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Genetic Variation and Revegetation Strategies for Desert Rangeland Ecosystems

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Abstract—Emphasis in rangeland revegetation has been placed on the selection of suitable species and on the development of techniques to increase establishment success. While the ecological consequences of deliberate revegetation have been examined extensively, relatively little attention has been paid to the genetic consequences of revegetation. Current interest among revegetation researchers has concentrated primarily on species composition within communities and not on genetic constitution of populations of individual species. Proper formulation of revegetation populations involves consideration of existing variation and accurate sampling of that variation. Improper sampling can lead to inbreeding, reduced genetic variation, poor adaptability, and a decrease in the overall stability of the revegetated ecosystem. Efficient plant breeding systems developed for use with crop plants can be adapted to produce more genetically appropriate populations for use in rangeland revegetation. Modification of one of these systems, Convergent-Divergent Improvement, may be especially effective for constructing genetically variable populations for use in revegetation of the highly diverse environments of arid rangelands.

There have been numerous, largely unsuccessful attempts to revegetate degraded desert rangelands in the southwestern U.S. (reviewed by Cox and others 1982; Cox and Jordan 1983; Roundy and Call 1988). A variety of reasons have been given to explain failures; however, genetic factors associated with the plants used in revegetation have not been implicated. There has been very little formal genetic improvement of plants for use in the revegetation of hot desert ecosystems (Wright 1975; Shiflet and McLauchlan 1986; Voigt and others 1987). Propagules (almost always seed) actually used in revegetation in these environments have been from a variety of sources including local populations of native species, nonlocal populations of native species, and introduced species (Cox and others 1982; Bainbridge and Virginia 1990; Jackson and others 1991).

Researchers have expended tremendous energy evaluating different plant species for use in rangeland revegetation (Cox and others 1982; Call and Roundy 1991;

James 1992). In a few cases, individual populations within preferred species have been evaluated for their revegetation potential (Hull and others 1978; McArthur and others 1983; Petersen and others 1987; Cox and others 1990). This evaluation and selection process necessarily involves at least indirect consideration of genetic factors since the differences between species and populations are largely genetically based. However, after species and place of origin, relatively little attention has been paid to the genetic composition of individual accessions of species selected for use in rangeland revegetation. Current interest among revegetation researchers in "biodiversity" (BLM 1990) also concentrates primarily on species composition within communities and not on genetic constitution of populations of individual species.

The methods in which propagules are initially collected and increased for use in revegetation may have significant effects on both success in establishment and long-term persistence of revegetated rangelands. There is some evidence that basic genetic considerations have been ignored during collection and increase of plant materials for revegetation (Millar and Libby 1989). Many of the species used in rangeland revegetation in the United States are developed within public programs, such as the USDA-SCS Plant Materials Program (Shiflet and McLauchlan 1986). The Plant Materials Program has been evaluating plant materials and plant establishment techniques for rangeland or cropland revegetation and critical area stabilization since 1933 (USDA-SCS 1990). In these programs, selected plant materials are produced in adequate quantities to allow for their use in revegetation trials, simulating actual use conditions. Concentrating on the improvement of SCS plant selection and propagation procedures may therefore have a significant direct effect on the genetic health of revegetated rangelands.

We have two main goals in this paper. First we will describe the fundamental genetic principles that should underlie the basic assembly of plant populations for use in revegetation. The possible negative consequences of not observing these principles will be briefly described. We will then present simple plant improvement strategies that may yield broadly adapted, genetically robust populations of self or cross-pollinated plants for use in rangeland revegetation. Throughout, our emphasis is on the use of native plants where genotypes in existing stands ("reference populations" from Aronson and others 1993) can be sampled.

Genetic Foundations

Evolutionary adaptation to a harsh and variable environment requires populations of organisms with sufficient supplies of genetic variation. This genetic variation represents the building blocks that permit organisms to evolve unique adaptations to the environment. We believe that understanding how genetic variation is organized within natural plant populations will help in developing populations for revegetation use. This should increase revegetation success and the population's long-term ecological vitality.

Genetic variation within plant species is organized hierarchically: among members of a family, among families within a population, among populations within a region, and among regions. The distribution of particular forms of genes (alleles) or genotypes describes the "genetic structure" of a species or population within a particular range of its distribution. Genetic structure of plant populations is largely determined by their mating system—the degree to which plants are self or cross-pollinated (Brown 1990). Effective collection and use of plants in revegetation demands some knowledge of their genetic structure in natural stands. Variation from complete cross-pollination to complete self-pollination (or apomixis) may occur within individual species. However, it is generally possible to roughly place most species within the cross to self-pollinated spectrum using floral, life history, or ecological factors (Loveless and Hamrick 1984). Species that are self-pollinated (or apomictic) tend to grow as disjunct populations. Generally there is very little variation within these populations since most individuals descend from self-pollination of a single individual. Most genetic variation in these species exists between populations. Alternatively, plants that are cross-pollinated tend to exhibit significant genetic variation both among individuals within individual populations as well as between populations (Millar and Libby 1989).

