

## GENECOLOGICAL CONSIDERATIONS IN GRASSLAND RESTORATION USING WILD-COLLECTED SEED SOURCES

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### ABSTRACT

Choice of species and seed sources to use in the revegetation of drastically disturbed lands depends on intended post-reclamation land use. When the intent is to return the land to predisturbance native plant cover and composition, the process can be termed ecological restoration. Seed sources for species used in restoration are usually wildland populations. Genecology deals with the ecological or adaptive significance of genetic variation within and among populations of plants. In contrast with plant breeding or biotechnological approaches, in restoration this knowledge is used to safeguard the genetic composition of source populations, restored populations, and populations adjacent to restored areas. Particular attention is paid to adequate sampling of source populations and to the maintenance of within-population genetic diversity through seed increase or nursery propagation phases. The goal is to initiate processes that will lead to the reestablishment of native ecosystems with diversity, resilience, and capacity for continued evolution, not to try to create static, idealized predisturbance vegetation.

### KEYWORDS

disturbed land reclamation; ecological restoration; genetic variation; propagation; seed transfer guidelines

### INTRODUCTION

The field of genecology, or ecological genetics, is concerned with the ecological or adaptive significance of genetic variation (Heslop-Harrison 1964; Antonovics 1976). It can be contrasted with traditional breeding and biotechnology, which focus on the elucidation, control, and manipulation of genetic variation for explicitly human ends (Jensen 1988). Genecological considerations are helpful when the goal is to imitate or facilitate natural processes of ecosystem recovery without distorting those processes, either wilfully or inadvertently.

Genetic variation at every level, from individual organism to population, ecotype, species, and beyond, is affected by processes of natural selection that are manifested in the interactions among organisms as well as between organisms and the nonliving world. Attributes that confer fitness in the natural environment inhabited by an organism may be different than those regarded as "superior" by plant breeders. For example, growth rate under favorable conditions shows major variation among populations or ecotypes of many native plant species (e.g., McArthur and Welch 1982). Growth rate is a manifestation of a complex set of physiological and developmental processes that can be optimized only through resource trade-offs with other character syndromes that affect survival, such as stress tolerance and anti-herbivore defenses (Grime 1977). The range of growth rates encountered in a population reflects the action of selection on whole organisms. Rapid growth rate may not be a very important component of fitness in a particular context, so that it can be and has been traded off for other attributes more central to survival at the whole organism level. When populations that represent adaptive responses to different selection regimes are brought together in an agronomic or breeding context, it is easy to conclude that slower-growing genotypes are "inferior" to those that grow rapidly and are thus more productive. The genecological approach is to quantify the differences in growth rate and to seek to understand the adaptive significance of this genetic variation, without ascribing value to any particular genotype over others. The existence of genetic variation

in growth rate is a fact, and the inference that this variation is the result of spatial and temporal variation in selection regimes is probably well-founded. But the conclusion that genotypes with faster growth rates are "superior" is clearly a value judgement based on human criteria and perspectives.

In any restoration project, one of the first set of choices to be made involves the source of any living plants, either as seeds or nursery stock, to be planted onto the disturbance. If the disturbance is small-scale and is surrounded by relatively intact native vegetation, the simplest and most genetically conservative approach is to collect from adjacent populations. But on large-scale disturbances, even the species composition of predisturbance plant communities may not be known, and populations of species to be used may no longer exist nearby. This greatly complicates the choices to be made. These include choice of species to be included in the restoration planting, of source populations for each species, and of methods of propagation or increase to be used in securing sufficient supplies of seeds or plants. These choices may impact not only the genetic composition and long-term success of the restoration planting itself, but also the genetic composition and survival of source populations and populations adjacent to the restored area.

### GENECOLOGICAL IMPACTS ON RESTORED POPULATIONS

The goal in restoration from a genecological perspective is to provide the restored plant community with the genetic diversity necessary not only to establish and survive in the short term but to be resilient in the face of events such as fire, insect or disease outbreaks, or severe drought, and capable of evolutionary change and adaptive response over the long term. This diversity is expressed at both species and infraspecific levels.

