appropriate” planting material should be appropriate in both the nature and amount of genetic diversity relative to the scale of the project. As noted by Kitzmiller (1990), the ceiling on genetic diversity is established by the seed collected. But that level of genetic diversity can be seriously eroded by subsequent events.

Two major examples of how genetic diversity can be reduced in a planting project are outlined below.

Inadequate sampling of genetic diversity in the seed (bulb, ramet, or other propagule) collection: This can result from making genetic collections from too few parent plants or from plants that are very close to one another, therefore more likely to be related. For example, a collection consisting of seeds from 10 closely related parent plants would likely have less genetic diversity than one composed of 10 unrelated or more distantly related plants. This applies to plant populations that are strictly or primarily outbreeding. If a species reproduces asexually, reductions in genetic diversity in the genetic collection can occur through inadvertently taking multiple samples (cuttings or other plant part) from the same individual. Depending upon the spatial genetic structure of the plant species, reductions in genetic diversity can also occur by sampling too few populations (relative to what is appropriate for the restoration site). Some references on genetic sampling guidelines include CPC (1991), Guarino and others (1995), and Guerrant (1992, 1996).

Narrowing of the genetic base through nursery practices: Some loss of seed or seedlings in the window between original collections and planting or seeding on the project site is not necessarily a problem. If the losses are random (that is, not linked to particular genes or gene combinations), then they will not change the original genetic composition of the sample significantly. High levels of mortality, however, can cause genetic erosion. And any nursery practices that favor some seeds or seedlings over others (that is, that constitute a “selection” of some individuals) can change the genetic composition of the original collection. In traditional plant improvement programs, such artificial selection is appropriate and, if successful, results in plants that are better suited to particular goals such as ornamental quality, palatability, productivity, or desirable site-specific characteristics. In restoration projects where the goals include restoration of genetic diversity, however, artificial selection may be less desirable, although it can still occur inadvertently (for example, Meyer and Monsen 1993). Nursery practices that select for uniformity in individuals (for example, in seed weight, germination time, or early height

growth) can decrease genetic diversity (Kitzmiller 1990; Elkasaby and Thomson 1996). This phenomenon is known as “genetic shift.” For example, a shift toward a more uniform germination response in garden-grown versus wild collections of blue flax (*Linum perenne* L. [Linaceae]) provided some evidence of inadvertent selection for nondormant, rapidly germinating seeds under conditions of greenhouse propagation (Meyer and Kitchen 1994). This possible reduction in genetic variability related to germination response could be problematic for restored populations if it represented a critical mechanism whereby seedbank persistence was ensured under widely different weather patterns. Improper handling or storage can shift the genetic base if the conditions are such that the more drought-tolerant or cold-tolerant individuals, for example, survive and others die. Some losses during the storage, nursery, or handling activities may simply be early elimination of plants that would die on-site in any event. However, if the selection pressures that we exert on the collections are not identical to those experienced in the natural condition, then some valuable genetic diversity may be lost. When seeds are not just grown but produced in the nursery, the layout of parental plants (if open-pollination is used) will also be important in determining the genetic composition of the seeds (for example, Reinartz 1995).

EXAMPLES OF GENETIC EROSION IN NATIVE PLANT SPECIES

For species that have lost large amounts of habitat and census number, it would be expected that considerable genetic diversity would also have been lost. This can be particularly serious for self-incompatible species (Figure 3). For example, loss of variation at loci controlling self-incompatibility in the remaining plants of an Ohio population of lakeside daisy or eastern fournerved daisy; (*Tetraneuris herbacea* Greene [Asteraceae]; formerly *Hymenoxys acaulis* (Pursh) Parker var. *glabra* (Gray) Parker) made it difficult for them to mate with one another to the extent that the population had produced no seeds for more than 15 y (Demauro 1993). This is because different self-incompatibility alleles are necessary to mate, and many of these had been lost from the population. In theory, polyploid species may be less susceptible to genetic erosion than diploid species (for example, Bever and Felber 1992; Glendinning 1989). However, an endangered tetraploid herb endemic to grasslands of southeastern Australia, *Swainsona recta* Lee (Fabaceae), suffered considerable genetic erosion despite its polyploid condition (Buza and others 2000).

