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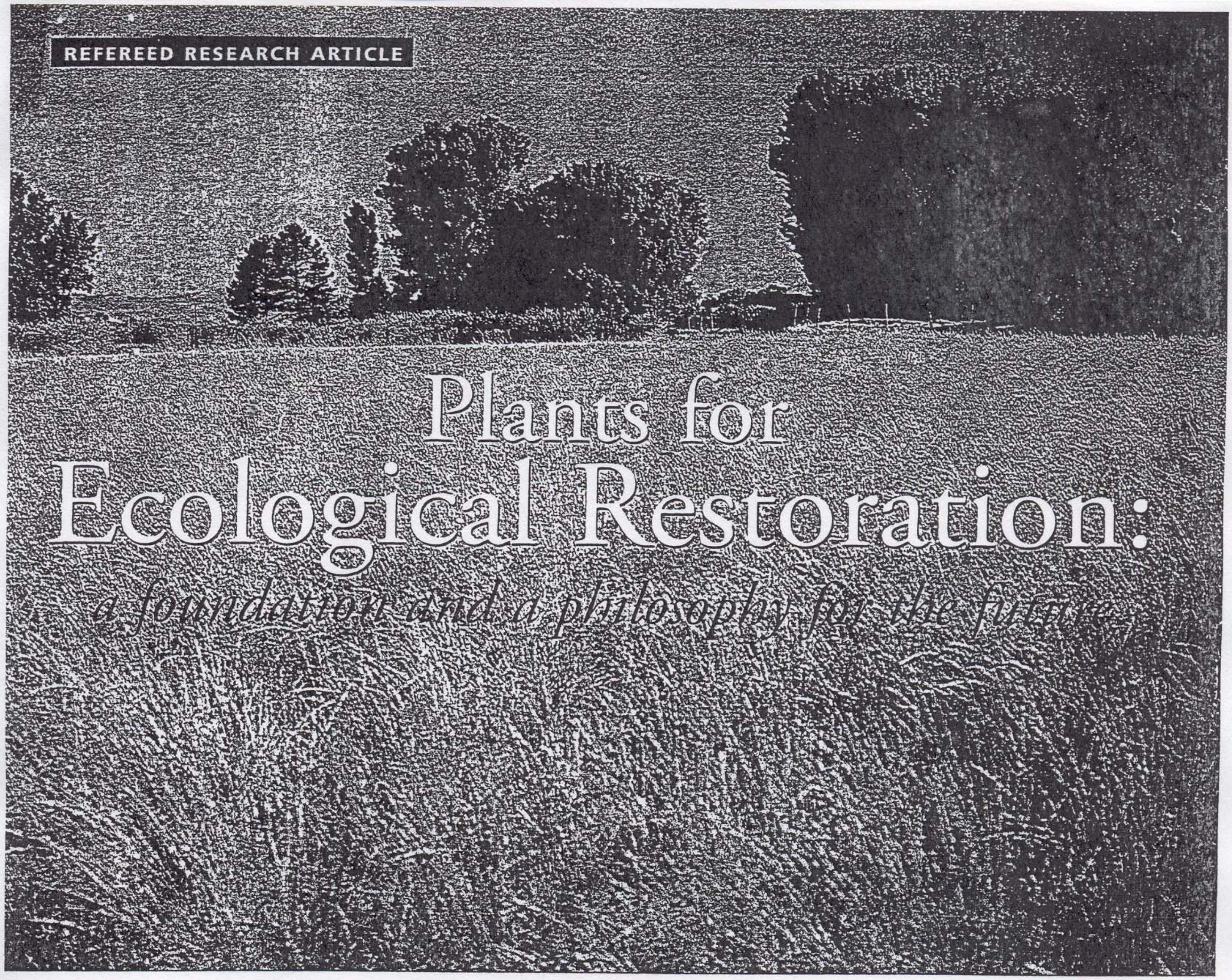

