

Sustainable Development and Biodiversity 7

M.R. Ahuja
S. Mohan Jain *Editors*

Genetic Diversity and Erosion in Plants

Indicators and Prevention

Volume 1

 Springer

Sustainable Development and Biodiversity

Volume 7

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Editors

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Indicators and Prevention

Volume 1



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Preface

The term erosion implies a gradual loss of something important that will eventually undermine the health or stability of dependent individuals or communities. As applied to genetic diversity, erosion is the loss of genetic diversity within a species. It can happen fairly quickly, as with a catastrophic event, or change in land use that removes large numbers of individuals and their habitat. Similarly, it can also occur more gradually and go unnoticed for a long time. Genetic erosion represents the loss of entire populations genetically differentiated from others, or the loss or change in frequency of specific alleles within a population, or the species as a whole, or the loss of allelic combinations in plants, trees, and animals.

Until the 1940s, the centers of origin of crop species and woody plants were considered limitless sources of genetic variability. After World War II, agriculture in developing countries suffered great changes. The expanded use of improved varieties resulted in the reduction of traditional varieties, a process called genetic erosion. The expansion of the agricultural frontiers also contributed to the risk of loss of the wild relatives of crop species. Some 10,000 different plant species have been used by humans for food and fodder production since the dawn of agriculture 10,000 years ago.

Yet today just 150 crops feed most humans on the planet, and just 12 crops provide 80 % of food energy, while wheat, rice, maize, and potato alone provide 60 % of staple food. Reduction of agricultural biodiversity means fewer options for ensuring more diverse nutrition, enhancing food production, raising incomes, coping with environmental constraints, and sustainably managing ecosystems. Recognizing, safeguarding, and using the potential and diversity of nature are critical for food security and sustainable agriculture. Biodiversity conservation targets three interdependent levels: ecosystems, species, and genes. Genetic erosion can represent the loss of entire populations genetically differentiated from others, the loss or change in frequency of specific alleles (i.e., different forms of a gene) within populations or over the species as a whole, or the loss of allelic combinations. Genetically eroded populations may be less competitive with introduced, new, invasive species. Genetic diversity is important to a species' fitness, long-term viability, and ability to adapt to changing environmental conditions. Genetic erosion can

be addressed at several levels in the spectrum of management activities. This book deals with a broad spectrum of topics on genetic erosion and biodiversity in crop plants, and trees.

We believe that this book will be useful to botanists, geneticists, molecular biologists, environmentalists, policy makers, conservationists, and NGOs working for the protection conservation of species in a changing environment.

M.R. Ahuja
S. Mohan Jain

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Chapter 1

Genetic Erosion: Context Is Key

Deborah Rogers and Patrick McGuire

Abstract Genetic erosion is a useful concept for conservationists, collection curators, natural lands managers, and practitioners of restoration and revegetation. However, there is variation in how the term has been used and how faithfully it follows from the genetic concepts upon which it was based. Genetic erosion is the loss of genetic diversity—often magnified or accelerated by human activities. It can result from habitat loss and fragmentation, but it also can result from a narrow genetic base in the original populations or collections or by practices that reduce genetic diversity. Just as loss of diversity is relative (to some baseline condition), so too is the biological significance of that loss, the management implications, and the human-applied value. Thus we emphasize the context in this chapter's treatment of genetic erosion. Although few species-specific guidelines are available, practitioners 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.

Keywords Genetic diversity · Reforestation · Restoration · Revegetation · Source materials · Inbreeding · Natural areas · Conservation

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1.1 Introduction

1.1.1 *Genetic Erosion—What Is It?*

Genetic erosion is the loss of genetic diversity—often magnified or accelerated by human activities. 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. This trend of changing agricultural techniques and land use and widespread transfer of improved cultivars led to the disappearance of traditional cultivars.

The term 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 and reflecting 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 focus on the anthropogenically related loss of genetic diversity in plant populations.