Loss of genetic diversity can occur in restoration or reintroduction projects in which the propagule source includes only a small number of parent plants or a small amount of genetic diversity. This change in genetic composition of a population caused by an origin consisting of a small number of individuals has been

called the “founder effect.” Such effects often include, in addition to lower genetic diversity, an increase in genetic drift and inbreeding, as described earlier. We are aware of founder effects in nature, such as those that occur when a few individuals found new populations as species migrate, over long periods of time, in response to climate change (for example, Ledig 1987). But founder effects can occur as a result of human activities, and over a much shorter period of time. For example, in a restoration effort for eelgrass (*Zostera marina* L. [Zosteraceae]), genetic analyses revealed that the transplanted eelbeds had significantly lower genetic diversity than natural undisturbed beds (Williams and Davis 1996). Moreover, subsequent studies showed that the loss of genetic diversity in the restored populations corresponded to lower rates of seed germination and fewer reproductive shoots, suggesting negative consequences for the restored populations (Williams 2001).

Some management practices may contribute to loss of genetic diversity. The perennial herb, Mead’s milkweed (*Asclepias meadii* Torr. ex Gray [Asclepiadaceae]), is a species federally listed as threatened, occurring primarily in prairie hay meadows in Kansas and Missouri, with a few small populations in Iowa and Illinois. The species can reproduce both sexually (and is self-incompatible) and asexually (through rhizomes). Over much of its remaining habitat, annual mowing has been common practice for more than a century. Some remaining habitat has been fire-managed since the mid-1950s, fire being a natural disturbance, historically, in these tallgrass prairie ecosystems. A comparison of genetic diversity between the 2 management methods provided evidence of much lower genetic diversity in the mowed sites than in the burned sites. Mowing usually removed the milkweed pods, preventing seed dispersal and sexual reproduction, and led to increased rhizomatous growth (Tecic and others 1998). Thus, genetic diversity was quickly lowered per unit area because of fewer and larger genetically distinct individuals. Over time, genetic diversity in the mowed area would likely continue to decline, as selection removed additional clones, and no new clones (from sexual reproduction) were recruited. Thus the continuing trend would be one of fewer, larger clones and less genetic diversity.

SOURCES OF NEW GENETIC DIVERSITY

New diversity is added to plant populations through mutation—the origin of all genetic diversity—and migration of genes from other populations. New combinations of alleles are formed through recombination. Mutations add genetic diversity to populations very slowly and generally spread slowly through the population and to other populations. The rate of spread is influenced by the reproductive rate, the nature of seed and pollen dispersal, and whether the mutation is affected by selection (for example, whether or not it has adaptive value). In any event, it can take many generations to have an appreciable frequency of the mutation, and this translates into extremely



Photo by Betsy Strauch

Figure 3. Loss of genetic diversity in a population of lakeside daisy (*Tetrannebris herbacea*) left them unable to reproduce.

long time periods if the regeneration times are long. Given the potentially long times to introduce meaningful levels of new genetic diversity, any influences that increase the rate of otherwise natural losses of genetic diversity (for example, through natural selection) can cause a net loss of genetic diversity.

Mutations can have positive, neutral, or deleterious effects for individuals and populations. Beneficial mutations are those that in some way improve survival or reproductive fitness. Plant species that are largely outbreeding have some—usually low—level of deleterious alleles. The sum of the fitness-reducing effects from these deleterious mutations is called the genetic or mutation load (for example, Crow 1993). So even in natural conditions, there is some genetic diversity that is undesirable, or at least not beneficial to the species.