Most self-pollinated species do not exhibit reduced fitness when related individuals are mated ("inbreeding depression") while cross-pollinated species are likely to display inbreeding depression. Because of their sensitivity to inbreeding, much more care must be taken in collecting and propagating populations of cross-pollinated species for use in revegetation. Sampling at least 50 to 100 genotypes that are widely dispersed in the reference population is crucial to avoid inbreeding in succeeding generations (Frankel and Soulé 1981). Similar attention to plant population size is crucial during seed multiplication in cross-pollinated species.

In addition to concerns about inbreeding, adequate sampling strategies are important in both cross and self-pollinated species in order to capture and maintain significant amounts of the genetic variation present in reference populations. Sampling too few individuals causes the population to experience a "bottleneck" and to lose genetic variation simply as a result of sampling error. In cross-pollinated species, loss of genetic variation is proportional to the number of plants sampled (Table 1). When population sizes are routinely low, bottlenecks are faced every generation and the effects are cumulative. This loss of genetic variation reduces long-term evolutionary potential (Frankel and Soulé 1981). With plants used in revegetation, drastic changes in genetic structure will be most deleterious when they occur during initial seed collection. Nothing done during subsequent seed production, short of introduction of additional genetic variation, will overcome initial sampling errors. These changes, referred to as genetic drift, would be associated with unpredictable performance and inability to adapt to changing environmental conditions. Sampling as many plants as possible (>100 individuals) is critical in constructing populations for use in native ecosystem revegetation regardless of mating system, growth habit, or site conditions. This practice minimizes problems associated with inbreeding, loss of genetic variation, or genetic drift.

Maintaining Genetic Variation

It is unclear how frequently genetic structure factors have been considered when plant populations have been constructed for use in revegetation. In the SCS Plant Materials Program, which represents the most organized of such efforts, plant materials are initially collected from a wide range of environments and grown at a common location. Accessions (individual collections) are evaluated for establishment and production characteristics at a single location. The accessions that exhibit superior qualities are placed in advanced tests where adequate amounts of propagules are produced for use in revegetation trials (Shiflet and MacLauchlan 1986). Since 1935 this program has released over 360 accessions for conservation use and greater than 53% of these have been native to the United States (Peterson and Sharp 1992). Traditionally, the SCS Plant Materials Program has compared and selected

Table 1—Retention of genetic variation in small populations (Frankel and Soulé 1981).

Population Size	Percentage genetic variation remaining			
	1 Generation	5 Generations	10 Generations	100 Generations
2	75	24	6	<1
6	91.7	65	42	<1
10	95	77	60	<1
20	97.5	88	78	8
50	99	95	90	36
100	99.5	97.5	95	60

single source populations that exhibited a desired or superior trait. But, it is unclear what portion of SCS releases are from single source populations. For example, 'Vaughn' sideoats grama (*Bouteloua curtipendula*), a widely used native grass, was originally collected from native stands near Vaughn, New Mexico in 1935 and then bulk-increased for commercial use (Hanson 1972). However, records do not state the number of individuals or sample size that comprised this release.

Underlying much of the plant selection in revegetation with native species is the assumption that adaptation to a revegetation site will be greatest in populations native to or adjoining the site (Vallentine 1989; Guinon 1993). Unfortunately, little solid research supports this assumption for highly disturbed desert sites. Limited research indicates that it may not always be true (McArthur and others 1983). While it is not possible to draw firm conclusions, there is some doubt whether single-source or local populations are necessarily optimum for use in rangeland revegetation. Moreover, the range of environments for potential use and the cost of collection and increase of propagules are both likely to be great for populations of plants for use in large-scale (>0.25 ha) rangeland revegetation. Together, these observations may suggest that such populations should have as wide a range of adaptability as possible. Ideally, these populations should contain genotypes adapted to essentially all of the typical native environments of the species. In self-pollinated or apomictic species, such genetically broad-based populations can be created by bulking equal numbers of propagules from representative populations from throughout the range (or a selected portion of the range) of the species. Because intermating between populations would be very infrequent, increase and maintenance of such bulk populations (or their components) would be relatively straightforward. However, because genetic recombination between different populations would be limited, the range of adaptation of the bulk population may be confined to environments very similar to those originally sampled. Genotypes able to successfully exploit intermediate environments may be infrequent. Nevertheless, because the total genetic variation that bulk populations contain will be greater than individual component populations, bulk populations of self-pollinated species should offer increased chances for successful establishment and persistence than populations derived from a single site (Marshall and Brown 1973).

