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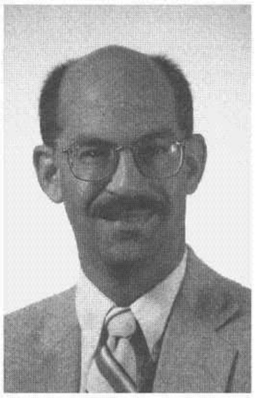

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Invited Synthesis Paper: Integrating genetic concepts into planning rangeland seedings

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Abstract

Choice of plant materials is a fundamental component of any rangeland rehabilitation, reclamation, or restoration project. We describe here an integrated approach for such decision-making. This approach considers site potential, desired landscape, seeding objectives, conflicting land use philosophies, appropriate plant materials, weed invasion, community seral status, and economic limitations. Technical limitations are considered in generating a plan that has the greatest potential for success. Determining whether native-site plant material is best depends on objectives, heterogeneity of the site's environment, uniqueness of the site, plant population size, and biotic or abiotic site disturbance. Fixation of alien genes into a population is referred to both as introgression, which may ensure maintenance of genetic variation critical for adaptation to a changing environment, and as genetic pollution, with the potential for swamping native cross-pollinating annual or short-lived perennial gene pools. Precautionary procedures during seed increase minimize genetic shift, which may be reversible, but genetic drift could result in permanent loss of desirable genes. A variety of germplasm classes, ranging from site-specific to widely adapted and varying in degrees of heterozygosity and heterogeneity should be considered. Material originating from multiple sites may increase the opportunity for natural selection. An understanding of the magnitude and nature of a species' genetic variation, its relationship to ecological adaptation, and its interaction with other ecosystem components contribute to informed decision-making. Though often unavailable, experience is the best guide for predicting performance of materials on non-native sites.

Key Words: genetic integrity, genetic pollution, introgression, natural selection, plant materials, polyploidy, rangeland weeds, succession

Land managers now have more options for species, seed sources, and seeding equiment, and additional options will be available in the future. Nonetheless, difficulties may arise in trying to balance the desired result with the reality of available biological, abiotic, and economic resources. Although not all concerned constituency groups may endorse a decision, detailed objectives and a coordinated plan are essential for inclusion of various viewpoints. This paper presents an approach to integrate genetic concepts into the seeding recommendation process (Fig. 1).

An improved understanding of rangeland species and their intraspecific genetic variation, i.e., ecotypes, biotypes, and chromosome races, should increase demand for a wider array of plant materials. Ultimately, an understanding of the association between ecological adaptation and genetic variation is the key to the choice of appropriate plant materials and their wise use on the land.

INITIAL STRATEGY

Site Potential and Desired Landscape

Site potential is influenced by climate, soil processes, fire frequency, existing vegetation, and landscape features. Loss of soil by erosion, invasion by undesirable plants, and unnatural increases in fire frequency reduce site potential (Allen 1995). The Snake River Plain and California grasslands exemplify how the combination of fire and weed invasion can lower site potential and limit land management options. When options are limited, land managers must make choices that otherwise may not have been preferred.

When topsoil has been removed, seedings of late successional species typically fail, especially if they are dependent on soil microbes such as mycorrhizae. Ectomycorrhizae are typically associated in an obligate manner with specific woody plant species, while arbuscular mycorrhizae associations are usually nonspecific with grasses and forbs (Allen 1996). Artificial inoculation is effective when undisturbed topsoil from the native site serves as the source of inoculum. Inoculation is most necessary when the scale of disturbance is great, eliminating nearby sources of inoculum. Inoculum may be applied by topdressing, as is often done in mineland reclamation, or it may be strategically applied with plants throughout the site to form inoculated patches. The inoculum may then spread throughout the site from the patches.

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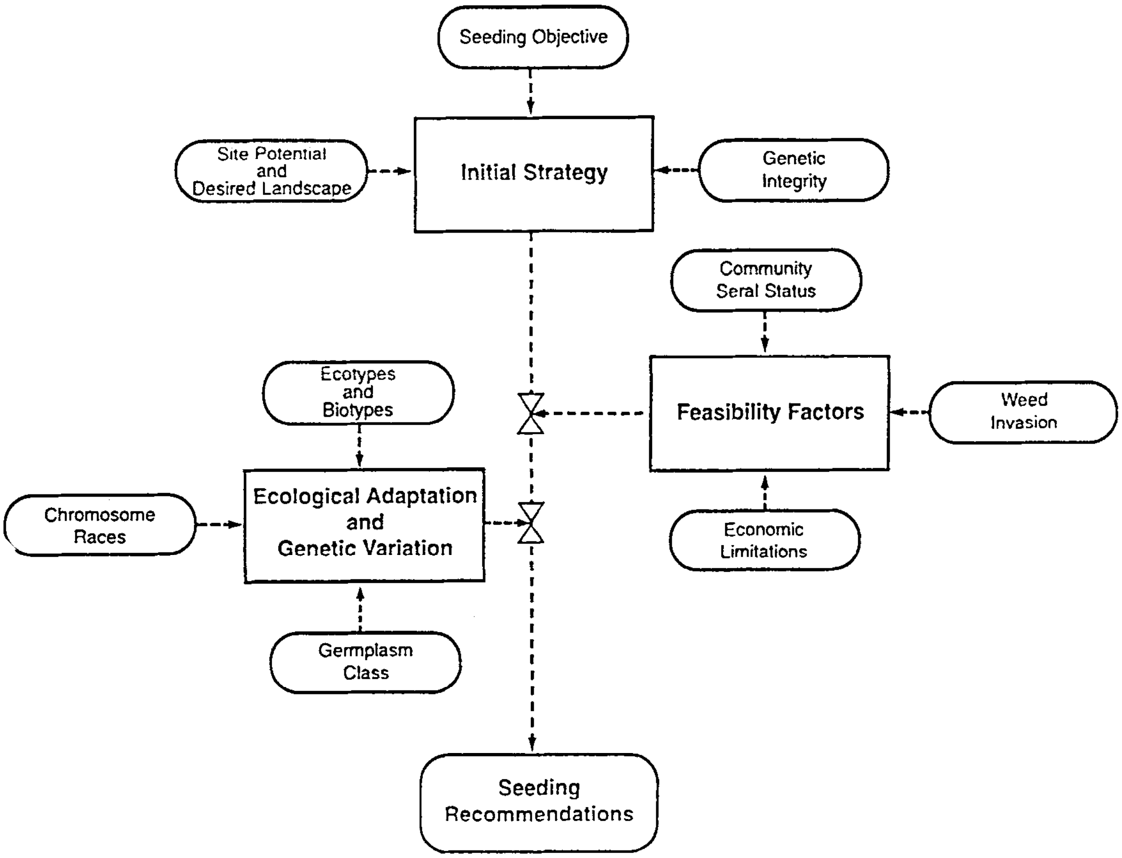

Fig. 1. Flowchart (Anonymous 1963) for making recommendations for rangeland seedings.

Because semi-arid western U.S. soils are typically high in P, response to inoculum in the region may be more often due to improved water relations than to nutrient uptake. Response to infection appears to be greater in warm-season than cool-season grasses.