Often it is deemed impractical to include large numbers of species in restoration plantings. A handful of dominant species are planted with the hope that species richness will subsequently increase on its own. This approach may be successful on small-scale disturbances where there are significant seed inputs from adjacent intact vegetation (e.g., Brown et al., 1996). On large-scale disturbances or on restoration sites surrounded by lands under human cultivation, any gain in native plant species richness would undoubtedly be much slower, if it occurred at all. Maximizing the number of species included in the initial planting is therefore more important on large-scale disturbances. Unfortunately, these are just the plantings where the economics and availability of adequate supplies of seed often militate against high-diversity mixes.

Species diversity in a seed mix must take into account not only the number of species but their relative proportions. If the mix is dominated by a few fast-growing grasses, adding small quantities of other species may not result in higher species richness in the restored community. One way to increase the chances of establishment for incidental species is to spatially separate them from the dominant species, e.g., in separate seed boxes (Plummer et al., 1968). If the site is spatially heterogeneous, it may be possible to spot-plant species that are adapted to less favorable microsites, such as rock outcrops, shallow or sandy soils, or saline areas. This would tend to result in increased species diversity over the site as a whole, with islands of

higher diversity in a matrix of grassland.

Intraspecific genetic variation is important to the success of restoration efforts in several ways. First, as mentioned above, many widely distributed native plant species exist as an array of genetically differentiated, locally adapted populations. Groups of populations that occupy similar ecological niches are sometimes referred to as ecotypes (Gregor, 1946). Ecotype is a broader and less well-defined concept than population. Sometimes ecotypic variation is described only with reference to a particular trait or syndrome. An example would be ecotypic differentiation in seed germination regulation syndrome, where adaptively significant, habitat-correlated variation in germination syndrome exists among populations of a species (e.g., Jain, 1982; Groves et al., 1982; Hacker, 1984; Meyer and Kitchen, 1994; Meyer et al., 1995). This genetic variation in germination response may or may not be correlated with variation in other traits. For example, in rubber rabbitbrush (*Chrysothamnus nauseosus*), variation in germination syndrome is correlated with climatic variation, while variation in achene mass is correlated with variation in soil texture and other microenvironmental characteristics (Meyer et al., 1989; Meyer, 1997). In pragmatic terms, ecotypes are defined on the basis of describable habitat characteristics, i.e., populations that occupy similar habitats are thought of as belonging to the same ecotype. The narrowness of the definition obviously hinges on the number of habitat attributes considered. Some species show more ecotypic differentiation than others, but the degree of differentiation has been documented for very few. Commercially important timber trees have perhaps been the best-studied of any native North American species; for example, western white pine (*Pinus monticola*) shows much less habitat specialization than Douglas-fir (*Pseudotsuga menziesii*), and seed transfer guidelines reflect this fact (Rehfeldt et al., 1984; Rehfeldt, 1989). Grasses have been said to exhibit less ecotypic differentiation than shrubs and forbs, but the exceptions are many (Kitchen and Monsen, 1994; Meyer et al., 1995). Latitudinal differences in flowering phenology can be particularly critical in long-term persistence of restored populations, e.g., of big bluestem (*Andropogon gerardii*; P. Allen, personal communication). Seed transfer guidelines such as those developed for timber species would be very useful to restorationists, but it is unlikely that the resources necessary to generate this information will be available for many native species. In the absence of this knowledge, the best approach is probably some degree of genetic conservatism. Generally speaking, when selecting populations to be used as seed sources in restoration of large-scale disturbances where local populations are no longer extant, the more closely matched the collection site habitat and the restoration site habitat, the more likely the planting is to succeed (Knapp and Rice, 1994; Meyer and Kitchen, 1995; Meyer, 1996). Geographic proximity is a necessary but not a sufficient condition; elevation, topographic position, soil type, and associated plant species are other useful matching criteria.

