
The Restoration Gene Pool Concept: Beyond the Native Versus Non-Native Debate

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Abstract

Restoration practitioners have long been faced with a dichotomous choice of native versus introduced plant material confounded by a general lack of consensus concerning what constitutes being native. The “restoration gene pool” concept assigns plant materials to one of four restoration gene pools (primary to quaternary) in order of declining genetic correspondence to the target population. Adaptation is decoupled from genetic identity because they often do not correspond, particularly if ecosystem function of the disturbed site has been altered. Because use of plant material with highest genetic identity, that is, the primary restoration gene pool, may not be ultimately successful, material of higher order pools may be substituted. This de-

cision can be made individually for each plant species in the restored plant community in the scientific context that ecosystem management demands. The restoration gene pool concept provides a place for cultivars of native species and noninvasive introduced plant material when use of native-site material is not feasible. The use of metapopulation polycrosses or composites and multiple-origin polycrosses or composites is encouraged as appropriate. The restoration gene pool concept can be implemented as a hierarchical decision-support tool within the larger context of planning seedings.

Key words: genetic adaptation, genetic identity, metapopulation, multiple-origin polycross.

Introduction

Uncertainty is often characteristic of the decision-making process when plant materials must be chosen for restoration. When one or more elements of the disturbed ecosystem are dysfunctional or missing altogether, description of pristine form and function is usually speculative. The primary objective of ecological restoration is “the reinitiation of natural succession that will lead to the reestablishment of ecosystem form and function” (Brown & Amacher 1999). Following this logic a “native” is fundamentally whatever contributes to this end.¹ Although native material may be preferred by the restorationist (Lesica & Allendorf 1999), whether material is native or not is a matter of scale (is it native at the species, race, or population level?) as well as a matter of adaptation, that is, ecological (does it interact with the biotic and abiotic elements of the ecosystem as it did before disturbance?) and physiological (what are its tolerance limits?) (Brown & Amacher 1999). Because no unambiguous answer can be offered to the question of what is native, these authors even suggested abandoning the use of the terms “native” and “introduced,” but they doubted that even that radical step would lead to a conceptual improvement. Here I attempt to make that conceptual improvement through delineation of what I term “restoration gene pools” (RGP).

Genetic Identity Versus Adaptation

To begin this discussion I define genetic identity and genetic adaptation. Nei (1972) measures the genetic identity between two populations on a scale from 0 to 1. If the genetic identity of populations X and Y is 1, then they have identical alleles with identical frequencies, that is, they are genetically synonymous. If their genetic identity is 0, they have no alleles in common at any locus, that is, X has one or more alleles at each locus, all of which are different from Y's alleles at each locus.

For a plant population to be *adapted* to a site, it must be able to persist and reproduce on the site and its progeny likewise. Brown and Amacher (1999) asserted that adaptability is defined by a *physiological range of stress tolerance* defined by genotype. It reflects the ability of the plant to adjust to a fluctuating environment by structural modification and physiological adjustment (Conrad 1983). Therefore, adaptability is not a unit of measure per se.

To understand the RGP concept one must first understand that maximizing genetic identity between the target plant population and the restoration plant material does not necessarily maximize genetic adaptation. Considering a target population from a particular site, a broad sample of seed taken from that site can be considered essentially genetically representative of the target, that is, their genetic identity approaches 1 except for sampling error. A sample of seed of the same species from a site genetically connected to the target site via pollen transfer or seed dispersal also has a relatively high genetic identity with the target site. Genetic identities of local populations disconnected from the target site may be lower but likely not as low as populations subjected to altogether different selec-

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¹Professionals in plant-related field tend to define “native” less strictly than the lay public (Smith & Winslow 2001).

tion pressures. And such populations of the given taxon have higher genetic identity to the target site than separate yet closely related taxa, which in turn have higher genetic identity to the target than disparate taxa.

This is not to say that the genetically connected population is better genetically adapted than the disparate taxon. Indeed, it is commonly experienced that unrelated taxa from a different hemisphere may have superior genes for adaptation to an *altered* site (and sites targeted for restoration are always altered). The primary objection to such a taxon is that it is not native; hence the long-standing emphasis on the native/non-native dichotomy. However, this is an issue of genetic identity rather than genetic adaptation.