Managers must identify the combinations of desired life histories required to create the desired ecosystem, i.e., the ecosystem of reference (Aronson et al. 1993). Sandy, gravelly, or rocky soils favor deep-rooted perennials, e.g., big sagebrush, while ephemerals tend to dominate in medium-to-heavy-textured soils with low infiltration rates (Noy-Meir 1973). Grasses may be short-lived perennials, e.g., Indian ricegrass [*Achnatherum hymenoides* (Roem. & Schult.) Barkw. = *Oryzopsis hymenoides* (Roem. & Schult.) Ricker = *Stipa hymenoides* Roem. & Schult.], or long-lived perennials, e.g., crested wheatgrass (*Agropyron* spp.). While some species readily regenerate from seed without management precautions, e.g., squirreltail [*Elymus elymoides* (Raf.) Swezey = *Sitanion hystrix* (Nutt.) J.G. Smith], others typically have poor seedling recruitment when livestock or wildlife numbers are high, e.g., curl-leaf mountain mahogany (*Cercocarpus ledifolius* Nutt. in T. & G.). Some species are predominately vegetatively propagated, e.g., western wheatgrass [*Pascopyrum smithii* (Rydb.) A. Löve = *Agropyron smithii* Rydb.]. Arrowleaf balsamroot [*Balsamorhiza sagittata* (Pursh) Nutt.] is a summer-dormant forb with a large tap root and deep soil penetration (Kitchen 1994), characteristics that confer longevity. Alternatively, Palmer penstemon (*Penstemon palmeri* Gray) and globemallow (*Sphaeralcea* spp.) produce abundant seed during seasons of plentiful moisture, but mature plants exhibit high mortality the following year. Such species are opportunistic but individual plants are short-lived.

Perennials low in productivity typically dominate the landscape of nutrient-poor habitats (Aerts and van der Peijl 1993), such as are found in the Intermountain Region. Highly productive perennials are typically absent in such environments because of their need for high nutrient turnover. In contrast, perennials with low productivity can maintain a high biomass equilibrium by conserving nutrients. Resources in these landscapes may become available in a "pulse-and-reserve" fashion (Noy-Meir 1973). For example, a rainfall event (pulse) may trigger buildup of a seed bank (reserve), which slowly declines until the next pulse.

Many researchers have investigated the "patchy" structure of natural ecosystems and its influence on ecosystem function. A cyclical pattern of shrub and grass establishment and mortality has been documented in the arid steppe of southern Argentina (Soriano et al. 1994). Several bunchgrass and shrub species displayed a chronological sequence as follows: initial shrub establishment, development of a bunchgrass ring surrounding and facilitated by the shrub, mortality of the shrub, and disintegration of the ring resulting from inter-grass competition.

Tongway and Ludwig (1990) described a landscape in eastern Australia consisting of a woodland community alternating along an elevational gradient with an intergrove community consisting of 2 distinct savannas. An *Eragrostis* savanna was present on gentle slopes above a *Monachather* savanna on level ground which, in turn, lies upslope from an *Acacia* grove. Hydrological flow concentrated nutrient ions, organic C, organic N, and available N in the woodland soil from the upslope *Eragrostis* savanna soil with the *Monachather* savanna soil intermediate. On a smaller scale, Ludwig and Tongway (1995) described nutrient patches associated with individual trees, logs, shrubs, and bunchgrasses built by fluvial and aeolian processes. Charley and West (1975) reported a "redistribution of capital" by shrubs in Utah. Soil beneath *Artemisia, Atriplex,* and *Coleogyne* shrubs was higher in total N, organic C, organic P, and often electrical conductivity than in bare interspaces.

Sharma and Tongway (1973) described how leaf fall and evaporative loss beneath canopies of 2 *Atriplex* species increased soil salinity and pH near the soil surface (accumulation zone), while salts were depleted in the rhizosphere directly beneath shrubs (depletion zone). In the compensation zone, situated vertically between the accumulation and depletion zones, the 2 forces were balanced and salt concentration was similar beneath and between shrubs. This ecosystem function has been termed "ion-pumping" (Tongway and Ludwig 1990). Richards and Caldwell (1987) described a similar phenomenon for water termed "hydraulic lift". When stomata were closed at night and on cloudy days, big sagebrush shrubs removed water from deeper moist soil, where roots were sparse, and released it in shallower dry soil, where roots were prolific. This makes deep soil moisture available to shallow-rooted species.

Tongway (1991) considers stable fertile patches prerequisite for proper function of the nutrient cycle and defines "degradation" as the breakdown of patch-maintaining processes. His proposed management goal is to maintain a full range of patches from small to large, providing sustainable production (Tongway 1991) and favorable habitat for vertebrate and invertebrate fauna (Ludwig and Tongway 1995). Tongway and Ludwig (1996) placed *Acacia* branches along the contour of a slope to intercept water, soil, and litter and create microsites for vegetation. This treatment increased soil N, organic C, infiltration rate, and respiration. Numbers of ants and perennial grass and shrub cover were also stimulated in the microsite environment.

When potential is heterogeneous within a site, the sculptured seeding approach is appropriate (Jacobson et al. 1994). Contrasting soil colors resulting from variation for soil type, topography, or moisture-holding capacity may delineate areas for separate seed mixtures or transplanting operations. Natural plant community boundaries often correspond to these variables. When arid ecosystems are poor in resources overall with fertility concentrated in patches, homogenization of the landscape, e.g., cultivation for seeding, is not advised (Whisenant 1995). Mechanical destruction of the patches may reduce soil nutrients, organic matter, and water availability throughout the landscape to a level below the establishment threshold for desirable plants. In these situations, confining seeding efforts to the fertile patches throughout the landscape is a better option than seeding the entire landscape. The restored patches may then serve as donor sites to adjacent untreated areas, stimulating autogenic succession.

Microbiotic soil crusts, a nonvascular component of the landscape, are considered pioneer life forms on degraded soils (Eldridge and Greene 1994). Crust composition may include mosses, liverworts, algae, lichens, fungi, bacteria, and cyanobacteria. They are found on soils ranging from high to low in bulk density (West 1990), but they are less stable on sands than on heavy-textured soils (Skujins 1984).

Nutrient cycling and soil stabilization functions are often attributed to crusts (Ladyman and Muldavin 1997), but additional empirical evidence must be gathered before their role in ecosystem function can be described and quantified (West 1990). Because crust composition varies greatly with constituent organisms and environment, broad generalizations regarding crust function are not useful (West 1990). Crusts may increase landscape stability by inhibiting wind and water erosion and enhance soil aggregates through the action of mucilaginous secretions (Eldridge and Greene 1994). Crusts also may contribute the majority of external N to desert and semi-desert ecosystems through the nitrogen-fixing ability of cyanobacteria (Ladyman and Muldavin 1997). Invertebrates may utilize crusts for food and habitat (West 1990).

Microbiota are alternatively viewed as competitors or facilitators of vascular plants (West 1990). Because crusts are easily destroyed by fire or overgrazing, interest in restoration by inoculation is high (Ladyman and Muldavin 1997). Growth and application of inoculants should be an important aspect of future research.