Plants for Ecological Restoration:

a foundation and a philosophy for the future

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ABSTRACT

Today's conservation concerns range from rare plant preservation to landscapes threatened by alien annuals. Effective action follows effective decision-making based on appropriately framed questions. We present the restoration gene pool (RGP) concept as a framework for choosing plant materials based on the priorities of the species, plant communities, systems, and landscapes threatened. We couch our discussion in an acknowledgment of 65 y of national plant materials progress that has evolved with society's priorities and has maintained a high degree of cooperation among participating entities. The plant materials program and its cooperators have contributed the bulk of the material and technology now used in ecosystem restoration and are our foundation for meeting conservation challenges of the future. Using a discussion of the genetics of native plant materials and 2 conservation challenges, we illustrate how the RGP concept can be used to select plant materials based on their ability to meet priority concerns.

*Genetic diversity in cross-pollinated native plants may be achieved by using broad-based populations. This field of P-7 bluebunch wheatgrass (*Pseudoroegneria spicata *(Pursh) A. Löve [Poaceae]) is an example of a multiple-origin polycross.*

KEY WORDS: gene pool, evolution, reclamation, conservation, restoration gene pool

NOMENCLATURE: USDA NRCS (1999) or cited literature

In the sense of ecological restoration, "native," refers to species existing in America when European settlers arrived and often implies sustainability (WDEQ 1994). Native plants are presumed to be adapted to their native sites and fully capable of reproduction on those sites. However, changes in local environments can prevent natural recruitment; ignorance, inexperience, seed cost and availability, or inadequate tools may interfere with effective re-establishment. In this paper we review past use of native plants for conservation and changes in social expectations that have influenced those plant materials choices. We also discuss the importance of ecotypic evolution to restoration efforts. We review some pressing conservation needs, then culminate our discussion by presenting the "restoration gene pool" (RGP) concept as a framework for choosing suitable restoration plant materials. The last 3 decades have produced an abundance of new knowledge about native plants and their environments. We are now responsible for logically applying that knowledge in environmental-management decisions. We believe the RGP concept will help us more effectively discharge that responsibility.

NATIVE PLANTS IN CONSERVATION: AN ACKNOWLEDGMENT

The ability of our native plant industry to respond to the growing demand for seeds has been largely due to our National Plant Materials Program that began with the USDA Bureau of Plant Industry nurseries, renamed Plant Materials Centers (PMCs) in 1954 (Norris 1989). The nurseries, a federal response to the Dust Bowl, were established in 1935 for the purpose of returning native grasses to plowed prairies and denuded rangelands (Norris 1989; Helms 2000). From inception, the plant materials program has been a cooperative effort with 137 cooperating entities in the US and Canada having participated in the development and release of plant materials (Meyer and others 1995). Cooperating entities include other federal agencies such as the Agricultural Research Service and the Forest Service, and state agricultural experiment stations, highway departments, resource management agencies, conservation districts, and universities. The program's first releases (1939 to 1942) were all species native to North America (Meyer and others 1995).

Social priorities of the time were soil conservation and production and it was soon evident that introduced species were meeting these objectives better than natives. The 1943 releases of 'Fischer' and 'Manchar' smooth bromegrasses (*Bromus inermis* Leyss. [Poaceae]) were the first of a succession of introductions. Introduced material comprised nearly two-thirds of all PMC releases through 1970 and were effectively used with the existing technology to meet the conservation and social objectives of the post-World War II era (Table 1).

TABLE 1

USDA plant material releases by time period, native (N) or introduced (I), and life form (adapted from Meyer and others 1995)

Life form	Time period							
	1934 – 1950		1951 – 1970		1971 – 1990		1991 – 1994	
	N	I	N	I	N	I	N	I
Grasses	15	20	23	36	58	16	15	8
Forbs	0	4	4	12	16	20	7	6
Woody plants	0	0	0	2	41	19	14	1
Totals	15	24	27	50	115	65	36	15
% Native	38		35		64		71	

Beginning in the 1970s and continuing into the 1990s, mining and other drastic land disturbances stimulated a growing concern for ecological restoration. Greater emphasis was placed on the value of plant community structure, diversity in species and life forms, and importance of diversity to secondary functions like seasonal food and shelter for native fauna. The new objective was restoration of all ecosystem functions and new social priorities emphasized native plants. PMCs responded to that emphasis (Table 1).