My point is that although we may prefer high genetic identity for restoration in theory, use of this material may be problematic in practice. This may be because the material of choice is unavailable, is difficult or expensive to propagate, or is no longer adapted to the altered environment. When any of the above hold, and we should be alert for such circumstances, we should act on alternate possibilities *without apology* because inaction may be even less desirable than implementing an action other than the preferred alternative (Jones 1997). Lesica and Allendorf (1999) pointed out that choice of the correct strategy depends on understanding trade-offs. The restoration practitioner must attempt to understand the degree and pattern of genetic variation for the target species, which can be thought of as its “genetic personality.” The correct approach, that is, the choice of which RGP (as described below) to use, depends on the target species itself and on the target environment.

An Introduction to the Concept

Here I adapt a concept developed for the discipline of breeding of cultivated plants for use by the discipline of restoration ecology. Harlan and DeWet (1971) defined the primary gene pool as the biological species, that is, all materials that easily cross, generating offspring with approximately normal fertility and segregation in succeeding generations. Harlan and DeWet’s secondary gene pool included all other biological species that have significant genetic incompatibility barriers to crossing but may cross with the primary gene pool under natural, albeit exceptional, circumstances. This “greater species” is termed a coenospecies (Clausen et al. 1939). Harlan and DeWet’s tertiary gene pool includes taxa that may be crossed with the species of interest but only through extreme measures that would probably occur at most rarely in nature. The tertiary gene pool is not a taxonomic unit but defines the extreme outer limits of the gene pool potentially useful to the plant breeder, albeit only with extraordinary artificial effort. Harlan and DeWet’s concept can be adapted for restoration. However, for restoration the primary and secondary RGPs encompass the same taxon as the target population, whereas taxa represented in the tertiary and quaternary RGPs are distinct from the primary RGP taxon.

The RGPs are ordered from primary to tertiary in descending level of genetic identity to the target population. The primary RGP consists of the target population itself or material genetically connected to it via pollen flow or seed dispersal, whereas the quaternary RGP consists of material of a different taxon from the target population altogether. Primary RGP material is preferred when it is available and when the ecological function of the target site has not been fundamentally altered in a manner that makes such material no longer adapted. But when either of these two conditions do not hold, materials from higher order RGPs may be substituted. In practice, secondary RGP material will be most commonly substituted when primary RGP material is simply unavailable. Tertiary or quaternary RGP materials will be substituted under the more challenging circumstances of major disruption of ecosystem function.

An Explanation of the Concept Using Bluebunch Wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve)

Primary RGP

Genetic identity of the primary RGP with respect to the target population is high. The genetic structure of the primary RGP retains the original levels of heterozygosity (genetic variation within an individual that may be documented by phenotypic variation among progeny) and heterogeneity (genetic variation between individuals as reflected by noncorrespondence of the progeny of one individual with those of another). The primary RGP also retains any biotypes (genetically controlled subpopulations with different form or function), that may have been present in the original population. The primary RGP includes only material from the target site plus adjacent areas that are genetically connected to the site via gene flow, that is, the metapopulation (Antonovics et al. 1994).

Metapopulations can be thought of as subunits of a species between which there is limited genetic exchange. A metapopulation may encompass sites that are ecologically different but lack genetic isolation from the target population. Selection pressure exerted by a heterogeneous environment must overcome gene flow from adjacent populations for natural selection to operate, which generally requires a landscape that permits isolation of local populations (Jones 1997). Moritz (1999) emphasized the importance of conservation of ecological and evolutionary processes in discrete historically isolated and independently evolving “evolutionarily significant units,” which appear to correspond roughly to metapopulations. This approach spares the biologist the technical difficulties of many likely redundant (ecologically and evolutionarily speaking) populations and is especially appealing to animal conservation biologists.