Seeding Objective

Reclamation

If natural regeneration following land disturbance, e.g., fire or mining, is anticipated to be insufficient to avoid erosion and weed invasion, quick coverage of the soil surface with vegetation is required. The Surface Mine Control and Reclamation Act of 1977 requires revegetation of minelands with species native to the site, but this requirement may not be compatible with the larger goal of matching plant materials with site condition. Bengson (1986) indicated that the soundest approach to mineland rehabilitation should involve a mix of native and introduced species. More important than the origin of the plant material is its seral status. Severely disturbed sites are often classified as early seral and are most appropriately seeded with early-seral species, either native or introduced. On oil shale disturbances in western Colorado, 6 years after seeding, Redente et al. (1984) found species composition of seeded mined lands was more affected by species composition of the initial seed mix than fertilization, irrigation, seeding method, or even ratios of lifeforms in the mix. In Montana, 3 mixtures of native species were seeded in early spring on coal surface-mined lands, chisel-plowed to a depth of 30 cm, and fertilized with 29.6 kg/ha N and 16.3 kg/ha P (DePuit et al. 1980). Species diversity declined through time, and after 2 years the most vigorous species dominated.

Restoration

When restoration is the goal, the emerging principles of restoration ecology must be considered. The Society for Ecological Restoration defines restoration as "the intentional alteration of a site to establish a defined indigenous, historic ecosystem" (Aronson et al. 1993). For reasons of morality, aesthetics, economics, and ecosystem function or "services", a pristine aesthetic state without evidence of man's interference may have maximal intrinsic value (West 1993). This view assumes that each species has a specific and unique role (Ehrlich and Ehrlich 1981). Restoration of arid or semi-arid lands usually is not economically feasible when the system has changed beyond the "threshold of irreversibility" (Aronson et al. 1993).

Ecological restoration efforts typically are initially concerned with particular species in the system including flagship, keystone, umbrella, and vulnerable species (Noss 1991). Flagship species attract particular attention because of their visibility. Keystone species are hypothesized to maintain community diversity through a pivotal role in ecosystem structure or function. Umbrella species, which have large area requirements, provide habitat protection for a wide array of additional species. Vulnerable, i.e., "threatened or endangered", species demand disproportionate attention because of their high risk of extinction. Ecological indicator species are used in programs to monitor system health (Landres et al. 1988). Noss (1991) emphasized the need to preserve ecological processes that transcend individual species, which has now become a concept of ecosystem management. This approach emphasizes conservation of species collectively rather than individually.

An alternative approach to restoration considers the ecological validity of functionally and structurally stable systems without emphasizing species composition *per se* (Johnson and Mayeux 1992, Walker 1992, West 1993). Citing examples including creosotebush [*Larrea tridentata* (Ses. & Moc. ex DC.) Cov.] and blackbrush (*Coleogyne ramosissima* J. Torr.), Johnson and Mayeux (1992) argue that constant reassembling of species is the norm in natural ecosystems, i.e., species composition is inherently unstable. This approach assumes that species can be added to or removed from an ecosystem without necessarily changing ecosystem structure or function. Species may substitute for one another because of biological redundancy (Westman 1990, Walker 1992). Proponents of this theory presume that introduced species can fill ecological gaps left by native species that have been lost from the system. They dispute the claim that native and introduced species play fundamentally different roles in ecosystems. While many taxonomically similar species exist for North American natives in the Old World or South America, their functional ecological equivalency remains hypothetical until tested.

Desired Plant Community

Recently, the concept of "Desired Plant Community" has been proposed (Task Group on Unity in Concepts and Terminology 1995a,b). Desired Plant Community refers to any managed plant community in which management does not accelerate soil erosion above a level considered "normal" for the site. Because soil erosion is difficult to measure directly, measurable site-specific attributes related to erosion such as canopy cover, plant basal area, plant density, plant lifeform, plant species, biomass production, or soil surface characteristics are determined instead. This concept for evaluating range condition does not categorize vegetation as to native or introduced. The concept originated with the Bureau of Land Management and has been adopted by the Society for Range Management with recommendations for implementation of a national rangeland inventory and assessment, adoption of educational programs to ensure understanding of the pertinent principles, and research to more correctly apply the concept. Pickett and Parker (1994) refer to the Desired Plant Community as the concept of "contingency" and suggest that it is encompassed within the goals of restoration. Direct and indirect human effects are considered elements of contingency (Pickett and Parker 1994, Jackson et al. 1995).

Genetic Integrity

The third consideration in assembling an initial strategy involves the philosophy of the individual, organization, or society concerning the genetic material for the site. Potential problems include invasion of adjacent communities, poor long-term survival of the material used, and lack of resilience to invasion by exotics. Belnap (1995) asserts that restoration is more than just vascular plant establishment. Intraspecific genetic variation for plant traits affecting the plants' compatibility with bacteria, fungi, nematodes, protozoa, invertebrates, and vertebrates, both above- and below-ground is likely important, but is poorly understood.

Genetic shift during plant propagation may lead to intentional or inadvertent selection of genotypes with lower levels of seed dormancy, less complex seed dormancy mechanisms, or larger seed size (Meyer and Monsen 1993). Meyer and Monsen (1993) propose that any shift of gene frequencies in the population may be unwise because the genetic basis for population persistence is not well understood. Genetic shift could conceivably lead to unadapted genotypes and eventually to seed bank depletion. However, in genetically heterogeneous material, some genetic shift is inevitable during seed production, harvesting, conditioning, and seedling establishment. Genetic shift can be minimized during seed increase by reducing plant mortality, harvesting across multiple dates, choosing an increase site similar to the target site, minimizing the number of years the nursery is harvested, replanting the nursery with original seed (Knapp and Rice 1994), harvesting equal amounts of seed per plant, harvesting seed only in moderate to heavy seed production years (Kitzmiller 1990), and maximizing the breaking of seed dormancy (Kitzmiller 1990, Meyer and Monsen 1993).

Despite the concerns of genetic shift discussed above, genetic shift may not always be undesirable, as it may improve adaptation. Gene frequencies may shift to a site-adapted equilibrium if seed production and seedling recruitment occur on the site. A mixture of seed from environments similar to the target environment would favor genetic shifts driven by natural selection (Knapp and Rice 1994).

Some argue that selection of an appropriate seed source for a restoration site can be made by matching plant communities, which presumably reflect the particular combination of climatic, microclimatic, topographic, and edaphic variables (Millar and Libby 1989, Meyer and Monsen 1993). Linhart (1995) advocates collection within areas of genetic similarity, e.g., no further than 100 m from the site for herbs and 1 km from the site for woody plants. Zones of genetic similarity would be expected to be narrower in self-pollinated than cross-pollinated species, particularly if habitats are fragmented.

Because of the risk of genetic pollution, i.e., the introduction of alien genes disruptive to site-specific adaptation, Linhart (1995) considers the use of plant materials from distant sites the worst option despite similarity of environment. Such genetic disruption has been termed "outbreeding depression". Millar and Libby (1989) expressed concern that the irreversible contamination of the native gene pool, which occurs when native and non-native site materials intermate, may affect dynamics at the community level, including coevolutionary processes. They also consider introduction of non-native site material a bigger risk than introduction of exotics because only the latter can be easily identified for eradication.