The plant materials program is now implemented by 26 PMCs across the nation and operated by the USDA Natural Resources Conservation Service and cooperating agencies and institutions (Gibbs 1995). During the last 3 decades of disturbed-land reclamation, PMC products have served us well. For example, 64% of the seeds used through 1994 by Wyoming's abandoned mineland reclamation program were of PMC releases (Richmond 1995). This does not appear to be atypical (Bucknam 1995). Releasing plant material compels an associated development of technology for planting, growing, harvesting, and processing seeds of the releases. Our national plant materials program has provided the major part of the knowledge, plant resources, and seed technology now being used in ecosystem restoration. We therefore acknowledge the program's contributions and call attention to its potential for cooperative work addressing today's conservation concerns.

TODAY'S AGENDA— GENE POOLS AND LANDSCAPES

Evolution in Action

Plant species often have ecotypes that have evolved in response to specific local conditions (Meyer and others 1989; Meyer and Monsen 1990; Booth and Haferkamp 1995; Jones and Johnson 1998; Bai and others 1999). Such habitat-correlated variation is evidence that natural selection may define or refine inherited characteristics which influence a population's ability to persist in the face of local or site-specific stresses. That wild-plant populations differ among locations has been regularly acknowledged in the literature and in recommendations for revegetation of disturbed areas (Thompson 1975; Gabriel 1981; Meyer and Monsen 1990; Pfannenstiel and others 1993). Sosebee and Wester (1995) wrote "In view of the accumulating information on ecotypic and polymorphic variation, ecologists can no longer regard all plants or populations of plants within a species as uniform. This view has implications in all areas of applied ecology." Today, that seems a profound understatement.

Local genotypes are likely to be most tolerant of local stresses. However, ample evidence indicates that non-local genotypes can flourish if they are adapted to the environment to which they are introduced. The utility of this practice has been documented by a survey of shrub seedings on 14 western reclaimed coal-mine sites. All sites were reclaimed for more than 10 y and had been seeded to mixtures of grasses and shrubs. In no instance do records indicate seeds were collected at or near the mine, but seedings have restored fundamental ecosystem functions and maintained acceptable levels of structural and species diversity (Gores 1995; Booth and others 1999). This and other evidence indicates that seeds collected from habitats where environmental challenges are similar to those of seeding areas can be used to successfully return a species to a disturbed site (Clary and Tiedman 1984; Geist and Edgerton 1984; Krzyszowska-Waitkus and others 2000; Vicklund 2000; Waage and others 2000). Plants and plant communities are in a constant process of selection and change (Johnson and Mayeux 1992). Harper (1977) writes "In many of the attributes that contribute to success within a population of neighbors, differences among populations within a species may indeed be greater than between species." Such interpopulation variance has been documented for germination characteristics of rabbitbrush (*Chrysothamnus* sp. Nutt. [Asteraceae]), sagebrush (*Artemisia* sp. L. [Asteraceae]), and winterfat (*Eurotia lanata* (Moq.) Pursh [Chenopodiaceae]; syn. *Krascheninnikovia lanata* [Pursh] Guldenstaedt.)(Meyer and others 1989; Meyer and Monsen 1990; Bai and others 1999). Harper (1977) further observed that " . . . the force of natural selection taken together with the estimates of high heritability of ecologically important attributes that are obtained by agronomists and others for plants brought from the wild, force the ecologist to treat natural populations as evolving systems . . . . Ecology is concerned with evolution in action . . . ."

"Ecological stowaways began to arrive with the earliest settlements."

- Aldo Leopold

Stutz (1982) recognized this when he recommended plant products selected for use on disturbed lands must be genetically rich in order to accommodate the array of existing environmental variables and also the new variables which are certain to appear as the habitat itself evolves. Stated in other words, seed mixtures should provide the basis for the physiological diversity needed to respond to environmental challenges. Diversity is a foundation from which stress defines the characteristics contributing to species sustainability. (Note that disturbed sites represent the majority, if not the totality, of sites where native materials are propagated.)