1.1.2 *How Is Genetic Erosion Measured?*

Efforts to quantify genetic erosion vary according to how genetic diversity is being measured. Implicit in the concept of genetic erosion is that there is a baseline against which erosion can be measured (Brown 2008). At a population genetic level, where diversity is measured as the number and frequency of alleles (i.e., different forms of a gene), erosion is expressed as a reduction in allele number and frequency. Many phenotypic and molecular genetic markers have been deployed to measure and monitor this level of genetic diversity, as exemplified by several chapters in the volume. At higher orders of biological organization, measures of genetic erosion still have population genetic diversity as an implicit foundation. At a species level, genetic erosion can mean reduced population sizes, loss of populations, and reduced range. At a landscape or ecosystem level, genetic erosion can mean a simplification of trophic levels in the system, reduction in numbers of species represented, reduced density of one or more represented species, and reduced diversity of represented species. At a farmscape level, genetic erosion has been quantified by the simplification of the agroecosystem moving from diverse commodities, variable habitats, and differing scales toward the monoculture extreme. At the level of national agricultural production, genetic erosion can be marked by a reduction in the numbers of different commodities produced, a reduction in the number and diversity of variants of any specific commodity, and by the replacement of older, presumably more genetically diverse commodity varieties by new, more uniform, often imported, commodity varieties (e.g., replacement of landraces by modern cultivars).

There is a genetic resources conservation perspective of genetic erosion as well. A key conservation objective is to capture and conserve samples of genetic diversity representative of the genetic diversity available in the targeted population, species, or environment for maintenance in either ex situ conditions (genebanks, gardens, arboreta, zoos, and animal parks) or in situ conditions (genetic reserves, natural areas, ecosystems, and on-farm situations). All conservation methods incur risks of genetic erosion that are inherent in such necessary practices as sampling, regeneration and propagation, culling, storage, and record keeping.

In general, genetic erosion at all these levels 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 within populations or over the species as a whole, or the loss of allele combinations. The ultimate loss of genetic diversity is the extinction of a species and on a national or global scale this loss of biological diversity has been measured traditionally by frequency of species extinctions.

1.1.3 How Does Genetic Erosion Take Place?

In many instances, the genetic diversity of a species or population may be severely degraded without an immediate loss in census number. For example, there are a few tree species in Canada or the US that are so diminished in presence that they have been federally listed as ‘endangered’ or ‘threatened’. However, there is serious concern about genetic erosion in forest tree species, as expressed at a 1995 international workshop on the status of temperate North American forest genetic resources (Rogers and Ledig 1996) and most recently in the State of the World’s Forest Genetic Resources report which noted that half the forest species reported by countries are threatened by genetic erosion in forest ecosystems (FAO 2014).

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. 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 (e.g., Templeton et al. 1990; Ledig 1992).

Even if genetic diversity is not lost immediately, it is often reduced gradually as populations become smaller (e.g., Lacy 1987). When organisms reproduce, the progeny or offspring that result do not necessarily contain all of the genetic diversity from the parental generation. The genes from some potential parent individuals may not be represented in the progeny because of random factors such as phenological and developmental differences, distance from other plants or inability to find a mate, environmental factors that affect reproduction, random mortality, and random abortion of embryos, among other factors. At each generation,

reproduction represents a sampling of the genetic diversity that was available in the parental generation—a sample that is affected by random processes. For example, rare alleles may be present in only a few individuals, increasing the probability that at some point, by chance, they are not passed to the next generation and will be lost forever from the population unless reintroduced (see discussion of ‘genetic drift’ below).

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 propagation activities associated with restoration, rehabilitation, or reforestation, particularly in large-scale projects or in captive breeding programs and reintroduction scenarios. For plant-focused 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 adapted to the target habitat (see Sect. 1.4 below for further discussion). 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.

Some management practices may contribute to loss of genetic diversity. The perennial herb Mead’s milkweed [*Asclepias meadii* Torr. (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 over a century. However, 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 populations under the two different management methods provided evidence of much lower genetic diversity in the mowed versus burned sites. As mowing usually removed the milkweed pods, preventing seed dispersal and sexual reproduction, this led to increased rhizomatous growth (Tecil et al. 1998). Thus, genetic diversity was quickly lowered per unit area because of fewer and larger genetically distinct individuals. However, 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.