If planned before disturbance, native-site seed can be collected for future projects (Beavers 1995). As of 1995, the National Park Service had contracted with the Natural Resources Conservation Service (NRCS) for seed production of about 400 indigenous populations of "known genetics" collected within park boundaries. After seed increase off-site at NRCS locations with similar elevation and climate, the seed is returned to the park for revegetation of sites disturbed by highway construction. When sites in need of rehabilitation, reclamation, or restoration have been permanently altered in 1 or more aspects, native-site plant material may no longer be best adapted or available. If so, a seed source with proven adaptation to the disturbance may be better adapted than that collected on-site prior to disturbance.

The loss of low-frequency genes as a result of genetic pollution through the mechanism of genetic drift, which involves stochastic fluctuations in gene frequency in small populations, may occur when pollen of non-native material "swamps" remnant native material of a reduced scale (Knapp and Rice 1994). Swamping may also lower population fitness by breaking up adaptive gene complexes. While recognizing the risks of genetic pollution, Knapp and Rice (1994) argue that collecting seed within a given radius of the planting site ignores environmental patchiness. Instead, they subscribe to Kitzmiller's (1990) concept of restricting planting of seed to that collected within the same "seed zone". Kitzmiller (1990) utilized 84 seed zones for conifers in California based on broad ecological and geographical features. Seed certification procedures for providing native-site verification for native rangeland grasses, forbs, shrubs, and trees are discussed under *Germplasm Class*.

Genetic pollution is synonymous with introgression, which involves hybridization followed by backcrossing and fixation of backcrossing types. Introgression has been recognized as an important evolutionary mechanism for nearly 50 years (Anderson 1949). Plants primarily derived from 1 taxon but with introgressed alien genetic material are more likely than F_1 hybrids to be fertile and adapted to some ecological niche. Introgression is widespread within rangeland species. Natural selection generates new adapted gene complexes from the novel genetic variation created by introgression.

Desert bitterbrush (*Purshia glandulosa* Curran) is reportedly derived from the introduction of alleles from Stansbury cliffrose [*Purshia mexicana* var. *stansburiana* (Torr.) Welsh = *Cowania stansburiana* Torr.] into antelope bitterbrush [*Purshia tridentata* (Pursh) DC.] and is found in California, Nevada, Arizona, and Utah in areas where the parents occur sympatrically (McArthur et al. 1983). These species easily hybridize in nature to the extent that McArthur et al. (1983) believe Stansbury cliffrose genes have introgressed into all antelope bitterbrush populations, even those outside of cliffrose's range. Stansbury cliffrose is often found on south and west-facing slopes, antelope bitterbrush occurs on north and east-facing slopes, and highly fertile hybrid populations are found along ridgetops.

In the northern part of its range, tetraploid fourwing saltbush [*Atriplex canescens* (Pursh) Nutt.] hybridizes with Gardner's saltbush [*Atriplex gardneri* (Moq.) D. Dietr.], which has resulted in speciation of *Atriplex aptera* Nelson, common on clay soils of Missouri River tributaries from Alberta to Nebraska (Stutz and Sanderson 1979). Similarly, in its southern extension, fourwing saltbush frequently hybridizes with *A. polycarpa* (Torr.) Watson, giving rise to *A. linearis*, common in western Mexico, southern California, and southern Arizona.

Numerous hybrids between populations of Indian ricegrass and various needlegrasses (*Stipa* spp.) also have been reported. While many of these hybrid populations are small, sterile, and endemic (Johnson 1945, 1960, 1962a, 1962b, 1963, Weber 1957), a spontaneously chromosome-doubled hybrid named Mandan ricegrass is highly fertile (Johnson and Rogler 1943, Nielsen and Rogler 1952).

Natural hybridization has led to new species through hybridization followed by chromosome doubling, e.g., *Achnatherum latiglume* (Swallen) Barkw. (= *Stipa latiglumis* Swallen) and *A. nevadense* (B.L. Johnson) Barkw. (= *Stipa nevadensis* B.L. Johnson). *Achnatherum latiglume* is a rare endemic found in sandy or rocky soils at the foot of talus slopes in the Yosemite Valley, Calif. (Pohl 1954). This new species ($2n = 70$) arose from hybridization of *A. occidentale* (Thurber) Barkw. ssp. *pubescens* (Vasey) Barkw. (= *S. elmeri* Piper & Brodie *ex* Scribn.) ($2n = 36$) and Lemmon needlegrass [*A. lemmonii* (Vasey) Barkw. = *S. lemmonii* (Vasey) Scribn.] ($2n = 34$). *A. occidentale* occupies the sandy alluvium of the valley floor, and *A. lemmonii* occupies the talus above the valley floor. The endemic, formed in a "hybrid zone", is intermediate in habitat preference and morphology between the 2 parents. It arose by hybridization between 2 species, followed by spontaneous chromosome doubling from 35 to 70, permitting the new species to reproduce sexually. *A. nevadense* ($2n = 68$), found along the eastern slope of the Sierra Nevada mountains and eastward across Nevada, arose from sterile hybrids of Letterman needlegrass [*A. lettermanii* (Vasey) Barkw. = *Stipa lettermanii* Vasey] ($2n = 32$) with western needlegrass [*A. occidentale* (Thurber) Barkw. = *Stipa occidentalis* Thurber] ($2n = 36$), with fertility restored by spontaneous chromosome doubling (Johnson 1962a).

Western wheatgrass ($2n = 56$), an allooctoploid, was probably generated by the hybridization of 2 tetraploids, beardless wildrye [*Leymustriticoides* (Buckl.) Pilger] ($2n = 28$) and thickspike wheatgrass [*Elymus lanceolatus* (Scribn. & J.G. Smith) Gould] ($2n = 28$) (Dewey 1975). These species are the only known species that have the chromosome content, morphological traits, habitat adaptation, germination characteristics, and reproductive systems required to generate western wheatgrass when hybridized.

New species may also arise from hybridization followed by backcrossing. Schechter and Johnson (1968) reported that *A. contractum* (B.L. Johnson) Barkw. [= *Oryzopsis contracta* (B.L. Johnson) Schechter] ($2n = 48$), a species limited to the Big Hollow region of southern Wyoming was sympatric with Indian ricegrass ($2n = 48$) and *Piptatherum micranthum* (Trin. & Rupr.) Barkw. [= *Oryzopsis micrantha* (Trin. & Rupr.) Thurb.] ($2n = 22$). *Achnatherum contractum* arose from hybridization between these 2 species followed by backcrossing to Indian ricegrass and additional generations of selfing. Apparently, large *P. micranthum* chromosome segments were incorporated in the new species, reproductively isolating it from Indian ricegrass despite their common chromosome number. Hybrids between these 2 species were found, but all were sterile.

Natural hybridization has been important in the differentiation and success of the *Artemisia* subgenus *Tridentatae* (McArthur et al. 1988). McArthur et al. (1988) demonstrated the presence of a hybrid swarm located at the ecotone of 2 diploid populations of big sagebrush (*A. tridentata* Nutt.). Mountain big sagebrush [*A. tridentata* ssp. *vaseyana* (Rydb.) Beetle] was present at the top of a slope on a residual soil, and basin big sagebrush (*A. tridentata* ssp. *tridentata*) was present beneath the slope on an alluvial soil. Coumarin and monoterpenoid data indicated the plants occupying the colluvium site on the slope itself were of hybrid origin. Stable zones of hybrids between diploid mountain big sagebrush and basin big sagebrush can be found in a narrow elevational zone along Utah's Wasatch Front (Freeman et al. 1991, Graham et al.