Genetic diversity may be achieved by using broad-based populations that have reproduced in various environments (Munda and Smith 1995) or by using seed-source bulks of a species or a group of closely related species (Stutz 1989; Munda and Smith 1995; Stutz and Estrada 1995). Both methods appear effective (Stutz and Estrada 1995). The recent development of P-7 bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve [Poaceae]) is an example of a multiple-origin polycross. It was generated by intermating 25 populations originating from 6 northwestern states and British Columbia (Larson and others

2000). The polycross-1 (PX_1; first intermating) and PX_2 (second intermating) generations will be maintained by the USDA Agricultural Research Service. Sale of P-7 seeds beyond generation PX_3 will be expressly prohibited to minimize dilution of plant-to-plant diversity that results from additional generations of intermating. Native Plant Solutions, a subsidiary of Ducks Unlimited Canada, is emphasizing "ecovars," selections of native plant species developed with equal emphasis on genetic breadth and agronomic characteristics (Wark and others 1995).

Challenges

Given the dynamic nature of plant populations and our increasing knowledge of genetics and evolution, how can we best meet today's environmental challenges?

The Challenge of Cheatgrass

One of the most serious conservation challenges we face is invasion of western shrublands, particularly sagebrush steppe, by alien annual grasses (Leopold 1980; Monsen and Kitchen 1994). Throughout the twentieth century, cheatgrass (*Bromus tectorum* L. [Poaceae]), or "cheat" for short, has invaded and endangered sagebrush communities by generating flammable understories (Leopold 1980; Monsen and Kitchen 1994). Cheat reduces productivity of mature native plants (Melgoza and Nowak 1991) and interferes with native plant recruitment. Although burned rangelands proximal to the mountain brush zone may recover (Ratzlaff and Anderson 1995), the more xeric sagebrush communities often deteriorate into cheat monocultures (Monsen and Kitchen 1994)(Figure 1). Our most successful defense to date has been introduced perennial grasses which co-evolved with cheat in Eurasia. Because they stay green longer into the growing season and are less likely to carry fire, they protect remaining shrub stands and return some diversity to burned landscapes (Pellant 1994).

Cheat is nearly ubiquitous in the West; particularly so in the California Mediterranean plant communities and in the interior sagebrush steppe. The possibility exists that genetic variation for competitive ability against cheat is present in native species populations. There is, however, a paucity of information on this subject and more investigations should be initiated to determine the salient traits for cheatgrass tolerance. A possible experimental approach is as follows: 1) assemble accessions from throughout a species' distribution, noting any that seem particularly tolerant of cheatgrass; 2) collect "passport" data for the site of each accession, that is, soil pH, texture, organic matter, and electrical conductivity; associated plant species; site aspect and slope; latitude and longitude; precipitation; temperature; 3) evaluate the accessions for a battery of physiological and morphological traits suspected to be related to cheatgrass tolerance; 4) use multivariate statistical techniques to define suites of correlated traits and to cluster similar accessions into discrete qualitative groups or, failing in this, to define a quantitative algorithm by which individual accessions may be compared; 5) verify the pertinence of specific trait(s) by comparing populations contrasting for the said trait(s) for competitive ability with cheatgrass; 6) validate specific accessions for high competitive ability with cheatgrass; 7) deposit samples of seeds of accessions (or bulks across homogeneous accessions as revealed in item 4 above) in the National Plant Germplasm System (NPGS 2000) and their passport data in the Germplasm Resources Information Network (GRIN 1999) for posterity; and 8) integrate items 2, 5, and 6 above with relevant abiotic variables such as fire treatments, herbicide applications, climatic regimes, soil characteristics, and micro-environmental features in designed field experiments.

If genetic variation for cheatgrass tolerance exists in native plant germplasm, then that germplasm should be conserved. Fire, or grazing that prevents natural seed dispersal, may be removing seeds and seedlings of populations that possess cheat tolerance. Fire in particular continues to extirpate cheat-infested native species populations. Each loss is a loss of native genetic material that potentially may have developed some tolerance to cheat.