Management plans for species conservation or habitat conservation may represent the best recommendations for maintaining genetic diversity in the targeted organisms that science can provide. Yet, there may still be inadvertent obstacles to preventing genetic erosion. In a managed area, there may be more than one target species with a management plan and the plans may be in conflict or the habitat management plan may conflict with the management plan for a target species within it.

Populations that are less genetically diverse may be more susceptible to pathogens (e.g., for plants: Schmid 1994) or other environmental stresses. Without genetic diversity, there is no adaptation and no evolution. Natural selection acts on genetic diversity; the more fit individuals survive and reproduce. Loss of genetic diversity reduces the ability of the population to adapt 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).

1.1.4 Is Reduction in Genetic Diversity Ever Useful?

Although reductions in genetic diversity are generally considered detrimental, there may be exceptions—such as reduction in the genetic load. For inbreeding species, typically found in plants, these detrimental alleles are rather quickly removed from the population because they are quickly exposed even when recessive, and the resulting individuals carrying them usually don't last long, or contribute much, if any, to future generations. For largely outcrossing species of plants and animals, 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 to selection. The 'uncloning' 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 (e.g., 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 (e.g., mildly or highly recessive), and the type of purging process (i.e., drift or selection, or their interaction) (Glémin 2003; these population genetic features are discussed further below).

Other than the obvious example of the benefit of losing deleterious alleles, one other context in which loss of genetic diversity may not be 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 Steudel (Poaceae) (Pellegrin and Hauber 1999), *Bromus tectorum* L. (Poaceae) (Bartlett et al. 2002), and *Setaria viridis* (L.) Beauv. (Poaceae) (Wang et al. 1995), although this is not a consistent feature among invasive species or populations (e.g., Pappert et al. 2000).

One direct and elegant example of loss of genetic diversity increasing invasive potential is the invasive Argentine ant [*Linepithema humile* (Mayr) Shattuck (Formicidae)]. A 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 et al. 2000).

In contrast, one genetic study of the common reed (*Phragmites australis*) provided an example of genetic erosion 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 (i.e., 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.

1.1.5 Who Is Paying Attention to Genetic Erosion?

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 (UNEP 1972). The lesson was that “*genetic uniformity is the basis of vulnerability to epidemics and, more generally, to biotic and abiotic stresses*” (Scarascia-Mugnozza and Perrino 2002). Concerns about genetic erosion were motivation for the initiation of a global network of genebanks to conserve agriculturally important genetic resources. From the initial agricultural focus, there was increasing concern for and attention to genetic erosion at all levels, reinforcing the assertion made for plant genetic resources by Brown and Brubaker (2002) that: “*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.*”

Genetic diversity, which underlies species diversity and is lost with species extinctions, has been often recognized in its own right as comprising one of three levels of biological diversity critical for conservation (for example, McNeely et al. 1990; Jensen et al. 1993; FAO 1999). Conservation of genetic diversity has been codified as a goal in several international strategies and instruments, such as the Convention on Biological Diversity (CBD 1992), the Global Strategy for the

Management of Farm Animal Genetic Resources (FAO 1999), the International Treaty for Plant Genetic Resources for Food and Agriculture (ITPGRFA 2004), and the Interlaken Declaration on animal genetic resources for food and agriculture (FAO 2007a). There is urgency associated with the current rate of genetic diversity 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 five 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 et al. 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.

At the international level, impacts of genetic erosion on biodiversity in general have been a focus by the Secretariat of the Convention on Biological Diversity. At the start of the century, the CBD’s Global Biodiversity Outlook 1 recognized declining genetic and species diversity and analyzed and recommended actions to address that decline (CBD 2001). The most recent revision and update of the CBD’s Strategic Plan adopted the Aichi Biodiversity Targets which include recognition of pressures on biodiversity and taking steps to alleviate them (CBD 2010). Initially focused on plant genetic resources, the mandate of the UN FAO Commission on Plant Genetic Resources for Food and Agriculture was broadened and its name became the Commission on Genetic Resources for Food and Agriculture. The inaugural state of the world report on animal genetic resources and the second state of the world report on plant genetic resources both emphasize the threats and mechanisms of genetic erosion and advocate documenting and monitoring at national levels the progress of genetic erosion (FAO 2007b, 2010). In each case, global plans of action have been established and national progress at adopting the facets of these plans is facilitated and monitored by the UN FAO for the Commission (FAO 2007a, 2011).