Another important geneecological consideration is the nature and extent of genetic variation within plant populations. There is considerable evidence to indicate that a major fraction of the genetic variation within native species occurs among individuals within populations (Hedrick et al., 1976; Jain, 1979). Because most of our experience has been with agronomic and horticultural plants, which have been bred or selected for genetic uniformity, major genetic variation among individuals of a wild plant population tends to surprise us. This genetic polymorphism is maintained through various mechanisms, but the most important is probably temporally varying selection (Hedrick, 1995). Wild plant populations experience different selection regimes in different years, due to variation in weather patterns, disturbance events, and other factors. They respond to these

differences with a shift in the proportions of contrasting genotypes that are suited to survive and reproduce better in contrasting selection regimes. Because selection regimes change every year, none of the genotypes are eliminated, and the result is genetic polymorphism. Genetic equilibrium in the Hardy-Weinberg sense is never reached, because the forces of selection keep changing. A population that loses some subset of its genetic polymorphism is in danger of extinction under specific selection regimes, so that surviving populations tend to be those that successfully maintain a full complement of adaptive genetic variation.

This is one reason why it is important to ensure that the restored plant population of a species contains as full a complement of genetic variation as possible. In contrast to the process of artificial selection to optimize certain traits and create genetically uniform "plant material", the restorationist tries to exert as little selection pressure as possible, not even inadvertent selection pressure, in transferring the genetic potential of an existing native plant population to a new population on the restoration site.

Guidelines for the maintenance of genetic diversity in restored populations have been outlined (Meyer and Monsen, 1993; Knapp and Rice, 1994; Meyer and Kitchen, 1995). The first step is to obtain as much of the genetic variation in the source population as possible in the process of collecting seeds or other plant parts for propagation. This means sampling from large numbers of plants, and not biasing the sample in favor of either apparently "superior" individuals or those that happen to be producing large quantities of seeds. Exactly how many individuals to sample from depends on the genetic structure and breeding system of the species, the size of the population, the degree of within-site environmental heterogeneity, and other factors, but the more individuals sampled, the larger the fraction of total genetic variation that will be included in the sample. If there is major variation among individuals in seed ripening phenology, it may be necessary to collect at two or more times during the season in order to obtain the full range of phenological variation. This variation may be quite important in terms of successful reproduction under alternative weather scenarios. Equal representation from a hundred or more widely spaced individuals will probably represent an adequate sample of most populations. Plants that are growing in proximity are often lineally related and more genetically similar on average than those separated by greater distances.

If an adequate sample of seeds or other plant parts collected from the source population is transferred directly to the restoration site, then the only selection pressures on the restored population are those imposed by the site itself, which should increase the proportion of genotypes adapted to conditions onsite at that particular time. But if it is necessary to intervene between the time of sampling and the introduction of plants onsite with some propagation technology, then there is ample opportunity to exert additional, unwanted selection pressure.

If seeds or cuttings are used to grow out nursery stock for outplanting, there are several points during the traditional propagation procedure where unwanted narrowing of the genetic base can take place (Meyer and Monsen, 1993). First, the process of cleaning seed can select against small but otherwise viable seeds. If the seeds require some dormancy-breaking treatment and the treatment applied does not break dormancy in all seeds, then genetic lines that produce a higher fraction of deeply dormant seeds will be selected against. If seeds are oversown in cells and thinned to the strongest seedling, undesirable selection against individuals with slower growth rates

may take place. The process of culling small individuals or roguing out extreme variants of any kind can also narrow the gene pool. Growing the plants out under conditions very different from the source and outplanting sites may result in directional selection and reduce subsequent fitness on the restoration site. These considerations are all strictly genetic, but of course not all the variation in seed size, plant growth rate, and other traits is genetically based. Traditional nursery practice is based on the sensible idea that apparently more fit individuals will have a better survival chance, whether or not their health and vigor is genetically based or only a plastic response to rearing conditions. Maintaining genetic diversity through the nursery propagation process thus requires the exercise of practices that are counter-intuitive. If the propagation is being carried out commercially, the growers should be given a clear explanation of the purpose of these somewhat unorthodox practices.