Although the ultimate source of genetic diversity is mutation, new genetic diversity can be introduced to a population through natural means, such as seed dispersal and pollination, or through artificial introductions, such as transplanting. The former usually occur slowly and new alleles would normally be in low frequency, at least initially. The latter can occur quickly and can dramatically change genetic composition. Whether introduced genetic diversity in plant populations is beneficial or detrimental will depend on the context. Some determining factors are the amount of genetic diversity remaining in the resident population, genetic differences between the resident and introduced plants, and breeding system (of both populations, if

different). Models have recently been developed in an attempt to predict when introducing new genetic diversity (and subsequent hybridizations) will be beneficial or detrimental. Key inputs to the models that affect the outcome include: 1) divergence between populations; 2) the genetic basis of outbreeding depression (disruption of local adaptation versus intrinsic coadaptation); 3) population parameters such as mutation rate and recombination rate; and 4) alternative management schemes (for example, 50:50 mixture versus one migrant per generation [Edmands and Timmerman 2003]).

Hybridization between populations may cause either increased fitness (hybrid vigor) or decreased fitness (outbreeding depression). Translocation between populations may therefore in some cases be a successful means of combating genetic erosion and preserving evolutionary potential (Edmands and Timmerman 2003). For example, supplementing genetic diversity in cases of high environmental variability or uncertainty (for example, Kitchen and McArthur 2001), or on altered sites, may be advantageous. In other cases, it could make the situation worse. If introduced plants are not well adapted in the long term but do survive to reproductive maturity, then the hybridization between the introduced and resident (or adjacent) plants can lower the fitness of subsequent generations (outbreeding depression) (for example, Hufford and Mazer 2003). But again, outbreeding depression is context dependent—more likely in cases where the parental populations are outcrossing and genetically distinct. Also, plants are notorious for variability in breeding systems, even within the same species. So uninformed mixing of plant populations—if the species is known to have population variability in its breeding system—could mean that plants with perhaps maladapted breeding systems could become established and disrupt locally developed, specific features of genetic recombination (Linhart 1995). Depending on the breeding system of the populations and the genetic basis of plant characteristics, it is also possible that the specific impacts will vary over time or over generations. So the negative impacts from either inbreeding or outbreeding depression might not occur in the first generation, but rather in subsequent ones. Alternatively, the negative effects might decrease over time, perhaps the result of natural selection.

IS LOSS OF GENETIC DIVERSITY EVER A GOOD THING?

Although reductions in genetic diversity are generally considered detrimental, there may be exceptions, such as reduction in the genetic load. For inbreeding plant species, these detrimental alleles are rather quickly removed from the population because they are exposed even when recessive, and the resulting individuals usually don't last long, or contribute much, if anything, to future generations. For largely outcrossing species,

the process takes longer because recessive alleles are more likely to be paired with more favorable dominant alleles and it takes longer for their exposure. The “uncloaking” and expression of these deleterious alleles is probably the explanation for much of the inbreeding depression observed when plant species experience higher-than-natural levels of inbreeding. The level of inbreeding depression depends on the nature of the deleterious mutations, the breeding system of the species, and the size of the populations (for example, Charlesworth and Charlesworth 1987; Lynch and Gabriel 1990). The efficacy of purging deleterious alleles is related to population size, the dominance level of the mutation (for example, mildly or highly recessive), and the type of purging process (that is, drift or selection, or their interaction) (Glémin 2003).