1995). Measurements of many morphological traits indicated a consistent linear change in hybrid index value along an elevational gradient (Freeman et al. 1991).

Considerable hybridization and introgression have been observed between the bunchgrass basin wildrye [*Leymus cinereus* (Scribn. & Merr.) A. Löve = *Elymus cinereus* Scribn. & Merr.] and the rhizomatous beardless wildrye where they are sympatric in the northern Great Basin, despite sterility of artificial hybrids (Dewey 1970a). Another bunchgrass, giant wildrye [*L. condensatus* (Presl.) A. Löve = *E. condensatus* Presl.], naturally hybridizes with beardless wildrye in California (Stebbins and Walters 1949). Though artificial hybrids proved sterile, the natural hybrid and its introgressed derivatives are common from the San Francisco Bay area south to Monterey County. The success of this natural hybrid is attributed to its combination of rhizomatous spread, vigor, longevity, a low fertility level, and human disturbance. This naturally occurring complex has proliferated in environments where neither parent is found.

Based on comparisons of artificial hybrids and field material, introgression of bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve = *Agropyron spicatum* Pursh.] into thickspike wheatgrass [*A. dasystachyum* (Hooker) Scribn. var. *dasystachyum* = *Elymus lanceolatus* (Scribn. & J.G. Smith) Gould ssp. *lanceolatus*] and streambank wheatgrass [*A. riparium* Scribn. & J.G. Smith = *E. lanceolatus* (Scribn. & J.G. Smith) Gould ssp. *lanceolatus* var. *riparium* (Scribn. & J.G. Smith) Bowden] has led to the development of the awned grasses *A. albicans* Scribn. & J.G. Smith (= *E. lanceolatus* ssp. *albicans* Scribn. & J.G. Smith var. *albicans*) and *A. griffithsii* Scribn. and J.G. Smith ex. Piper [= *E. lanceolatus* ssp. *albicans* var. *griffithsii* (Scribn. & J.G. Smith) A.A. Beetle], respectively (Dewey 1970b). Repeated backcrossing to thickspike or streambank wheatgrass is likely responsible for increased fertility of the hybrid derivatives. The presence or absence of lemma awns and pubescence distinguishes these 4 taxa (Dewey 1969). Dewey (1970b) also presented evidence supporting the introgression of thickspike wheatgrass into bluebunch wheatgrass as the causal mechanism for introduction of rhizomes into some populations of this species.

These examples indicate that hybridization between taxa, compilation of taxa, and introgression into taxa have been and will continue to be important, naturally occurring mechanisms for generating new genetic material in rangeland plant populations, sometimes leading to speciation. Introgression ensures maintenance of genetic variability, which may be critical in adaptation to changing biotic or abiotic conditions.

Often hybridization leads to an evolutionary dead end. The species *Agropyron saxicola* (Scribn. & J.G. Smith) Piper was determined to be a sterile triploid hybrid, which commonly forms between bluebunch wheatgrass ($2n = 14$) and bottlebrush squirreltail ($2n = 28$) (Dewey 1964). Slender wheatgrass [*Elymus trachycaulus* (Link) Gould ex Shinners = *A. trachycaulum* (Link) Malte] X foxtail barley (*Hordeum jubatum* L.) (Boyle and Holmgren 1955), slender wheatgrass X spreading wheatgrass [*E. scribneri* (Vasey) M.E. Jones = *A. scribneri* Vasey] (Dewey 1963), blue wildrye (*E. glaucus* Buckl.) X big squirreltail (*Sitanion jubatum* J.G. Smith) and blue wildrye X bottlebrush squirreltail (Stebbins et al. 1946, Stebbins and Vaarama 1954), and basin wildrye X bottlebrush squirreltail (Dewey and Holmgren 1962) also commonly occur naturally, but are sterile hybrids.

Genetic pollution is more frequent in predominantly cross-pollinating than self-pollinating or apomictic taxa because of the former's greater gene exchange. While hybridization between native-site and nonnative-site genotypes can occur, resultant seedlings will be competitively disadvantaged compared to native-site seedlings unless the hybrids are more fit, the reverse of Linhart's (1995) outbreeding depression. However, hybrids well adapted in the short-term may not be well adapted in the long-term. Physical displacement by aggressive introductions of species not present on the native-site has been termed "biological pollution" (Howarth 1983). Native-site populations of long-lived perennials will not be displaced merely by introduction of nonnative-site material. The native-site population has the competitive advantage of being well-established, whereas the nonnative-site material must establish from seed. Therefore, the issue of genetic or biological pollution is most important for cross-pollinating annuals or short-lived perennials.

Some surprising situations with released plant materials have arisen in western North America. 'Appar' "Lewis flax" (*Linum perenne*) (Pendleton et al. 1993) and 'Shoshone' "beardless wildrye" [*Leymus multicaulis* (Kir. & Kar.) Tzvelev] (Asay and Jensen 1996) are not natives, as first thought, but are members of corollary introduced species instead. These introduced materials, recollected in the New World, performed so well in seeding trials compared to their native relatives that they were released as cultivars. Johnson and Mayeux (1992) refer to an alien species that functions as part of the natural vegetation as a "new native".

Obviously many viewpoints exist concerning the genetic integrity issue. As is common in science, collection of data may be straightforward, but their interpretation may stir controversy. The issue of genetic integrity is one that has been interpreted differently by various scientists and has been shaped by personal opinion as much as scientific interpretation. Both science and personal opinion are important in decision-making; thus, land managers should try to understand how these arenas interface rather than emphasizing one at the expense of the other.

FEASIBILITY FACTORS

Community Seral Status

After an initial strategy is identified, it must be interfaced with practical matters of feasibility (Fig. 1). The traditional Clementsian model of plant succession presumes a series of plant communities that replace each other, beginning with a pioneer community and ultimately reaching a stable climax community (Clements 1916). This model views the ecosystem as a "balance of nature", the so-called "equilibrium paradigm" (Pickett et al. 1992), and presumes that the ecosystem is closed, internally regulated, climatically equilibrated, generally devoid of human activity, and relatively static unless disturbed (Jackson et al. 1995). The contrasting "flux-of-nature" view (Johnson and Mayeux 1992, Jackson et al. 1995) or "nonequilibrium paradigm" (Pickett et al. 1992) presumes that ecosystems are open, greatly influenced by outside forces, capable of movement via a variety of multiple pathways, and inclusive of human activity, which is considered to be simply another natural disturbance. Emphasis is on the process rather than the end point, as in Clementsian thinking. Equilibrium may be included in this paradigm as a special case.