If the purpose of propagation is to increase the quantity of seed available for seeding onto the restoration site, there are some additional considerations. Seed increase fields should be established directly from wild-collected seeds whenever possible, as every generation in cultivation has the potential to exert additional selection pressure. The seed increase site should be as much like the source and outplanting sites as possible, and agronomic practices such as fertilization and irrigation should be kept to a minimum. If possible, a dormancy-breaking treatment that ensures first-year germination of all seeds should be applied. This will reduce selection favoring low seed dormancy. Low dormancy may be advantageous in agronomic settings, but variable seed dormancy is a key aspect of the survival strategy of many native species and must be retained for long-term population survival (e.g., Meyer et al., 1995). This implies a knowledge of seed physiological ecology for each species being cultivated.

Seeding rates or stock outplanting in seed increase fields should result in plant spacing that minimizes competition among individuals. This may not maximize seed production on an area basis, but there is usually a wide range of densities that results in maximum seed yield (Harper, 1977). The goal is to aim for the low end of this range, with the object of encouraging the survival of genotypes that may be poor competitors in an agronomic setting but that have attributes which enhance survival in the wild.

#### **GENECOLOGICAL IMPACTS ON SOURCE POPULATIONS**

Seed collection from wildland populations is a commercial enterprise in the western United States. This industry has grown up in connection with state and federal programs for rehabilitation of depleted game ranges, and now services private buyers as well, especially the market associated with mined land reclamation. Until recently the industry has been essentially unregulated in terms of impacts on the wildland populations where collection takes place. The decision to collect from a particular population in a given year is an economic one based on seed quality and quantity and consequent effects on harvest efficiency. Shrub populations that produce frequent good seed crops and that have features that make them logistically easy to harvest (e.g., upright growth form, monospecific stands) are harvested more frequently than those that lack these features. Repeated harvest year after year has unknown and possibly deleterious effects on the source population. As long as the harvest technology involves manual harvest of fully mature seeds, a considerable fraction of the seeds produced may shatter and thus escape harvest; this probably reduces impacts on the harvested populations. Mechanized methods of harvest such as combining have more potential for damage, including direct damage associated with disturbance and removal of excessive

biomass as well as longer term negative consequences associated with systematic removal of all seeds produced in a particular year. These latter impacts will be especially negative if the practice is carried out in successive years.

It may seem that plant populations produce seeds far in excess of what they need to perpetuate themselves, but this excess production is tied to features of the ecology of each species, including interactions with seed and seedling predators. For example, shrubs that mast fruit rely on a bumper crop of seeds every few years to saturate the needs of seed predators and permit some seeds to escape predation and establish as seedlings (Kelly, 1994). Thus there is a possibility that, if human collectors harvest a sizeable fraction of the seeds every year, those seeds that are left behind will never be sufficient to saturate predator needs. In this case it is probably better from the point of view of the plant population to collect in intervening years rather than in mast years, but economic considerations would clearly dictate harvesting in the mast year, when time spent in the labor of collection is more profitable.

The problem of impacts on harvested populations are more acute when the intent is to harvest large quantities of seed, enough to seed directly onto large-scale disturbances. If the seed collection is to be used to propagate nursery stock or plant seed increase fields, the return on seed is much higher and the quantities needed much less. As the demand for native seed for use in the restoration of large-scale disturbances increases, seed production in an agronomic setting will undoubtedly become more important. As discussed above, this has its own problems, but a move in this direction will tend to mitigate effects on source populations. Species such as big sagebrush (*Artemisia tridentata*), whose seeds can be harvested in large quantities from wildland stands, will probably continue to be harvested directly from the wild. In the western United States, this usually means harvest from public lands, a practice that can be regulated through a permitting system in order to minimize negative impacts and provide accurate seed source information to buyers (Young, 1995).