Other than the obvious example of the benefit of losing deleterious alleles, one other context in which loss of genetic diversity is not necessarily disadvantageous is that of exotic invasive plant species. When exotic plant species are introduced to a new environment, they often experience what is called a “genetic bottleneck” as the introduced plants just represent a sample—perhaps a very small sample—of the entire range of genetic diversity of the species. Although in theory the loss of genetic diversity could serve the invasion potential of plant invaders, this remains largely unconfirmed by conclusive experimental evidence. Some studies have revealed low levels of genetic diversity within populations of some invasive species including *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae) (Pellegrin and Hauber 1999), *Bromus tectorum* L. (Poaceae) (Bartlett and others 2002), and *Setaria viridis* (L.) Beauv. (Poaceae) (Wang and others 1995), although this is not a consistent feature among invasive species or populations (for example, Pappert and others 2000). A genetic study of the common reed (*Phragmites australis*) provided an example of loss of genetic diversity within native plant populations by invasion of exotic genotypes of the same species. More specifically, comparisons among historical and extant samples of native populations of common reed in the US showed that certain historical haplotypes (the genetic diversity was measured with alleles of closely linked loci in chloroplast DNA) seem to have disappeared and that one haplotype is now very widespread and invasive in the US, probably a more recent introduction to the US and possibly of Eurasian origin (Saltonstall 2002). In this case, the species is also clonal—a trait that could be beneficial to the invasive haplotype. So although the direct advantage of the narrow genetic base of the invader was not demonstrated in this study, the haplotype is highly successful and apparently outcompeting conspecific locals despite little genetic diversity. One direct and elegant example of loss of genetic diversity increasing invasive potential is the invasive Argentine ant (*Linepithema humile* Mayr [Hymenoptera: Formicidae]). A recent genetic study revealed that the Argentine ant has substantially less genetic variation in its introduced populations—even though they occur over a

wide geographic area—than in its native range, and that the loss of diversity is associated directly with a behavioral change that allows the introduced ants to have widespread ecological success (Tsutsui and others 2000).

HOW CAN GENETIC EROSION BE MANAGED?

For agricultural crops, solutions or mitigations have focused on *ex situ* conservation—seedbanks, genebanks, and others. This approach allows genetic diversity to be maintained even if it is not currently represented in agricultural practice. In addition, genetic research on some agriculturally important crops is comparing genetic diversity between modern and historic cultivars and even with the progenitor wild plant species, where possible. This information helps to illuminate current or to predict future problems of genetic erosion, allowing an appropriate management response.

For native plant species, we focus on conservation of genetic diversity *in situ*, although *ex situ* conservation methods are certainly an appropriate parallel conservation strategy, particularly for rare or endangered species or those experiencing high mortality or rapid loss of habitat. (See, for example, Brown and Briggs [1991] and Guerrant and others [2004] for information on genetically appropriate collection procedures for *ex situ* genetic collections.) However, *ex situ* conservation is not an effective or reasonable substitute for *in situ* conservation. These are complementary, rather than alternative, conservation strategies (for example, Falk 1987; Given 1987). *Ex situ* collections, for example, are only a sample of the natural range of genetic diversity in the species and are removed from the influence of natural selection and thus cannot accrue new adaptations over time. They are also vulnerable to financial constraints or downsizing, chronic losses in diversity depending on storage methods, catastrophic losses from equipment failures or fires, among other issues (for example, McGuire and Qualset 1990).

Avoiding losses of habitat or fragmentation of habitat (that can interrupt sharing of genes between populations, for example) are important management practices. But this level of stewardship is often beyond the control of natural areas managers and those other professionals associated with restoration projects. At the level of specific revegetation or restoration projects, there are some actions that can be taken to lessen the risk of genetic erosion. All of the following recommendations are provided within the context of native ecosystem (or species) conservation—which could include projects that are considered revegetation, restoration, mitigation, or other. If that is not the primary goal of a planting project, these points will be less relevant.

Review the basic biology of the restoration species (in particular, the breeding system, asexual or sexual reproduction, dioecious or monoecious, and general life

form—such as annual, perennial, or shrub). A good deal of common sense can be derived from these life-history features that can be applied to genetic collections. For example, if the species is dioecious (for example, poplar and willow), genetic collections need to consider a balance of males and females if collecting vegetative material rather than seeds (see Landis and others 2003). If collecting from conifers that have serotinous cones held on the trees for years, collecting from cones at different levels in the canopy will sample seeds from different cone crops, and probably reflect more genetic diversity than collecting from one cone crop only. If the plant species is known to reproduce asexually, be particularly careful not to collect seeds or vegetative propagules from just one or a few clones.