Against this backdrop of a range of levels at which to measure genetic erosion and a range of impacts from populations to national and international levels, one can opine that the term genetic erosion may have become too vague to be useful. For example, currently the UN FAO urges its member nations to report periodically on the extent of genetic erosion through several mechanisms, such as the country reports expected from each member nation as the foundation for state-of-the-world reports on plant, animal, and forestry genetic resources. In addition, the global plans of action for plant and animal genetic resources each have priority actions relevant to reporting the status of genetic erosion. However, the types of responses to such efforts to collect information vary greatly as does the resulting value of the responses. On the one hand, presenting quantifiable data, studies have been done documenting displacement of breeds and local varieties, genetic marker-based assessments of genetic diversity in collections, in wild populations, or in breeding populations have been reported, and national surveys of varietal

diversity in specific crops have been conducted. Such information is extremely limited given the global scale of these reporting efforts. On the other hand, in spite of great efforts by international, regional, and national organizations, responses are sometimes almost statements of faith: “*If introduced, modern cultivars are being grown, there must have been a concomitant loss of local cultivars or landraces.*” Or: “*If climate change impacts increase in severity, there will necessarily be increased erosion of genetic diversity.*” The weakness is the absence of a specific context for specific questions about genetic erosion. Accordingly, we will focus in this chapter on one specific context for genetic erosion: that of natural, wild populations and plant restoration and revegetation.

1.2 Genetic Erosion—Dynamics of Genetic Diversity

Genetic diversity is always changing—over space and over time. Spatially, it sometimes reflects patterns in the environment (i.e., abiotic conditions such as elevation, soil moisture gradients, or climatic patterns, or biotic conditions such as predator, pollinator, or microbial interactions), suggesting adaptation of organisms to their conditions. But whether the genetic diversity is adaptive or not, it is constantly in motion over the landscape, moving by migration and through pollen and seeds and other propagules and being lost through mortality—both random and selective. The general arena in which much of reproductive activity and genetic movement occurs is called the ‘population’—which, for many species, is a ‘virtual entity’ and difficult to identify in the field.

Genetic diversity also changes over time as a result of random factors. For example, whether a particular seed—with its inherent genetic diversity—germinates and survives depends, to some extent, not only on its compatibility with its environment, but also on 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 the survival of its progeny. With each generation, genes are reshuffled and recombined, to greater or lesser extents depending on breeding systems, population structures, and selection. For plants for example, the longevity and life form of the species (e.g., annual, perennial, long-lived woody species), the ploidy level (e.g., diploid or tetraploid), the mode of reproduction (e.g., asexual, sexual, or some combination; dioecious or monoecious), and the breeding system (e.g., 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.

The relationship between population size and loss of genetic diversity has been well established and quantified, with Wright’s (1931) work being seminal. Generally, small populations tend to lose genetic variation by genetic drift (a random process) much more quickly than larger populations. And the shorter the

generation length (i.e., time to reproductive maturity), the more rapid the diversity loss in absolute time (e.g., Frankham et al. 2004). There is considerable theory and empirical research on the relationship between population size and genetic diversity and a review of that literature is beyond the scope of this paper. See, for example, Falk and Holsinger (1991) and Ellstrand and Elam (1993) for some reviews. 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 (e.g., Karron 1987, 1991; Hamrick and Godt 1990; Gitzendanner and Soltis 2000; Cole 2003). However, it is important to note 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 (e.g., Frankham et al. 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 (i.e., in an individual (diploid) plant, there are two copies of the same allele rather than two different alleles for a given locus), and decreases the level of heterozygosity. In general, increased homozygosity (in particular, of partly recessive, mildly deleterious alleles) leads to reduced reproduction and survival (i.e., lower reproductive fitness) and ultimately to increased risk of extinction (Charlesworth and Charlesworth 1987; Charlesworth and Willis 2009). Hence, this cascade of events that results from increased inbreeding has been described as ‘inbreeding depression’ (Falconer 1981).