The state-and-transition model as applied to rangelands (Westoby et al. 1989, Friedel 1991, Laycock 1991) presents an alternate viewpoint of plant community changes, namely that environmental changes may be cataclysmic rather than gradual and that improvement from a degraded state requires crossing a threshold, not easily accomplished. Transitions may be induced naturally or by man and may represent favorable opportunities or undesirable hazards (Westoby et al. 1989). A state-and-transition model is used to explain why some abused rangelands do not recover following cessation of livestock grazing. Application of state-and-transition models to arid and semi-arid lands is gaining acceptance (Box 1992, Borman and Pyke 1994).

The seral position of revegetation species should be identified and considered in decision-making. For example, slender wheatgrass, blue wildrye (*Elymus glaucus* Buckl.), Canada wildrye (*E. canadensis* L.), and mountain brome (*Bromus marginatus* Nees) are short-lived perennials that typically do not persist in seedings on semi-arid sites. Successional position of semi-arid species is believed to be related to how they cycle N and P (Redente et al. 1992, McLendon and Redente 1994). Early-seral species, such as bottlebrush squirreltail, typically take less time following establishment to produce seed, while late-seral species, such as basin wildrye, may take several years to reach reproductive maturity. Many late-seral grasses, such as western and thickspike wheatgrasses and beardless wildrye, rely mostly on vegetative propagation and produce decreasing amounts of seed as stands age. Crested wheatgrass stands are extremely stable (Marlette and Anderson 1986), and seedling recruitment on undisturbed sites is believed to be minimal in the Columbia River Basin (Harrison et al. 1996). Some introduced species such as crested wheatgrass and smooth bromegrass (*Bromus inermis* Leyss.) may be considered "too competitive", but this probably is a reflection of their late-seral status. If a monoculture is undesirable on a late-seral site, multiple late-seral species of diffferent lifeforms should be seeded or transplanted.

Weed Invasion

A second feasibility factor is the potential for weed invasion or a pre-existing infestation (Fig. 1). A weed is "a generally unwanted organism that thrives in habitats disturbed by man" (Harlan and deWet 1965). Effective reproductive systems and seed dispersal mechanisms are 2 traits common to successful weedy colonizers (Baker 1965). High phenotypic plasticity and interspecific competition are also characteristics of successful weeds (Lewontin 1965).

We commonly think of weeds as being introduced. West (1993) emphasized that introduced species are not inherently threatening, but that their acceptability depends on how they fit into the ecosystem. Native species can also become weeds as a result of anthropogenic perturbation of ecosystems. The irony of these native weeds is that they were part of the ecosystem long before they became weedy. Predicting which species will become a weed and where is an almost impossible task.

Weed control alone is inadequate to curb large-scale infestations (Sheley et al. 1996). The objective should be to shift ecosystem dynamics toward a healthy and diverse plant community that will be weed-resistant because most niches are occupied. Such a community could be the "desired plant community" previously discussed. Sheley et al. (1996) term this ecological approach a "successional weed management system". It requires an understanding of disturbance, colonization, and differential species performance. Weeds often gain a foothold in patches created by disturbance, including roadsides. To guide succession in the desired direction, management techniques such as herbicide treatment, grazing, burning, prevention of weed seed introduction, biocontrol, manipulation of soil nutrients, and seeding may be employed. For example, introduction of ephemeral, early-seral species may influence soil properties to favor desired late-seral species.

Economic Limitations

The third feasibility factor involves an economic consideration of costs and benefits resulting from action or inaction (Fig. 1). Assuming restoration is technically feasible, the extent to which it can be accomplished depends on availability of funds, especially when competing with less-expensive projects. Restorationists, in particular, must think in terms of economic as well as ecological sustainability.

Rangeland seedings are expensive and are usually implemented only when other management options are unable to improve land condition. Moreover, the probability for failure is high on some sites with consequences that may be less desirable than if no action were taken. This is the primary reason why many rangeland rehabilitation and revegetation efforts have emphasized low-risk introduced species. Whether limited funds are to be disbursed to a few highly visible projects or to general efforts directed at controlling aggressive weeds, for example, is a matter of public policy. Many important projects are overlooked because of limited funding, while less critical projects are implemented because an agency has appropriated substantial funding for specific projects within its jurisdiction.

The size of a project and availability of plant material generally determine whether restoration is realistic (Belnap 1995). Ambitious restoration efforts may be expended on small-scale projects if local seed sources are available. For large-scale projects, especially for regions where the original flora is no longer present, restoration efforts may not be possible. The magnitude of financial investment required for large-scale projects usually discourages their implementation in favor of smaller, more manageable projects. In these large-scale efforts, use of introduced plant materials or generally available native-species cultivars may be the only feasible option when seeding is necessary. Monsen and McArthur (1995) advocate the use of the most effective rehabilitation species regardless of origin on sites where potential has been reduced by disturbance. Alternatively, for sites with intact soil topography and hydrologic function, they argue the management objective should be restoration to a natural state.

Following reconciliation of the initial strategy with feasibility factors, a desired community species array should be assembled (Fig. 1). To effectively implement an integrated approach for choosing plant materials, the ecological adaptation/genetic variation of the species available should be considered (Fig. 1).

ECOLOGICAL ADAPTATION AND GENETIC VARIATION

Ecotypes and Biotypes

The distribution of a species and its genetic variation depend on many variables. Edaphic features such as soil texture, fertility, and drainage are important. Average growing season temperature,

temperature extremes, and length of growing season also are important and are related to latitude, altitude, and topography. In addition, the average and extreme amounts and seasonal distribution of precipitation are critical and vary across the North American West, particularly with altitude and between coastal, Intermountain, and Great Plains regions. A species is considered ecotypic when its populations, termed ecotypes, tend to be adapted specifically to local conditions (Odum 1971) instead of exhibiting general adaptation throughout the species' range.

Some species display inherently more genetic variation than others (Knapp and Rice 1994). The presumption that a genotype will not perform well in an environment different from its native site is not as good a guide as experience. For example, Indian ricegrass is highly ecotypic, e.g., while typically found in areas of low precipitation, it also grows in saturated soils at the edge of Lesser Slave Lake, Alta. (pers. obs.). However, green needlegrass [*Nassella viridula* (Trin.) Barkw. = *Stipa viridula* Trin.], a relative of Indian ricegrass distributed throughout the Great Plains from Alberta to New Mexico, exhibits remarkably little genetic variation throughout much of its range (pers. comm., John G. Scheetz). Likewise, Apache plume [*Fallugia paradoxa* (D. Don) Endl.] shows minimal variation despite ranging from central Nevada and California to northern Mexico and west Texas (McArthur et al. 1983). Considerable genetic variation in western wheatgrass across latitude and longitude has led to the release of varieties from Kansas, Colorado, New Mexico, Nebraska, North Dakota, Montana, and Alberta (Asay 1995). Tall, erect, nonsprouting populations of antelope bitterbrush are not adapted to environments where fire is a factor, but short, decumbent populations may resprout following fire (Blauer et al. 1975). Lewis flax (*Linum lewisii* Pursh) populations differ greatly for longevity and seed dormancy (Kitchen 1994). Shadscale [*Atriplex confertifolia* (Torr. & Frem.) Wats.] from the cold desert regions exhibits multiple seed dormancy mechanisms, while warm-desert populations germinate more easily (Sanderson et al. 1990).