When purchasing plants for conservation-related projects, check with the nursery as to source, collection methods, and conditions for growing out the plants. Even if appropriate (for your project) genetic sources or genetic data are unavailable, it is important to fully portray your needs and expectations to those who provide revegetation materials. As noted by Buis (2000), “They may not know, but if customers keep asking, eventually the nurseries will start answering.” Create a need; express an expectation.

Seed (or other propagule) collection methods should consider not just the locale of the collections but the number of parent plants in the collection and their distance from one another. For outbreeding plant populations, if there is no evidence to the contrary, assume that plants close to one another may be more genetically similar than those farther apart. As such, collecting from many adjacent plants would sample less genetic diversity than spacing the collections more widely (for example, Millar and Libby 1989).

If using cultivars of native species, avoid excessive use of one or a few cultivars unless there is reason to believe they contain appropriate levels of genetic diversity for the project site.

Nursery activities should aim to maximize the proportion of seeds that become healthy plantable seedlings (Kitzmilller 1990). Good nursery management, based on awareness of possible genetic variation in seed characteristics, germination requirements, and growth patterns, can take measures to avoid inadvertent selection and minimize the impact on the genetic diversity of the original collection (Campbell and Sorensen 1984; Meyer and Monsen 1993).

General common-sense measures such as these can dramatically decrease the risk or severity of genetic erosion in native-plant populations. Such improvements in the conservation of the genetic diversity of plant populations are not conditional on the development of more quantitative or specific guidelines.

ACKNOWLEDGMENTS

I greatly appreciate the helpful comments provided on an earlier draft by Patrick E McGuire and 3 anonymous reviewers. I thank Joseph DiTomaso, Ruth Hufbauer, John Gaskin, and Marie Jasieniuk for their guidance on the literature of genetic aspects of invasiveness in plants.