The Snake River Birds of Prey National Conservation Area in southwestern Idaho, U.S.A., home of the greatest

concentration of nesting raptors in North America, serves as our target site. This is a land area of 196,000 ha along a 130-km stretch of the Snake River, so how would one interpret the primary RGP? Consider the metapopulation of bluebunch wheatgrass in this area. Bluebunch wheatgrass is wind pollinated, and gene dispersal is probably restricted only by geographical barriers and proximity to neighbor populations. Let us consider three possible situations (Table 1): example A, material from a single site within the National Conservation Area; example B, a random intermating or "metapopulation polycross" (MPPX) among materials from various sites within the metapopulation; and example C, material from a single site genetically connected to the others but ecologically distinct in terms of edaphic characteristics, which exert selection pressure.

Materials of examples A and B both possess genetic identity at the "very high" level. However, example B, the MPPX, possesses two potential advantages over example A, a single-site seed source: (1) protection against inbreeding in this cross-pollinated species and (2) a broader sampling of genetic variation.

If the plants from which seeds are to be harvested at the single site are a "remnant" of the original population and plants are positioned so far apart that cross-pollination is limited by distance, for instance, then seed harvested off of the remaining plants may be selfed, an abnormal and deleterious condition for bluebunch wheatgrass. This danger in harvesting seed from scattered remnant plants is realized when this sort of material is used for restoration. A normal population of bluebunch wheatgrass is heterozygous and heterogeneous, that is, each plant in the population is non-inbred and genetically unique. A variety of self-incompatibility mechanisms discourage the production of weak inbred progeny by putting pollen produced by the same plant at a competitive disadvantage relative to pollen from other genotypes (Briggs & Knowles 1967). ("Genotype" as referred to here is at the organism level, i.e., genes within the organism, not at the single-gene level or at the population level.) These mechanisms minimize selfing and crossing within the same "mating type," especially when pollen of other genotypes is present. Inbreeding depression may also occur when crosses are not limited by distance. If two closely positioned bluebunch wheatgrass plants happen to be closely related, as is often the case when seed dispersal is limited (Waser & Price 1989), their progeny will be inbred.

Bluebunch wheatgrass will produce only a small amount of selfed seed when isolated from other bluebunch wheatgrass plants and that seed will be inbred with respect to the parent. Looking at the next generation, if seedlings arising from selfing do survive and reproduce, pollination by the parent or sister plants will lead to additional inbreeding, though not as great an increment as the prior generation. The result would not only be inbred individuals but now also an inbred population. This loss of genetic variation is typical (Clegg & Brown 1983) of what has been referred to as a "founder event" (Mayr 1963). Heterozygosity itself

Table 1. Genetic identity, genetic variation, and adaptation relative to the target of primary, secondary, tertiary and quaternary restoration gene pools for reseeding perturbed bluebunch wheatgrass sites in the Snake River Birds of Prey National Conservation Area.

Gene Pool	Relationship to Target						
	Genoplasm Origin	Ecosystem	Site	Taxon	Genetic Identity	Ecological Adaptation	Genetic Variation
Primary, example A	Bluebunch wheatgrass (BBWG) from a single Birds of Prey site	Same	Same	Same	Very high	High (excepting inbreeding)	Low
Primary, example B	Birds of Prey BBWG metapopulation polycross (MPPX)	Same	Multiple similar	Same	Very high	High	Moderate
Primary, example C	Birds of Prey BBWG (distinct microhabitat)	Same	Different	Same	High	High	Low
Secondary, example D	P-7 BBWG multiple-origin polycross (MOPX)	Different	Different	Same	Moderate	Moderate	High
Secondary, example E	cv. Whitmar, Goldar	Different	Different	Same	Low	Subject to testing	Low
Tertiary	a) Tetraploid race of BBWG b) Doubled diploid × tetraploid hybrids	Different	Different	Closely related	Very low	a) Low b) Subject to testing	a) Low b) Very high
Quaternary	"Successful introductions," e.g., crested wheatgrass, Old World <i>Pseudoroegneria</i> , Snake River wheatgrass cv. Secar	Different	Different	Distantly related	Dissimilar	Very high	Variable

may confer adaptive advantage, as in wild barley (*Hordeum sponatum* K. Koch) where heterozygous genotypes of this self-pollinating species are more prevalent in microsites subject to microclimatic fluctuations (Nevo et al. 1986).