#### **GENECOLOGICAL IMPACTS ON ADJACENT POPULATIONS**

Another consideration when transferring the genetic potential of a source population to a new population on the restoration site is any possible negative impacts on the genetic composition of populations in adjacent areas. This is another good reason to use adjacent populations as source populations if they are still extant. Cases are known where remnant animal populations were negatively impacted by introduction of nonadapted nonlocal genotypes, but such evidence is largely lacking for plants (Knapp and Rice, 1994). However, some land management agencies in the United States, notably the National Park Service, have interpreted their mission to preserve intact ecosystems to include the idea of preserving local gene pools for each species, or at least of not actively introducing nonlocal genes into these gene pools (Hassell, 1993). One school of ecological genetics holds that the genetic constitution of a population consists of complexes of genes; these must occur together in an individual if the adaptive response controlled by the complex is to be maintained (Linhart, 1995). According to this idea, introduction of nonlocal genes could disrupt these adaptive complexes and result in reduced fitness. There undoubtedly are complexes of genes that function together to produce, for example, normal development in individual organisms. Evolutionary canalization results in the fixing of these genes in complexes, and in fact every normal individual of the species must possess them. In other words, this may not be a part of the genome where much adaptively significant variation occurs. The presence

of adaptively significant variation among individuals of a population reflects the non-equilibrium nature of selection pressures, as mentioned above. It is hard to see how increasing this variation could have a deleterious effect on the population as a whole. Maladapted genes would be eliminated by the selection regime, while genes that increased fitness would be incorporated into the population gene pool. It seems that a decrease in the amount of genetic variation would be much more likely to have long term negative effects than an increase. Plant populations do not evolve in a vacuum; gene flow between populations always plays some part in the evolutionary process. And superimposed over among-year variation in selection pressure is secular change, particularly climatic change. A plant population in situ must respond to such change either with a plastic phenotypic response or a change in gene frequencies, or else suffer local extinction (Jain, 1979). At the same time, new habitats that come within the range of adaptation of the population may be opening up, permitting migration into previously unoccupied areas. This suggests that the gene pool of a population is not a static entity that can be preserved, but is instead a much more fluid entity whose composition changes every time an individual dies or a new zygotic combination is formed. Notwithstanding the logic of this line of reasoning, our nearly complete ignorance of the effects of introduction of nonlocal genes into plant populations should encourage us to meddle with local gene pools as little as possible. In any case, the more overlap between the genetic composition of the restored population and that of the adjacent populations, the more likely the restored population is to have the requisites for survival.

#### **PREADAPTATION TO DISTURBANCE AND SITE AMELIORATION**

Some people claim that conditions on drastic anthropogenic disturbances can be so far outside the norm that no naturally-occurring plant populations are sufficiently adapted to establish and persist on them. This is only rarely the case. Not all drastic disturbance is anthropogenic, and most plant communities contain native early seral species that are adapted for colonization of disturbed sites. One restoration strategy is to plant these early seral species first and give them time to initiate the successional processes that permit colonization by later seral species. These later seral species can then be planted into the established vegetation or be allowed to colonize on their own, depending on the proximity of seed sources. The procedure is one of facilitating and perhaps accelerating successional processes that would eventually occur, perhaps over a very long time frame, without human intervention.

Even some soils contaminated with heavy metals can eventually be colonized by native plants (Antonovics et al., 1971). This process may require in situ evolution and be quite slow, prompting the suggestion that breeding could produce “plant materials” preadapted for such disturbances and thus able to colonize them quickly. Unfortunately, breeding for a single trait such as copper tolerance involves trade-offs with other survival traits, both in naturally occurring and artificially-selected populations (Hickey and McNeilly, 1975).