REFERENCES

- Bartlett E, Novak SJ, Mack RN. 2002. Genetic variation in *Bromus tectorum* (Poaceae): differentiation in the eastern United States. *American Journal of Botany* 89:602–612.
- Bever J, Felber F. 1992. The theoretical population genetics of autopolyploidy. *Oxford Surveys in Evolutionary Biology* 8:185–217.
- Brown AHD, Briggs JD. 1991. Sampling strategies for genetic variation in *ex situ* collections of endangered plant species. In: Falk DA, Holsinger KE, editors. *Genetics and conservation of rare plants*. New York (NY): Oxford University Press. p 99–119.
- Brown AHD, Brubaker CL. 2002. Indicators of sustainable management of plant genetic resources: how well are we doing? In: Engels JMM, Ramanatha Rao V, Brown AHD, Jackson MT, editors. *Managing plant genetic diversity*. Oxon (UK): CABI Publishing. p 249–262.
- Buis S. 2000. Writing woody plant specifications for restoration and mitigation practices. *Native Plants Journal* 1:116–119.
- Buza L, Young A, Thrall P. 2000. Genetic erosion, inbreeding, and reduced fitness in fragmented populations of the endangered tetraploid pea *Swainsona recta*. *Biological Conservation* 93:177–186.
- Campbell RK, Sorensen FC. 1984. Genetic implications of nursery practices. In: Duryea ML, Landis TD, editors. *Forest nursery manual: production of bare-root seedlings*. Dordrecht (Netherlands): Martinus Nijhoff. p 183–191.
- Charlesworth D, Charlesworth B. 1987. Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* 18:237–268.
- Cole CT. 2003. Genetic variation in rare and common plants. *Annual Review of Ecology, Evolution, and Systematics* 34:213–237.
- [CPC] Center for Plant Conservation. 1991. Genetic sampling guidelines for conservation collections of endangered plants. In: Falk DA, Holsinger KE, editors. *Genetics and conservation of rare plants*. New York (NY): Oxford University Press. p 225–238.
- Crow JF. 1993. Mutation, mean fitness, and genetic load. In: Futuyma D, Antonovics J, editors. *Oxford Surveys in Evolutionary Biology*. Vol. 9. Oxford (UK): Oxford University Press. p 3–42.
- Demauro MM. 1993. Relationship of breeding system to rarity in the lake-side daisy (*Hymenoxys acaulis* var. *glabra*). *Conservation Biology* 7:542–550.
- Edmands S, Timmerman CC. 2003. Modeling factors affecting the severity of outbreeding depression. *Conservation Biology* 17:883–892.
- Elkassaby YA, Thomson AJ. 1996. Parental rank change associated with seed biology and nursery practices in Douglas-fir. *Forest Science* 42:228–235.
- Ellstrand NC, Elam DR. 1993. Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology and Systematics* 24:217–242.
- Falk DA. 1987. Integrated conservation strategies for endangered plants. *Natural Areas Journal* 7:118–123.
- Falk DA, Holsinger KE, editors. 1991. *Genetics and conservation of rare plants*. New York (NY): Oxford University Press. 283 p.
- Frankham R, Ballou JD, Briscoe DA. 2004. *A primer of conservation genetics*. Cambridge (UK): Cambridge University Press.
- Futuyma DJ. 1979. *Evolutionary biology*. Sunderland (MA): Sinauer. 565 p.
- Gitzendanner MA, Soltis PS. 2000. Patterns of variation in rare and widespread plant congeners. *American Journal of Botany* 87:783–792.
- Given DR. 1987. What the conservationist requires of *ex situ* collections. In: Branwell D, Hamann O, Heywood V, Syngé H, editors. *Botanic gardens and the world conservation strategy*. London (UK): Academic Press. p 103–116.
- Glémin S. 2003. How are deleterious mutations purged? Drift versus non-random mating. *Evolution* 57:2678–2687.
- Glendinning D. 1989. Some aspects of autotetraploid population dynamics. *Theoretical and Applied Genetics* 78:233–242.
- Guarino L, Ramanatha Rao V, Reid R, editors. 1995. *Collecting plant genetic diversity: technical guidelines*. Wallingford (UK): CAB International.
- Guerrant EO. 1992. Genetic and demographic considerations in the sampling and reintroduction of rare plants. In: Fiedler PL, Jain SK, editors. *Conservation biology: the theory and practice of nature conservation, preservation, and management*. New York (NY): Routledge, Chapman and Hall Inc. p 321–344.
- Guerrant EO. 1996. Designing populations: demographic, genetic, and horticultural dimensions. In: Falk DA, Millar CI, Olwell M, editors. *Restoring diversity: strategies for reintroduction of endangered plants*. Washington (DC): Island Press. p 171–207.
- Guerrant EO, Havens K, Maunder M, editors. 2004. *Ex situ* plant conservation: supporting species survival in the wild. Washington (DC): Island Press. 424 p.
- Hamrick JL, Godt MJW. 1990. Allozyme diversity in plant species. In: Brown AHD, Clegg MT, Kahler AL, Weir BS, editors. *Plant population genetics, breeding, and genetic resources*. Sunderland (MA): Sinauer. p 43–63.
- Hufford KM, Mazer SJ. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecology and Evolution* 18:147–155.
- Karron JD. 1987. A comparison of levels of genetic polymorphism and self-compatibility in geographically restricted and widespread plant congeners. *Evolution and Ecology* 1:47–58.
- Karron JD. 1991. Patterns of genetic variation and breeding systems in rare plant species. In: Falk DA, Holsinger KE, editors. *Genetics and conservation of rare plants*. New York (NY): Oxford University Press. p 87–98.

Sun Gro Horticulture's Recipe for Success

Forestry/Native Plant Production

- ✓ **Sunshine Forestry/Native Plant Growing Mixes**
- ✓ **Nutricote Controlled Release Fertilizer**
- ✓ **Sunshine Peat Moss**
- ✓ **Technigro Water Soluble Fertilizer**
- ✓ **Strong-Lite Vermiculite**

Start with Sunshine Forestry/Native Plant Growing Mixes, specially developed for seedling production.