Loss of genetic diversity can occur in restoration or reintroduction projects, where the seed or propagule source included only a small number of parent plants or a small amount of genetic diversity. This change in genetic composition of a population because of 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 which can lead to an increase in 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. (e.g., 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 eel beds 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).

Inadequate sampling of genetic diversity in the seed (bulb, ramet, or other propagule) collection can lead to reduced genetic diversity in subsequent populations. 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 et al. (1995), and Guerrant (1992, 1996).

1.2.1 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 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 (e.g., through natural selection) can cause a net loss of genetic diversity.

Mutations can have positive, neutral, or deleterious effects for the individuals and populations. Beneficial mutations are those that in some way improve survival or reproductive fitness. Plant species that are largely outbreeding also 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 (e.g., Crow 1993). So even in natural conditions, there is some genetic diversity which is undesirable, or 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 occurs 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 (e.g., 50:50 mixture vs. 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 (e.g., Kitchen and McArthur 2001), or on altered sites, may be advantageous. However, 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) (e.g., Hufford and Mazer 2003). But again, it 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 inbreeding system—could mean that plants with perhaps maladapted breeding systems will get 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, but rather subsequent, generations. Alternatively, the negative effects might decrease over time, perhaps the result of natural selection.

1.2.2 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. For example, loss of variation at loci controlling self-incompatibility in the remaining plants of an Ohio population of lakeside daisy [*Hymenoxys acaulis* (Pursh) Parker var. *glabra* (Gray) Parker (Asteraceae)] reduced mate availability to the extent that the population had produced no seeds for over 15 years (Demauro 1993). In theory, polyploid species may be less susceptible to genetic erosion than diploid species (e.g., Glendinning 1989; Bever and Felber 1992). However, an endangered tetraploid herb endemic to

grasslands of southeastern Australia, *Swainsona recta* A.T. Lee (Fabaceae), suffered considerable genetic erosion despite its polyploidy condition (Buza et al. 2000).

1.3 Genetic Erosion—the Importance of Context

Two frames provide important context for evaluating the significance of genetic erosion and appropriate responses: that of the nature of the species or population and, secondly, the management objective(s). The first frame refers to the status of the species in the wild (abundant to rare) and its degree of manipulation (natural to impacted to domesticated). For example, genetic erosion would have different impacts if detected to be a serious threat to natural populations of an abundant native plant species (i.e., cascading effects throughout the ecosystem) than if detected in a (naturally) rare species. Similarly, genetic erosion is a natural consequence of domestication of wild species, where minimally genetic diversity is ‘repackaged’ and typically also reduced in the domesticated plant products. Loss of genetic diversity in a wild relative of a domesticated plant, though, could be of concern because of the loss of opportunity it represented in finding valuable new traits or new combinations. In naturally or artificially rare species or populations (e.g., those that have been assessed as ‘endangered’ or ‘threatened’ under statutes such as the US. Endangered Species Act), genetic erosion could undermine restoration and recovery efforts, and act as the precursor to extirpation or extinction.

The management objective(s) of the plant species or population is the second frame critical to interpreting the significance of and response to genetic erosion. Even within the context of ‘natural areas management’ there is a diverse array of objectives 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, providing access and infrastructure for recreation and other activities, or serving as a reservoir for species harvested wild from nature and for species useful as gene resources for crop plants. The primary focus for this chapter 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 nonnative species may be appropriate, at least as a nurse crop to help restore soil stability or quality.

Within this topic of genetic erosion in natural plant communities, one could address maintaining genetic diversity within the populations, reintroducing 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.

1.4 Genetic Erosion—Management and Mitigation Practices

The most appropriate and effective preventative, management, or restorative practices for the impacts of genetic erosion will depend on context and management objectives. For agricultural crops, solutions or mitigations have focused on facets of ex situ conservation—such as seedbanks, genebanks, in vitro culture banks, and nurseries and gardens. 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 predict future problems of genetic erosion, allowing an appropriate management response.