Perhaps a less interventionist approach is to use some kind of amendment to ameliorate the site temporarily, to permit the establishment of early seral natives. Liming acidic mine spoils in an alpine tundra community in Montana permitted establishment from seed of species selected on the basis of their ability to invade other kinds of disturbed sites and resulted in successional change and an increase in native species richness in the ensuing years, while unlimed plots showed no recovery (Brown et al., 1996).

Another argument for the use of exotic or genetically manipulated “plant materials” is in the context of degraded North American cold desert grasslands, where conversion from high-diversity sagebrush-bunchgrass communities to a dysclimax of exotic annual grasses, principally cheatgrass (*Bromus tectorum*), has occurred over millions of acres (Billings, 1990). Forage grasses such as crested wheatgrass (*Agropyron cristatum*) have been bred or selected to have seedling establishment attributes that make them better able to establish than native late seral species on cheatgrass-dominated sites. Unfortunately, these same attributes make it difficult for native species to establish on crested wheatgrass-dominated sites (e.g., Blaisdell, 1949). One alternative approach involves planting early seral native perennial bunchgrasses such as squirreltail (*Elymus elymoides*). These grasses are sometimes able to establish into cheatgrass, but can themselves give way to later seral native species. Elucidating the particular scenarios of soil nutrient status and seasonal precipitation pattern that permit squirreltail and similar natives to invade cheatgrass will increase the practicality of this approach.

There is considerable evidence that soil nitrogen status plays a major role in mediating the rate of successional change in many plant communities, including sagebrush-bunchgrass communities (Tilman, 1990; McLendon and Redente, 1990, 1991, 1992). Soil amendments that reduce available nitrogen show promise as a way of tipping the scale of competitive interactions in favor of native species (Belnap and Sharpe 1995). Introduction of a carbon substrate stimulates microbial activity and results in a temporary tie-up of nitrogen into unavailable forms. The weedy winter annuals are nitrogen-limited in this situation and cannot fully deplete soil moisture reserves, thus permitting survival of native perennial seedlings through the summer. This method has also been proposed as a way of speeding establishment of natives in competition with weeds in North American prairies (Morgan, 1994). It represents an alternative to the notion that the only way to “beat the weeds” in grasslands is to introduce exotic or improved “plant materials”.

#### **CONCLUSIONS**

This discussion has been based on the premise that the objective in reclamation of disturbed land is to restore native predisturbance vegetation. A salient question is the extent to which this premise is in conflict with the objective of establishing forage species for livestock production. The two objectives are clearly not always mutually exclusive. If the predisturbance vegetation was adapted for grazing use by large herding ungulates, then there is every reason to think that the restored vegetation will be equally adapted, if it is given adequate time to establish prior to the introduction of livestock. It may take years or decades for the restored vegetation to reach a successional state that resembles predisturbance conditions.

Not all vegetation types that include perennial grasses are adapted for grazing use, even with very careful management. Restoration of predisturbance plant communities on a drastic disturbance in a matrix of degraded or desertified grassland provides an opportunity to try to recreate plant communities that were present prior not only to drastic disturbance, but prior to grazing abuse. These restored communities might ultimately be useful in the study of whether or not the ecosystem in question can be grazed at all without the inevitable changes in species composition and site physical characteristics that indicate degradation.

A scientific practice that aims to imitate and facilitate natural processes rather than serve human-defined ends implies a whole different set of assumptions and attitudes about the natural world and our place in it. The perspective of breeders and biotechnologists

who regard living plants as “materials” to be manipulated may be contrasted to the humility and willingness to learn from nature that is needed to undertake successful ecological restoration. Those who work in restoration know that efforts so far have been crude at best, and that there is far more to learn about the complex processes of natural recovery in any ecosystem (Packard, 1994; Allen, 1995). The paradigm shift from control and exploitation to a participatory relationship with the natural world may seem like a luxury to some. But this shift does not imply a lack of human need or impact. It focuses on the reciprocity of the relationship, and it emphasizes that the gift of human consciousness includes a responsibility toward the natural world, the world that generates and includes us.

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