Ecologically distinct biotypes, genetically fixed variation within a population of a species, may broaden the population's adaptation to local conditions. For example, Indian ricegrass displays intrapopulation genetic variation for seed size, which is correlated with seed dormancy (Young and Evans 1984, Jones and Nielson 1996). We have found populations of squirreltail var. *longifolium* with early and late-maturing biotypes, also under genetic control, near Almont, Colo. and Colmor, N.M. (unpub. data). While the *Neotyphodium* endophytic fungus is present in most plants of most populations of robust needlegrass [*Achnatherum robustum* (Vasey) Barkw. = *Stipa robusta* (Vasey) Scribn.], some populations are predominantly uninfected (unpub. data).

In general, genetic variation varies only gradually across a species' geographical distribution in cases where the species exhibits traits such as cross-pollination, a continuous range, a long-lived perennial life history, or early-successional seral status (Millar and Libby 1989). Genetic variation among populations is greater in species that exhibit self-pollination, disjunct distributions, an annual or short-lived perennial life history, or a late-successional seral status. Gymnosperms often exhibit greater genetic variation among populations than angiosperms.

Chromosome Races

Chromosome races, results of either chromosomal rearrangements or polyploid increases in chromosome number, exist in several rangeland species and usually correspond to different ranges or habitats. Knowledge of the chromosome race adapted to the site can help identify preferred material for seeding. Standard tetraploid crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult.] arose by natural hybridization between 2 diploids, *A. mongolicum* Keng from the more arid lands of western Inner Mongolia and the "fairway" type, *A. cristatum* (L.) Gaertn., from the more mesic lands of eastern Inner Mongolia (Asay et al. 1992). Hsiao et al. (1989) demonstrated that these diploid species differed by a chromosome translocation, a structural rearrangement in which 2 chromosomes have exchanged segments.

Bluebunch wheatgrass may be diploid or autotetraploid, with the less common tetraploids adapted to mesic ponderosa pine (*Pinus ponderosa* Lawson) woodlands or shrubby grasslands in eastern Washington, northern Idaho, or southern British Columbia (Dewey 1984, Carlson 1986). Basin wildrye may be tetraploid or octoploid (Dewey 1984). Octoploids of basin wildrye, e.g., 'Magnar', are predominantly glaucous (blue), while tetraploids, e.g., 'Trailhead', are non-glaucous (green). Octoploids of basin wildrye predominate in southern British Columbia, eastern Washington, and northeastern Oregon, while tetraploids occur elsewhere in the species' distribution. Salina wildrye [*Leymus salinus* (M.E. Jones) A. Löve] may also be tetraploid or octoploid, but the distribution of the 2 races is unknown (pers. comm., Kevin B. Jensen).

Ecotypes of switchgrass (*Panicum virgatum* L.) are correlated with chromosome number and chloroplast genome. Lowland ecotypes are tetraploid ($2n = 4x = 36$) and upland ecotypes are mostly octoploid ($2n = 8x = 72$) (Hopkins et al. 1996), though both chromosome races were found together in 17 of 28 upland ecotype sites in 7 midwestern states (Hultquist et al. 1997). Lowland and upland ecotypes can also be distinguished by cytotype, designated as 'L' and 'U', respectively, as differentiated by restriction fragment length polymorphisms of chloroplast DNA (Hultquist et al. 1996). Upland plants are fine-stemmed, semi-decumbent, and with a spreading base. Lowland plants may be taller and are coarse-stemmed, erect, and bunched.

Keeler et al. (1987) reported hexaploid and octoploid plants of big bluestem (*Andropogon gerardii* Vitman) coexist, yet remain reproductively isolated. The 2 chromosome races were not distributed in any ecological pattern within a site (Keeler et al. 1987) and may be considered "functionally equivalent" (Keeler 1992). Populations with high frequencies of individuals greater than $6x$ were more common at the extremities of the species' range (e.g., Nebraska, Kansas, and Florida) than near its center (e.g., Iowa, Missouri, Illinois, and Ohio) (Keeler 1990, 1992).

Similar information for shrub species has been summarized by McArthur (1989) and Sanderson et al. (1989). Shadscale is an autoploid series ranging from diploid to decaploid, with tetraploids most common (Stutz and Sanderson 1983, Sanderson et al. 1989, Sanderson et al. 1990). Decaploids are tallest, followed by diploids, then tetraploids and octoploids; hexaploids are shortest. Diploid seedlings are shorter and more broad-leaved than polyploid seedlings. Diploids are often stratified above polyploids at the same site, which may correspond to levels above and below the surface of Pleistocene lakes. Polyploids are generally adapted to more xeric environments than diploids, and hexaploid and higher races are adapted to more saline environments than diploids or tetraploids.

Creosotebush is diploid with a low-growing, broad, compact growth habit in the Chihuahuan Desert; tetraploid with a tall, slender, open-growth habit in the Sonoran Desert; and hexaploid with an intermediate growth habit in the Mojave Desert (Yang 1970). Yang (1970) hypothesized that the hexaploid race arose from hybrids between diploids and tetraploids. The North American tetraploid was hypothesized to have arisen from hybrids between the North American diploid and a diploid from northern Argentina.

Douglas rabbitbrush [*Chrysothamnus viscidiflorus* (Hook.) Nutt.] is widely distributed in North America as an autoploid series of diploids, tetraploids, and hexaploids. In this species, however, chromosome number does not correlate closely with geographic variables among its 5 subspecies. Subspecies *viscidiflorus* may be found at all 3 ploidy levels, ssp. *lanceolatus* and ssp. *puberulus* are diploid or tetraploid, and ssp. *axillaris* and ssp. *planifolius* are strictly diploid (Anderson 1986). When they occur together, diploid populations of ssp. *viscidiflorus* are prevalent at cooler, wetter, higher-elevation sites than hexaploids with tetraploids intermediate. A similar relationship is present for ssp. *lanceolatus* with diploid populations occurring at higher elevations than tetraploids. Subspecies *puberulus* tetraploids, however, are found at higher altitudes than diploids, but this may be partly compensated by their increased frequency at lower latitudes. The diploid ssp. *axillaris* and *planifolius* are found in the warmer, drier portions of the species' range.

Fourwing saltbush is another widely distributed shrub in North America. While the most common var. *occidentalis* (Torr. & Frem.) Welsh & Stutz is autotetraploid, diploid and autoploid populations at 6*x*, 12*x*, 14*x*, and 20*x* levels occur (Sanderson and Stutz 1994). Polyploids are woodier, slower growing, and smaller statured than the diploid populations from which they are derived (Stutz and Sanderson 1979). Ploidy level has been correlated with soil texture in adjacent portions of southern New Mexico and west Texas (Dunford 1984). Diploids are found on sandy dunes, hexaploids occur in the medium to fine-textured soils of the Rio Grande flood plain, and the most common tetraploids are present in sandy dunes and heavier-textured mesa soils.

Big sagebrush (*Artemisia tridentata* Nutt.), the most abundant shrub in North America, has 5 major subspecies that are adapted to various combinations of precipitation level, altitude, and soil depth (McArthur 1994). Diploids are generally larger and faster growing than tetraploids (McArthur and Welch 1982). Populations of basin and mountain big sagebrush may be diploid or tetraploid, while Wyoming (ssp. *wyomingensis* Beetle & A. Young) big sagebrush is tetraploid with occasional hexaploid plants. Snowbank [ssp. *spiciformis* (Osterh.) Goodrich & McArthur] big sagebrush is diploid (pers. comm., E. Durant McArthur).