For native plant species, the focus is predominantly 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 information on genetically appropriate collection procedures for ex situ genetic collections, Brown and Briggs (1991) and Guerrant et al. (2004)). However, ex situ conservation is not an effective or reasonable substitute for in situ conservation. These are complementary, rather than alternative, conservation strategies (e.g., Falk 1987; Given 1987). Ex situ collections, for example, are only samples 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 (e.g., Chap. 3 of FAO 2010).

Avoiding losses of habitat or fragmentation of habitat (that can interrupt sharing of genes between populations, for example) are important management practices. In addition to habitat conversion and fragmentation, loss of population size and genetic diversity can also arise through the imposition of additional and incompatible management objectives, or even from unintended consequences. For example, the population size of one of the five extant populations of *Pinus radiata*—*P. radiata* var. *binata*—on Guadalupe Island, Mexico, had declined to fewer than 500 trees by 1957 (Bannister 1965) and to approximately 200 by 2001 (Rogers et al. 2006) because of introduced goats and extreme grazing pressure that resulted (Fig. 1.1). However, after an extreme effort was successfully launched to remove the goats, natural regeneration resumed although the genetic impacts of



Fig. 1.1 The Guadalupe Island population of *Pinus radiata* was in serious decline at the time of a census in May 2001, with no evidence of any regeneration

this reduction in population size are still being assessed (Fig. 1.2). But this level of stewardship is often beyond the control of natural areas' managers and those other professionals associated with restoration projects. Nevertheless, genetic erosion of native plant populations in protected open spaces or conservation areas can be lessened by practices and policies that promote (genetic) connectivity among habitat fragments. Because of the diversity of jurisdictions involved at the landscape level, government directives (e.g., ordinances) and policies of nongovernmental organizations (NGOs) that have influence on environmental decisions can be important. For example, a large and active NGO in the State of California—the California Native Plant Society—has developed a guidance document that recommends, for horticultural landscaping, the use of known local sources of native plant species, thus providing some genetically appropriate continuity where landscaped areas and private gardens may connect fragments of natural populations (CNPS 2001). At the US national level, protections for endangered or threatened plant species that specifically address genetic considerations such as protection of minimum viable populations, restoration with genetically appropriate materials, and maintenance or establishment of connectivity among populations (when appropriate), can minimize the occurrence of genetic erosion. However, there is rarely sufficient species-specific information to support such policies, where they exist and requirements are often more general. For example, a review of recovery



Fig. 1.2 Following removal of the goats, natural regeneration was evident just a few years later in 2008 (Photo credit Richard Hawley)

plans for 24 federally listed plants in California revealed that in only 10 cases was research on genetic issues recommended, in only 7 cases were concerns expressed for contamination of local populations from introductions, and in 1 case was monitoring for genetic variation specifically addressed (D. Elam, unpublished 2005 survey, US Fish and Wildlife Service, Sacramento CA USA).

Revegetation or restoration projects—whether they occur at local or landscape spatial scales—provide a significant opportunity to lessen the risk of genetic erosion. (Alternatively, if conducted without genetic considerations, these projects can represent a major source of genetic erosion.) The genetically appropriate decision is often framed as ‘planting local’—which refers to planting or seeding with a genetic source that is locally adapted. Geographic distance is often used as a proxy for genetic distance to give more specific guidance for ‘local’ collections. However, there is little relationship between the two and more meaningful guidance can be derived from the species’ life-history traits. Use of genetically appropriate sources for restoration events can be more important, even critical, for species that are rare, threatened, or endangered. A current effort is underway to develop such specific genetic guidelines for a federal-threatened and state-endangered species in California—San Diego thornmint [*Acanthomintha ilicifolia* (Gray) Gray (Lamiaceae)] (Figs. 1.3 and 1.4). Results from parallel allozyme analysis, ploidy assessment, and common-garden studies suggest strong



Fig. 1.3 San Diego thornmint (*Acanthomintha ilicifolia*) is an annual plant restricted to San Diego County in California USA and Baja California Norte in Mexico. It is endangered because of habitat loss and fragmentation in California (Photo credit Sarah Godfrey)

differentiation—with evidence of considerable local adaptation—among populations (Lippitt et al. 2013; Hipkins and DeWoody 2014).