Or start with Sunshine Grower Orange, the peat moss grade that was developed in partnership with the forest seedling industry.

Nourish your seedlings with Nutricote to provide them with the precise amount of nutrients they need to grow over the long-term.

Additional feeding with Technigro fertilizer may be needed to give your seedlings the extra nourishment they need during early growth.

And finally, cover your seeds with Sunshine Vermiculite to ensure they are always moist.

Combine together and watch your seedlings GROW!

From seedling to sapling to standing timber, the recipe for success is no secret... strong growth depends on superior growing ingredients. That's why Sun Gro has been working with the Forest and Native Plant Industry for over a decade to provide premium growing mixes and peat moss, water-soluble fertilizer and horticultural minerals. We are now pleased to offer Nutricote Controlled Release Fertilizer to our ever-growing product mix. To find out more about our forest and native plant products, call your Sun Gro representative today!

SUNSHINE *nutricote*

SUN GRO
HORTICULTURE
www.sungro.com

Strong-Lite. TECHNIGRO

Western Region Customer Resource Centers: Hubbard Oregon 1-800-842-3256 or Seba Beach Alberta 1-888-797-7328.

Manufactured outside of Canada by Sun Gro Horticulture Distribution Inc., 13011 N.E. 40th St., Suite 100, Vancouver, British Columbia, Canada V4N 4C4. • Distributed in Canada by Sun Gro Horticulture Inc. (Canada), 10100 Highway 103, Box 190, Seba Beach, AB T0B 0B0 Canada. © 2004 Sun Gro Horticulture Canada Ltd. All rights reserved. • Sun Gro, Sunshine, Strong-Lite and Technigro are registered trademarks of Sun Gro Horticulture Canada Ltd. • Nutricote is a registered trademark of Sun Gro Horticulture Canada Ltd. • Technigro is a registered trademark of Sun Gro Horticulture Canada Ltd.