Broom snakeweed [*Gutierrezia sarothrae* (Pursh) Britt. & Rusby] may be diploid or less commonly tetraploid, but the 2 races occupy the same sites, range across a common distribution, and are not easily morphologically separated (Solbrig 1971). Despite their overall similarity, tetraploids display larger morphological features when compared with diploids from which they were derived.

Diploid and autotetraploid races of hopsage [*Zuckia brandegei* (Gray) Welsh & Stutz = *Grayia brandegei* Gray] can be distinguished phenotypically (Stutz et al. 1987). Diploids are primarily restricted to south-central Utah and northeastern Arizona, while the larger-statured tetraploids are found to the east, west, and north.

Germplasm Class

When deciding on a final seeding recommendation, the germplasm class of plant materials must be considered in concert with their adaptation. Seed of released cultivars has been most commonly used in the past because of its availability and reasonable cost. Several other options are available, however, for increasing intraspecific genetic diversity.

If the best match of plant material and site cannot be predicted, a seed mixture with a broad genetic base provides opportunity for on-site natural selection (Kitzmiller 1990). To increase genetic variation for self-pollinated species, seed from various genetically heterogeneous sources may be purchased and blended together in bulk mixture (Munda and Smith 1995). Seeding of defined, multiple biotypes may be sensible based on the characteristics of the ecosystem you are trying to emulate (Jones and Nielson 1996). For cross-pollinated species increased variation may be accomplished through the use of a multiple-origin polycross, the product of random intermating among genotypes from defined geographical areas (Millar and Libby 1989). Munda and Smith (1995) adapted the convergent-divergent plant breeding improvement scheme of Lonnquist et al. (1979) designed for maize (*Zea mays* L.). Populations from throughout the targeted range are intermated into 1 population at the single convergent location. Then this population is increased at several divergent locations simultaneously and equal amounts of seed of surviving plants are bulked between and within locations and intermated at the convergent location. This cycle may be repeated as many times as desired. The objective of this breeding scheme is to augment genetic variation and widen adaptation.

The use of local seed sources has been championed recently; while an expensive option, it is technically feasible (Beavers 1995). If the species is cross-pollinated and the stand is sparse, however, the few seeds that can be collected from distant plants will be mostly self-pollinated and suffer from inbreeding depression. When screened for allozymes across 14 polymorphic loci, the heavy seed fraction in a Scots pine (*Pinus sylvestris* L.) population from northern Sweden exhibited more heterozygosity than the light seed fraction (Szmidt 1987). He concluded that culling light seed would effectively reduce homozygosity in the population.

Cultivar release of material with a minimum of genetic manipulation following lengthy collection of supportive data is a long-standing practice with native species in the United States. Alternatives include any of 3 "fast-track" germplasm classes (source-identified, selected, and tested) of non-genetically manipulated certified seed. This certification process verifies county and elevation of a native-site collection that has not undergone genetic manipulation (Young 1994, 1995). Thus, this approach is of great relevance when a local seed source is desired.

The 3 germplasm classes range from low stringency (source-identified) to high stringency (tested). The source-identified class is not compared with other collections of the same species. The selected class is compared with other collections, and data are compiled. The tested class is progeny tested to assure that the desired traits that are observed are heritable. Most rangeland germplasms currently being released for commercial use are native grasses of the selected class. Release of materials as source-identified, selected, or tested germplasm is preferred compared to a traditional variety release when commercial seed sources are inadequate, specific ecotypes for restoration are needed, a high potential for immediate use is present, or commercial potential is limited to a small number of sites. Information regarding these germplasms is available through seed dealers specializing in native seed, state seed certification officials, or the USDA-NRCS Plant Materials Centers.

Ducks Unlimited Canada has adopted the "ecovar" (ecological variety) concept for development of native plant materials for revegetation (Wark et al. 1995). In recognition that seed yield, shattering, and dormancy are important for practical reasons, equal emphasis is placed on maintenance of a broad genetic base and improvement of seed-related characteristics. Ecovar development avoids rigid selection for genetic uniformity in favor of retention of a broad range of genetic potential.

Overview and Future Directions

Rehabilitation, reclamation, or restoration of rangeland may be required because of unwise resource use or disturbance due to fire, highway construction, mining, or erosion. Important components of the initial strategy include site potential, desired landscape, seeding objectives, and genetic integrity of the plant material that could be used in the seeding. Each aspect should be considered individually and in combination. Feasibility factors, including the potential for weed invasion, seral status of the existing plant community, and economic limitations, necessarily may limit certain aspects of the initial strategy. After the needs of the project have been interfaced with biotic, abiotic, and economic realities, appropriate plant materials should be identified. An understanding of the association between ecological adaptation and genetic variation of species targeted in the desired community species array should be considered in choosing appropriate plant materials. Released cultivars as well as bulks of genotypes, multiple-origin polycrosses, multiple biotypes, local seed sources, source-identified seed, and ecovars should all be considered when selecting plant materials.

Site-specific planning of seedings is important and should be encouraged. For this planning to be successful, however, it will need to meet the intended uses of the land, work within a realistic ecological framework, and recognize biological and economic realities, both opportunities and limitations. After an array of plant materials is assembled, technology to restore the site to the desired landscape should then be applied.

The concern that finely tuned genetic complexes may be disrupted by material collected distant from the site has been termed "genetic pollution". Hybridization and backcrossing among related cross-pollinating taxa, however, has long been recognized as a component of the naturally occurring evolutionary mechanism of introgression. Introgression between related cross-pollinating plant taxa generates novel genetic material, which natural selection can either mold into adapted gene complexes or discard. Alternatively, genetic pollution may have deleterious consequences, particularly with annual or short-lived perennial cross-pollinating species. For self-pollinating or apomictic plants, hybridization with off-site material will be less frequent. Native-site, long-lived perennials will generally persist *in situ* upon introduction of off-site material of the same species, regardless of mode of reproduction.

Genetic issues are important because seeded material must not become weedy; must be able to reproduce, recruit seedlings, and survive environmental fluctuations; and must be compatible with other ecosystem components, i.e., soil biota and terrestrial fauna (Belnap 1995). Degree of genetic variation varies greatly among species. Germplasm of some species is adapted across a wide range while that of others is much more site specific. When biotypes occur, their presence provides an argument for maintenance of fundamentally different genotypes on the same site. If chromosome races exist, their geographical distribution and site adaptation should be considered. Future research should be directed towards an improved understanding of the ecological adaptation of genetic variation in rangeland species and its interaction with other ecosystem components.

For seeding recommendations in the future, a multiplicity of materials featuring a variety of germplasm classes should be provided. However, lack of sustained demand for these products may limit their development. Demand will be influenced by project size and cost (Belnap 1995). These products must be profitable enough to attract the seed and nursery industry. If this occurs, we anticipate that the industry will continue to specialize in order to deliver many of the low-volume plant materials needed.

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