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



Fig. 1.4 San Diego thornmint is restricted to heavy clay soils and gentle slopes such as the population in the foreground here. Its habitat requirements and loss of habitat to development have placed the species on the endangered list in California (*Photo credit Sarah Godfrey*)

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 (i.e., that constitute a ‘selection’ of some individuals) can cause the resulting genetic composition to differ from that of the original collection. In traditional plant improvement programs, this artificial selection is appropriate and, if successful, results in plants that are better suited to particular goals such as ornamental interest, palatability, or productivity. However, in restoration projects where the goals include restoration of genetic diversity, artificial selection may be less desirable, although it can still occur inadvertently (e.g., Meyer and Mosen 1993). Nursery practices that select for uniformity in individuals (e.g., in seed weight, germination time, or early height growth) can decrease genetic diversity (Kitzmilller 1990; El-Kassaby 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 exerted 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 physical arrangement of parental plants (if open-pollination is used) will also be important in determining the genetic composition of the seeds (e.g., Reinartz 1995).

A large percentage of angiosperm species have been described as polyploid. Differences in chromosome number may correlate with differences in fitness (Keeler 2004), dispersal (Linder and Barker 2014), or community interactions (Thompson et al. 2004), and may indicate limitations in sexual compatibility (Burton and Husband 2000). Yet the chromosome number of natural populations, whether or not known, is rarely considered in conservation or management strategies. Because chromosome number is not easily predicted (i.e., there can be much variability for chromosome number within a family or genus) and it is not often measured even in the context of genetic studies and thus it is not considered in management or restoration decisions. As a result, planting with the inappropriate cytotype may occur in restoration events, which may result in swamping and eventual erosion of the less common cytotypes or disrupting cytotype-related adaptations. If chromosome numbers cannot be counted directly, relative genome size can be reasonably inferred either from DNA content via flow cytometry (direct evidence) or allozyme banding patterns (indirect evidence).

In managed natural areas or genetic reserves, where inbreeding has been identified as a major risk for the target populations, supplementing genetic diversity may be necessary. Bijlsma and Loeschke (2012) suggest three ways of doing this: increasing gene flow between the target population and nearest other populations of the species (this assumes previous larger undivided population); increasing population size (enlarging the habitat might also achieve this); and facilitating genetic exchange with more distant populations and even populations from different habitats (this is the most extreme suggestion and the risk of swamping local adaptation must be balanced by the current risk of loss of the population due to inbreeding and inability to adapt). Beatty et al. (2014) emphasize the need for monitoring and quick action if augmentations are indicated, since the level of genetic diversity in a population can become too low for such remedies.

1.5 Concluding Recommendations

We offer these recommendations in the context of native ecosystem (or species) conservation—which could include projects that are considered revegetation, restoration, mitigation, or other. If conservation of genetic diversity of native plant species is not a primary management objective, these points will be less relevant.

1. 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, genetic collections need to consider a balance of males and females if collecting vegetative material rather than seeds. 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 to not collect seeds or vegetative propagules from just one or a few clones. Species that exhibit a high level of selfing will generally require more genetic samples to obtain the same level of diversity as a comparable species that exhibits a high level of outcrossing (Lawrence et al. 1995).
2. Planning for conservation and restoration activities should include some minimum survey of chromosome number, at least in plants where polyploidy is known within the family, where easily detectable phenotypic differences don't correspond with different chromosome numbers, and especially where rare or endangered species are involved. The most conservative approach would include chromosome number as a criterion for seed collection zones, for example, restricting the transfer of germplasm between populations of different cytotypes.
3. 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 information are not always available, 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.
4. 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 might be more genetically similar than those farther apart. Thus, collecting from many adjacent plants would sample less genetic diversity than spacing the collections more widely (e.g., Millar and Libby 1989).
5. 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.
6. Nursery activities should aim to maximize the proportion of seeds that become healthy plantable seedlings (Kitzmilller 1990). Good nursery management—that is 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).