About 1948, Aldo Leopold (1980) noted a hopeless attitude toward cheat. He wrote, "There is as yet, no sense of pride in the husbandry of wild plants and animals, no sense of shame in the proprietorship of a sick landscape." That is no longer true. The current danger is that in our zeal to culture native plants, we overlook biological realities. Our management policies must recognize the reality of cheat's current competitive dominance (Harris 1977; Melgoza and Nowak 1991; Nasri and Doescher 1995a, b), as well as the potential for discovery of cheat-tolerant genotypes of native species. Protecting remaining native-plant populations must be our first sagebrush-steppe priority.

Conserving Rare Genotypes

A broadening of gene pools among natives threatened by cheatgrass and other environmental challenges will increase the odds of ultimate success. However, we recognize that broader gene pools may also pose a risk of hybridizing, and thus compromising, rare plant genotypes.

Both challenges reviewed above—the loss of sagebrush steppe landscapes to cheat and conservation of rare genotypes—illustrates the breadth of conservation challenges and the respective decisions that must be made and implemented in future resource management. It is to the decision-making process of future management that we wish to address the remainder of our paper.

SELECTING PLANT MATERIALS FOR ECOLOGICAL RESTORATION

The mental structures people create to make organized decisions are called "frames." Frames keep complexity within the dimensions that our minds can manage and no one, not even the greatest genius, can make a rational decision without framing (Russo and Schoemaker 1989). Russo and Schoemaker continue, "But beware: Any frame leaves us with only a partial view of the problem. Often people simplify in ways that actually force them to choose the wrong alternatives." For restoration purposes, stereotyping plant materials into the traditional native-introduced dichotomy may be a simplification that forces sub-optimal choices. To avoid over-simplified frameworks we suggest using the restoration gene pool (RGP) concept when selecting plant materials for ecological restoration.

RESTORATION GENE POOL

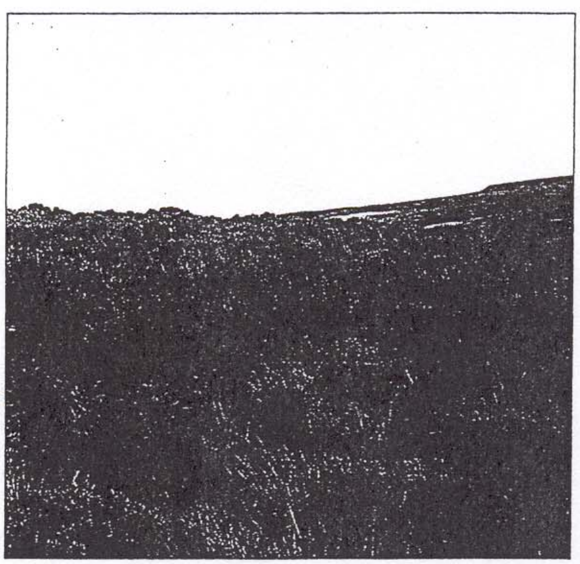
The RGP concept divides plant materials corresponding to a particular target population into primary, secondary, tertiary, and quaternary restoration gene pools based on their relationship to the target. This concept was converted from a scheme devised by Harlan and de Wet (1971) that categorizes genetically improved germplasm. The RGP concept works as well for noncultivated species for restoration as does Harlan and de Wet's scheme for cultivated species.

The primary RGP pool includes germplasm genetically identical to the population of interest as a result of proximity and genetic connectivity, that is, the metapopulation (Table 2). Catalina Island mountain mahogany (*Cercocarpus traskiae* Eastw. [Rosaceae] (also, *C. betuloides* Nutt. var. *traskiae* (Eastw.) Dunkle. [C.T. Eastw.] (Munz and Keck 1968)) has declined to 7 adult trees on the southwest side of Santa Catalina Island (Los Angeles County, California) as a result of grazing by introduced herbivores (Rieseberg 1991). Ecological restoration has involved the use of plants from the primary RGP, that is, rooted cuttings from surviving trees. This approach is feasible because of the small area involved.