The second advantage of the MPPX (Table 1, example B) is that it may have greater genetic variation than example A. Alleles that may have been absent by chance in example A because of genetic drift due to small population size (Barrett & Kohn 1991) are likely present in example B. Although it could be argued that these alleles lower the genetic identity of the MPPX relative to example A, this is only because example A is a sample of the metapopulation and the sample may be a biased estimator of the metapopulation. In actuality the MPPX has greater genetic identity relative to the metapopulation than example A.

An interesting question is posed by the subpopulation positioned on a distinct microhabitat (Table 1, example C). At work here are opposing forces of (1) selection for alleles conferring specific adaptation to the microhabitat and (2) gene flow from the surrounding metapopulation that reintroduce alleles conferring general adaptation to the macrohabitat (Grant & Antonovics 1978). Selection for alleles conferring specific adaptation can only occur if they are already present in the population or can be generated by mutation. The microhabitat must also be strong enough to exert selection pressure and/or the landscape dissected enough to provide isolation from incoming gene flow that counters the selection pressure (Jones 1997). Therefore, it cannot be assumed that a distinct microhabitat results in a distinct genetic array, but there are many cases where this has been documented (Huenneke 1991). Conversely, if a distinct genetic array occurs, it may result from restricted gene flow (i.e., a "bottleneck") or from an adaptive response to environmental patchiness (Huenneke 1991). Careful consideration should be given to whether the MPPX would successfully meet project objectives for such microhabitats or whether more specialized material adapted to the microhabitat is required (Hickey & McNeilly 1975).

Secondary RGP

Use of the primary gene pool, as described above, is often not feasible. The most common reasons are lack of seed and poor adaptation to an altered landscape. When it has been determined that either of these factors preclude use of the primary RGP, the secondary RGP should be considered. The secondary RGP is a more palatable alternative to the primary RGP when the genetic array of the target species is distributed in a general fashion across its range (continuous variation among populations), for example, sea-plaintain (*Plantago maritima* L.) (Gregor 1946) and scots pine (*Pinus sylvestris* L.) (Langlet 1959). This alternative is less preferable when the genetic array of the target species is packaged in more or less discrete and distinct subunits that are adapted to fluctuations of environment

in space (discontinuous variation among populations), for example, tidy-tip (*Layia platyglossa* [F. & M.] Gray) and *Potentilla glandulosa* Lindl. (Clausen et al. 1947).

Species that are widespread, long-lived, and cross-pollinating package more of their genetic variation within populations and less between populations (continuous variation among populations) than species that are endemic, ephemeral, and self-pollinating (discontinuous variation among populations) (Hamrick et al. 1991). On average, self-pollinating species had five times greater genetic diversity among populations than cross-pollinating species because of much greater gene flow among populations for the latter group. Stebbins (1950) stated that a species' pattern of genetic variation depends on whether interchange of genes between individuals or populations is more or less free, resulting in a continuous pattern, or whether interchange of genes is restricted by isolating mechanisms, resulting in a discontinuous pattern.

Genetic identity of the secondary RGP is lower than that of the primary RGP because the former consists of material originating from various disjunct sites, those that are genetically disconnected from the target population. Despite its lower genetic identity relative to the target population, material of choice of the secondary RGP may nonetheless be as well or better adapted to the target site. This may simply be a matter of likelihood because, except in the case of the endemic, the secondary RGP provides more genetic material from which to choose than the primary RGP.

On the other hand "outbreeding depression" may occur when local material crosses with nonlocal material of the same taxon. This may result when (1) hybrid material is less adapted to local conditions than the original local material or (2) hybridization disrupts the genetic balance of genes per se in the population, termed "intrinsic coadaptation" (Templeton 1986). For example, Waser and Price (1989) found that seed set in scarlet gilia (*Ipomopsis aggregata* [Pursh] V. Grant) was greatest for progeny arising from crosses between parents separated by an "optimal outcrossing distance," that distance at which inbreeding depression among relatives (greater among nearby plants) is balanced by outbreeding depression (greater among distant plants). The fitness of progeny arising from either selfing or crossing of distant plants was relatively inferior, and these authors suggested that the outbreeding depression of the latter was explained by reduced adaptation to the local environment of the maternal parent.