The bulk population concept can be extended to cross-pollinated species with the potential that genotypes with adaptation to intermediate environments can be produced. We propose that this could be achieved by using a plant breeding strategy originally developed for corn (Convergent-Divergent Improvement, hereafter "CDI") (Lonnquist and others 1979). In its simplest form, this procedure is initiated with collection of propagules from populations of the desired species located throughout the targeted range (Fig. 1). This is followed by equal bulking of these propagules and planting at a single location (Convergence) where plants are allowed to randomly interpollinate. Equal amounts of seed (produced from interpollination) from each individual plant is then bulked. This bulk seed is then used at selected locations within
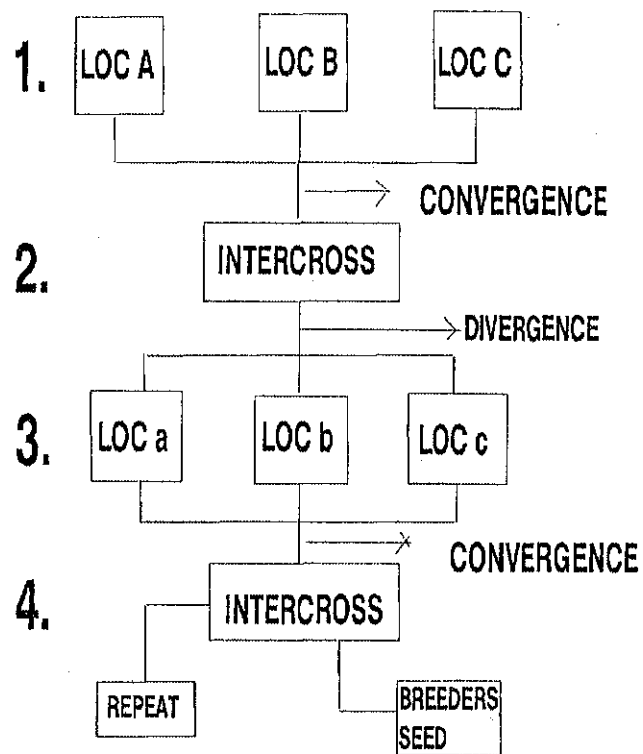

Figure 1—Flow diagram describing the four basic steps in Convergent-Divergent Improvement with populations from three environments. Step 1: Propagules are collected from separate locations within the natural range of the species. Step 2: Propagules are bulked with equal representation of locations, planted at a single location, and allowed to randomly intermate (Convergence). The resulting seed may be released directly for use in revegetation. Step 3: Samples of seed produced in Step 2 are sown/transplanted at locations representative of the environments the improved population would be used in (Divergence). Step 4: Propagules of plants persisting at field locations are collected, bulked, planted at a single location, and allowed to randomly intermate (Convergence). Seed may be released for use in revegetation or subjected to another cycle of divergence.

the targeted area (Divergence). The "selected locations" are locations that best simulate where the plant is to be used. Equal amounts of propagules (plants or seed) of surviving plants at these selected locations are then collected, brought back to a single location, and planted in a crossing block to simulate and facilitate random cross-pollination (Convergence-cycle 2).

CDI should result in cross-pollinated populations that have:
- A wide range of genetic variation, including novel genotypes not present in any of the originally sampled populations
- Proven ability to establish at variable locations and environments

- The capability to be no more time consuming or expensive than the traditional SCS-Plant Materials Program methods of selection and increase of single-source populations.

Conclusions

In the SCS Plant Materials Program it may take 12 to 15 years to test, select, and release for commercial production a superior plant material. CDI could reduce this to less than 10 years. Furthermore, the use of bulk populations of self-pollinated species or CDI with cross-pollinated species has the potential to produce a product that has a better chance for successful establishment and persistence, potentially reducing the cost of revegetation projects.

Currently, the Tucson Plant Materials Center is implementing CDI and the production of bulk populations for three species: Spike dropseed (*Sporobolus contractus*); Mesa dropseed (*Sporobolus flexuosus*); and Slim tridens (*Tridens muticus*). By fall of 1995 we will have our initial bulk populations (Convergence) for the above species and will begin planting into their targeted areas (Divergence) by summer of 1996.

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