The secondary RGP, which circumscribes the traditional biological species aside from the target population, is geographically isolated from the target population (lower in "identity"), but it may remain sufficiently adapted to the target site. Two examples are a polycross with relatively high genetic variation, and single-site populations with relatively low genetic variation (Table 2). Single-site populations originating from sites with climatic parameters similar to the site of interest are candidates for restoration at the secondary RGP level. Presently this is the predominate choice for most commercial ecological restoration. It is this application of the secondary RGP (single-site populations) that has prompted some western state crop improvement associations to develop programs for "source-identified seeds" (Young 1995).

The tertiary RGP includes germplasm of taxa intimately involved with the evolution of the species of interest, but genetically isolated from the modern gene pool of the target population by such mechanisms as hybrid sterility or polyploidy. The quaternary RGP includes taxa at most distantly related to the species, but that may serve as substitutes for the

Figure 2 • Left to right: A healthy sagebrush steppe community in the western US. Cheatgrass invades the sagebrush community. Highly flammable cheatgrass creates high-intensity conflagrations that sagebrush is unable to survive. The result is a cheatgrass monoculture.



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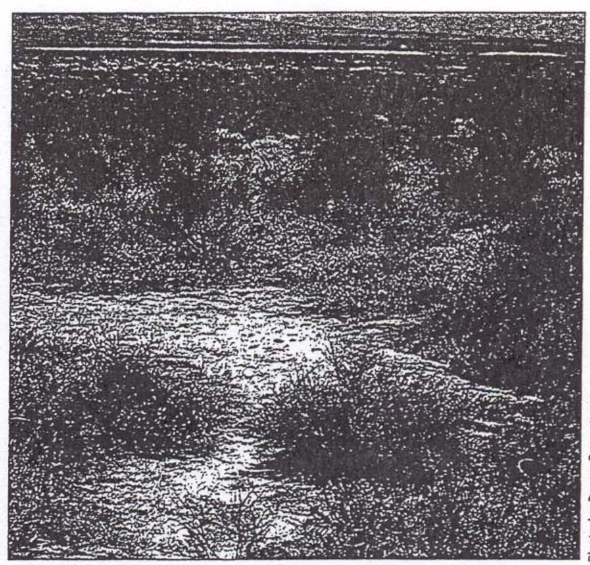

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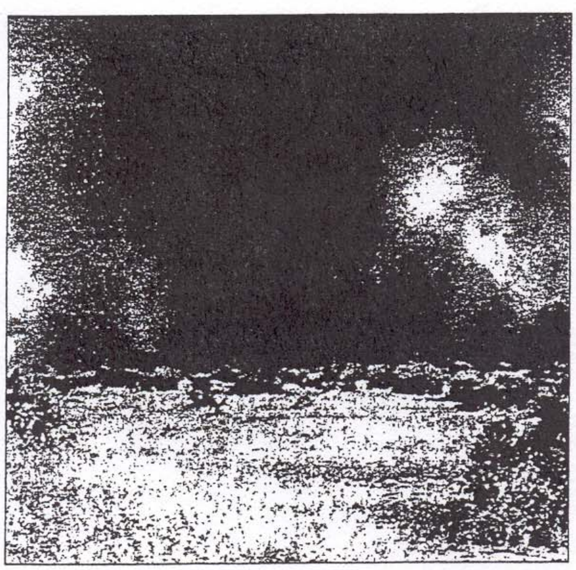
target population in respect to ecosystem structure and function. It may be implemented when primary, secondary, and tertiary RGPs are inadequate, at least initially, to succeed under strenuous conditions, for example, the cheatgrass challenge.

Recognition of diversity within species and coenospecies (the set of populations, some perhaps extraspecific, which are interfertile) raises questions regarding how we should conserve existing rare genotypes given the myriad of challenges to native ecosystems. Conservation priorities will differ by circumstance and problems. One may be concerned that non-local material introduced to a site will not grow or reproduce, and therefore will not contribute to community structure or diversity. An alternative concern may be that non-local material will grow, reproduce, and by hybridizing, contaminate the local gene pool, that is, outbreeding depression. (This concern is limited to cross-pollinating annuals and short-lived perennials [Jones and Johnson 1998]). By identifying conservation priorities and target populations for a particular situation, resource managers can then use the RGP concept to logically frame questions about available plant materials, financial resources, and long-term resource management.