These workers also found open-pollinated progeny of Nelson's larkspur (*Delphinium nelsonii* Greene) plants to be more fit in their own maternal environment than open-pollinated progeny derived from parents located more than 50 m away (Waser & Price 1985). On the other hand remarkably similar genotypic arrays have been found among populations of the facultative apomict, Sandberg bluegrass (*Poa secunda* Presl.), from southern Idaho and central Washington, U.S.A., nearly 600 km apart (Larson et al. 2001). Based on reciprocal transplant experiments

Schemske (1984) demonstrated that selection had occurred for local adaptation to forest edge, mid-woods, and inner woods environments by *Impatiens pallida* Nutt., a self-pollinating annual. Obviously, species differ in the degree of site specificity and generalizations across species cannot be expected to hold.

Clewell and Rieger (1997) recognized that exclusive use of local material may sometimes sacrifice "genetic flexibility." A multiple-origin polycross (MOPX) (Table 1, example D) may provide a more genetically flexible secondary RGP alternative to cultivars. This sort of strategy may be preferred over the primary RGP when site disturbance has been so great as to render local material unadapted (Guerant 1996). The attractive feature of the MOPX is its higher genetic variation compared with the primary RGP and to cultivars originating from a single site (secondary RGP, example E). High genetic variation confers two advantages: (1) an increased likelihood that genes for adaptation will be present in an MOPX than in a single accession and (2) natural selection will operate more easily on genetic material possessing greater diversity.

P-7, an MOPX bluebunch wheatgrass germplasm, was generated by polycrossing 25 accessions originating in six states and British Columbia (Larson et al. 2000). This material was developed because of the two advantages cited above relative to the two previously existing cultivars, Goldar and Whitmar, both of which are derived from single point of origin populations in southeastern Washington, U.S.A. P-7 has more unique alleles and greater nucleotide diversity than Goldar or Whitmar. After introduction of the material to a restored site, such material is expected to vary genetically in response to the environment over several generations.

Cultivars Goldar and Whitmar (Table 1, example E) both exhibit excellent seed production. Although they are widely available at a reasonable price, they may not possess the drought tolerance to be adapted to the Snake River Birds of Prey National Conservation Area. Regarding the secondary RGP in general, some have expressed reservations about introducing nonlocal plant material when remnant local material is extant, because the latter material may be genetically "swamped," particularly if they outcross (Knapp & Rice 1994). A related issue is competitive exclusion of remnant local material by nonlocal material, which is unaffected by breeding system. Despite these reservations there is a place for cultivars of native species in restoration, and it is in the secondary RGP.

Although material with innately high seed production occurs frequently in the tristate area where Washington, Oregon, and Idaho converge, seed production of southwestern Idaho bluebunch wheatgrass germplasm is consistently poor. Therefore, the secondary RGP is a reasonable alternative to the primary RGP in this bluebunch wheatgrass example. If bluebunch wheatgrass material with good seed production could be found in a region more similar to southwestern Idaho in climate, it might be preferred over the currently available cultivars.

The importance of genetic variation has been underappreciated in conservation biology because of the lack of empirical data and the training of scientists in this field (Montalvo et al. 1997). Whether high or low genetic variation is preferred is a matter of the scale of the intended use and the structure of a typical population. Lesica and Allendorf (1999) recommended high genetic variation when both the degree of disturbance and the size of the disturbed area to be restored were high. I argue that for planting across a regional area, an MOPX is suitable for a species like bluebunch wheatgrass that exhibits continuous genetic variation. But when a species' genetic variation is rather discontinuous, as is often the case with self-pollinated species (Hamrick et al. 1991), such an approach may be less appropriate.

DeMauro (1993) used the secondary RGP to rescue Illinois populations of the lakeside daisy (*Hymenoxys acaulis* [Pursh] K. L. Parker var. *glabra*) threatened by extirpation because all surviving individuals were of the same mating type and therefore were not interfertile. She introduced genetic material from Ohio and Canada to restore fertility and to ensure continued representation of Illinois germplasm in restored populations.