- Kitchen SG, McArthur ED. 2001. Native or not: subjective labels and their application in wildland plantings. *Native Plants Journal* 2:21–24.
- Kitzmiller JH. 1990. Managing genetic diversity in a tree improvement program. *Forest Ecology and Management* 35:131–149.
- Lacy RC. 1987. Loss of genetic diversity from managed populations: interacting effects of drift, mutation, immigration, selection, and population subdivision. *Conservation Biology* 1:143–158.
- Landis TD, Dreesen DR, Dumroese RK. 2003. Sex and the single *Salix*: considerations for riparian restoration. *Native Plants Journal* 4(2):111–117.
- Ledig FT. 1987. Genetic structure and conservation of California's endemic and near-endemic conifers. In: Elias TS, editor. *Conservation and management of rare and endangered plants*. Sacramento (CA): California Native Plant Society. p 587–594.
- Ledig FT. 1991. Secret extinctions: the loss of genetic diversity in forest ecosystems. In: Fenger MA, Miller EH, Johnson JF, Williams EJ, editors. *Our living legacy: proceedings of a symposium on biological diversity*. Victoria (BC): Royal British Columbia Museum. p 127–140.
- Ledig FT. 1992. Human impacts on genetic diversity in forest ecosystems. *Oikos* 63:87–108.
- Linhart YB. 1995. Restoration, revegetation, and the importance of genetic and evolutionary perspectives. In: Roundy BA, McArthur ED, Haley JS, Mann DK, compilers. *Proceedings: wildland shrub and arid land restoration symposium*. Ogden (UT): USDA Forest Service, Intermountain Research Station. General Technical Report INT-GTR-315. p 271–287.
- Lynch M, Gabriel W. 1990. Genetic load and the survival of small populations. *Evolution* 44:1725–1737.
- McGuire PE, Qualset CO, editors. 1990. *Genetic resources at risk: scientific issues, technologies, and funding policies*. Davis (CA): University of California, Genetic Resources Conservation Program. Report No. 5.
- McNeely JA, Miller KR, Reid WV, Mittermeier RA, Werner TB. 1990. *Conserving the world's biological diversity*. Washington (DC): World Conservation Union, World Resources Institute, Conservation International, World Wildlife Fund-US, and the World Bank.
- Meyer SE, Kitchen SG. 1994. Life history variation in blue flax (*Linum perenne*: Linaceae) seed germination phenology. *American Journal of Botany* 81: 528–535.
- Meyer SE, Monsen SB. 1993. Genetic considerations in propagating native shrubs, forbs, and grasses from seed. In: Landis TD, technical coordinator. *Proceedings, Western Forest Nursery Association symposium; 1992 Sep 14–18; Fallen Leaf Lake, CA*. Fort Collins (CO): USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. General Technical Report RM-GTR-221. p 47–54.
- Millar CI, Libby WJ. 1989. Disneyland or native ecosystem: genetics and the restorationist. *Restoration and Management Notes* 7:18–24.
- Pappert RA, Hamrick JL, Donovan LA. 2000. Genetic variation in *Pueraria lobata* (Fabaceae), an introduced, clonal, invasive plant of the southeastern United States. *American Journal of Botany* 87:1240–1245.
- Pellegrin D, Hauber DP. 1999. Isozyme variation among populations of the clonal species, *Phragmites australis* (Cav.) Trin. Ex Steudel. *Aquatic Botany* 63:241–259.
- Reinartz JA. 1995. Planting state-listed endangered and threatened plants. *Conservation Biology* 9:771–781.
- Rogers DL, Ledig FT. 1996. The status of temperate North American forest genetic resources. Davis (CA): University of California, Genetic Resources Conservation Program. Report No. 16.
- Saltonstall K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proceedings of the National Academy of Science of the United States of America* 99:2445–2449.
- Scarascia-Mugnozza GT, Perrino P. 2002. The history of *ex situ* conservation and use of plant genetic resources. In: Engels JMM, Ramanatha Rao V, Brown AHD, Jackson MT, editors. *Managing plant genetic diversity*. Oxon (UK): CABI Publishing. p 1–22.
- Schmid B. 1994. Effects of genetic diversity in experimental stands of *Solidago altissima*: evidence for the potential role of pathogens as selective agents in plant populations. *Journal of Ecology* 82:165–175.
- Tecic DL, McBride JL, Bowles ML, Nickrent DL. 1998. Genetic variability in the federal threatened Mead's milkweed, *Asclepias meadii* Torrey (Asclepiadaceae), as determined by allozyme electrophoresis. *Annals of the Missouri Botanical Garden* 85:97–109.
- Templeton AR, Shaw K, Routman E, Davis SK. 1990. The genetic consequences of habitat fragmentation. *Annals of the Missouri Botanical Garden* 77:13–27.
- Tsutsui ND, Suarez AV, Holway DA, Case TJ. 2000. Reduced genetic variation and the success of an invasive species. *Proceedings of the National Academy of Sciences of the United States of America* 97:5948–5953.
- USDA NRCS. 2004. The PLANTS Database, version 3.5. URL: <http://plants.usda.gov> (accessed 18 Aug 2004). Baton Rouge (LA): National Plant Data Center.
- Wang RL, Wendel JF, Dekker JH. 1995. Weedy adaptation in *Setaria* spp. I. Isozyme analysis of genetic diversity and population genetic structure in *Setaria viridis*. *American Journal of Botany* 82:308–317.
- Williams SL, Davis CA. 1996. Population genetic analyses of transplanted eelgrass (*Zostera marina*) beds reveal reduced genetic diversity in southern California. *Restoration Ecology* 4:163–180.
- Williams SL. 2001. Reduced genetic diversity in eelgrass transplantations affects both population growth and individual fitness. *Ecological Applications* 11:1472–1488.
- Wright S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–159.

AUTHOR INFORMATION

Deborah L Rogers
 Assistant Research Geneticist
 Genetic Resources Conservation Program
 University of California
 One Shields Avenue
 Davis, CA 95616
debrogers@ucdavis.edu