If a site to be restored has not been so disturbed in either a biotic or abiotic manner to significantly alter ecosystem structure and function, the restorationist's goal should be to approximately match the target for both mean and variance for as many ecologically significant traits as possible. Operating from the RGP concept, the restorationist will judge a material's adaptation; ideally, adaptation must be both centered (matching mean) and robust (matching variance). Brown and Amacher (1999) point out that adaptation is not merely a unit of measure (mean), but also a physiological range of tolerance (variance). Robustness of a population refers to its "buffering capacity." Buffering capacity may be a consequence of: 1) phenotypic plasticity of individuals, the ability of an individual to morphologically or physiologically respond to an array of environments (Coleman and others 1994; Silvertown 1998); or 2) the direct result of genetic variation among individuals within the population.

All too often, sites targeted for revegetation have been so disturbed that the original structure and function have been destroyed. Under such circumstances, matching the target for both mean and variance may be inadequate. Plant materials may require more consistent germinability, greater seedling vigor, increased seedling recruitment, and greater tolerance to stresses such as competition for water, light and nutrients, or to herbivory or fire, that is, "greater" means. These are biologically valid reasons for looking beyond the primary RGP. There are also valid technological reasons for looking beyond the primary RGP.

Ideally, one would match the genetic diversity of the target population both quantitatively and qualitatively in the restoration plant material. In practice, the genetic diversity of the target population may be unknown, particularly if it has been extirpated. Even when the target population is not extirpated a presumption of low genetic diversity based on gross morphology may be misleading. Consider the self-pollinated and morphologically homogenous 'Rimrock' Indian ricegrass (*Achnatherum hymenoides* (Roemer & J.A. Schultes) Barkworth [Poaceae]). Although this material has little visible plant-to-plant variation, Jones and Nielson (1999) have found great variation for seed dormancy within the cultivar. In both situations—the extirapated population and the apparently homogenous population—the restorationist would be well advised to look beyond the primary RGP to a secondary RGP source that will provide broader genetic resources needed for long-term success (Stutz 1982, 1989).



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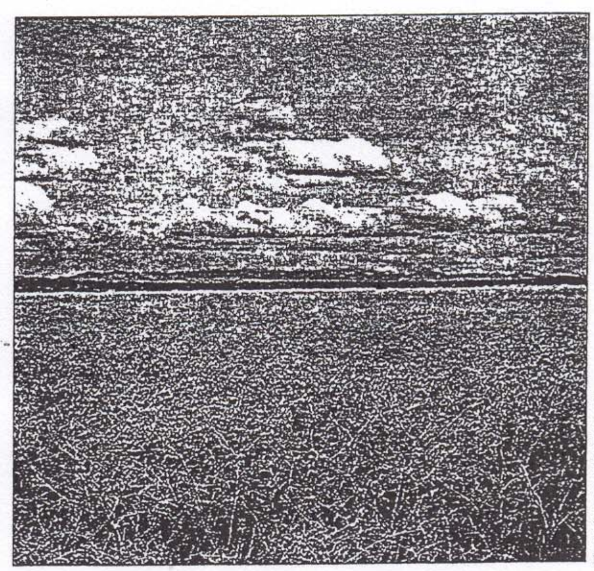

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TABLE 2

Tabular characterization of the restoration gene pool concept

		Relationship of restoration gene pool to target		
Germplasm source	Restoration gene pool	Taxon	Genetic identity	Ecological adaptation
Single (target) site or multiple sites genetically connected to target site [a]	1°	same	very high	high
Multiple sites throughout distribution (multiple-origin polycross) [b]	2°	same	moderate	moderate
Cultivars of single-site origin [c]	2°	same	low	subject to testing
Closely related taxa, including native and introduced material hybridized to target taxon [d]	3°	closely related	very low	subject to testing
Introductions [e]	4°	distantly related	dissimilar	very high

Examples using bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love):

[a] Material from any single location or from multiple connected locations with genetically identical material.
[b] P-7 (a population generated using 1 tetraploid and 24 diploid populations from 6 states (US) and British Columbia, Canada).
[c] The cultivars Whitmar and Goldar which were developed from single native-site populations.
[d] The tetraploid race of bluebunch wheatgrass or hybrids such as *P. spicata x Elymus lanceolatus* (North American native)(Asay and others 1991b) or *P. spicata x Elymus repens* (introduced)(Asay and others 1991a).
[e] Successful introductions such as crested wheatgrass (*Agropyron desertorum* (Fisch. ex Link) Schult; or, the distantly related Snake River wheatgrass (*Elymus wawawaiensis* J. Carlson & Barkw.).

Conservation of an ecological site is a different conservation objective from conservation of a species or genotype and proper use of the RGP concept requires differentiation and prioritization among these types of conservation objectives. Some restorationists have argued that "the very worst option is to use seeds from very far away" (Linhart 1995); such concerns are termed "outbreeding depression" (Linhart 1995) or "swamping" (Knapp and Rice 1994). While their validity varies tremendously with distribution of genetic variation and life history of the species concerned, they do point to the necessity of off-site germplasm conservation, that is, conservation for posterity in a gene repository, in addition to on-site conservation. On-site conservation is the preferred approach by many ecologists because evolutionary processes may continue unimpeded. Our contention is that off-site conservation is an underutilized stopgap measure that is able to mitigate losses when on-site conservation fails through biotic or abiotic disturbance, and is a means for preserving the option to use the primary RGP.

Germplasm threatened by outbreeding depression or swamping can, and should, be collected for long-term off-site storage. The National Plant Germplasm System (NPGS 2000) is an appropriate repository for this sort of material. While small-scale seed increase for restoration may be impractical on large-acreage projects, it is rapidly becoming a cottage industry that is responding to small-scale specific needs. The USDA Forest Service (Region VI) and The Nature Conservancy have taken the lead in contracting with seed producers to do off-site seed increases for on-site implementation (Jones 2000). Small-scale seed increase requires the economic incentive necessary to attract seed growers to produce relatively small volumes, but this is an industry niche that is particularly attractive to the smaller seed companies.

An effort to encourage and coordinate the deposits of such small-scale seed-increase germplasm in the NPGS should be made. This could be accomplished by seed certification officials dealing with source-identified seeds (Young 1995) by requiring the deposit as a precondition for issuance of certification tags. Over time, this would partially obviate the need for cumbersome seed collecting expeditions on the part of the research or land management sectors, allowing them to concentrate their resources on the most threatened material. In practice, certification is generally not sought in contract grow-outs. Rather, it is more common when a seed grower or company wishes to offer specialty items in their product line. But the practice of routine NPGS deposit could be encouraged among restorationists by making it a professional obligation. Stored germplasm would then be available for future restoration needs as primary or secondary RGP material.

SUMMARY AND CONCLUSIONS

We have looked toward the future with an acknowledgment of past accomplishments. The cooperative efforts which have embodied our national plant materials program have contributed the bulk of the material and technology now used in ecosystem restoration and are a foundation upon which future work can be based. The complexity of today's natural resource challenges suggests the need for effective plant-material choices that will put measurable conservation on the ground. Each problem requires its own solution based on the priorities of the species, plant communities, systems, and landscapes that are threatened. We offer the RGP concept as a format for logical application of all acquired knowledge of ecotypic evolution, genetics, and plant materials. We believe that instead of asking if a plant is native, the questions should be:

- What are the conservation concerns and why?
- What is the relative importance of these concerns and why (priorities)?
- What plant materials will most effectively meet the priority concerns?
- How closely related are these plant materials to the target populations and what interactions are likely to occur among local and seeded populations?
- What are budgetary and technical considerations related to the situation?
- Given the above, what plant material will best address first-priority concerns?

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