Tertiary RGP

When efficacy of the target taxon itself is dubious, use of related taxa or hybrids of such taxa with the target taxon, that is, the tertiary RGP, may be used. This is appropriate when the site has been so highly disturbed that ecosystem function has been altered. This is the kind of impact cheatgrass (*Bromus tectorum* L.) has had on the fire regime and vegetation of the Snake River Birds of Prey National Conservation Area (Billings 1994).

Because the tertiary RGP consists of taxa distinct (or separated by dependable genetic isolation mechanisms) from the taxon of the target population, its genetic identity is considerably lower than the primary or secondary RGPs. These materials are closely related to the taxon of interest but are separated by a genetic barrier. An example would be a polyploid race that is genetically isolated because of its chromosome number.

Enhanced vigor may be contributed by the related taxon either directly or through a heterotic response in a hybrid. Although bluebunch wheatgrass in our target area is diploid ($2n = 14$), tetraploid ($2n = 28$) populations also exist. Direct use of tetraploid bluebunch wheatgrass populations would not be used because they are not necessarily more vigorous than diploid populations. However, based on results with other perennial Triticeae grasses, there is reason to believe that hybrids of chromosome-doubled diploid X tetraploid bluebunch wheatgrass populations can display desirable interploidy heterosis. "Hycrest" crested wheatgrass (*Agropyron desertorum* [Fisch. ex Link] Schult. ($2n = 28$) × chromosome-doubled *A. cristatum* [L.] Gaertn. ($2x = 14$; $4x = 28$)), for example, is larger and more robust than either of its parents (Asay et

al. 1985). We have also seen heterosis for hybrids between doubled tetraploid and octoploid races of basin wildrye (*Leymus cinereus* [Scribn. & Merr.] A. Löve). McArthur et al.'s (1988) work detailing hybridization between subspecies of big sagebrush (*Artemisia tridentata* Nutt.) is another good example of the use of the tertiary RGP. Although such material is only occasionally available, in specific instances it provides an additional option for the restorationist.

Quaternary RGP

The quaternary RGP exhibits low genetic identity relative to the target population, but its adaptation ranks high. Its appeal lies in its ability to tolerate or repair an ecosystem whose structure and function have been drastically altered. The quaternary RGP may include Old World, Australian, or South American corollaries to our native species. It may also include species native to North America (though, by definition, presumed not to have been present at the target site before disturbance) that can substitute for the target species.

The role of the quaternary RGP may be thought of as a vicarious one when primary, secondary, and tertiary RGPs are not feasible. Taxa other than the target taxon may serve similar roles in ecosystem structure and function yet be more robust, meaning they are better able to tolerate ecosystem stresses such as competitive weeds, altered edaphic or hydrological conditions, or modified fire regimes. Taxa that display similar ecological functions are said to belong to the same "functional group" (Chapin et al. 1992; Walker 1992). Although this term may refer to a list of species with similar function in a single naturally occurring ecosystem, here it refers specifically to species that may be ecologically redundant to the target taxon but originate in different ecosystems besides that of the target site (Johnson & Mayeux 1992). These workers view the presence of any particular species or population as non-critical relative to the presence of all pertinent components of ecosystem structure and function. It should be mentioned here that proponents of the "rivet hypothesis" will argue that ecosystem roles of species are more complementary than redundant (Ehrlich & Ehrlich 1981).

For the present example three taxa come to mind for inclusion in the quaternary RGP. *Pseudoroegneria strigosa* M. Bieb. (A. Löve) ssp. *aegilopoides* from Russia is an Old World counterpart to our native bluebunch wheatgrass (Jensen et al. 1995). Its distant relatedness to our native is shown by the low levels of viable pollen and absence of seed set in the Asian-North American hybrids. Nevertheless, this Asian bluebunch wheatgrass has exceptional grazing tolerance not characteristic of the native bluebunch wheatgrass. This grazing tolerance is of particular adaptive significance in western North American rangelands in the public domain. As a result of legislative mandate modern grazing pressure may be higher than at the time before European settlement.

Second, Snake River wheatgrass (*Elymus wawawaiensis* J. Carlson & Barkworth) cv. Secar (Carlson & Barkworth 1997) is currently being used successfully on the National Conservation Area. This bunchgrass is native to the lower portion of the Columbia and Snake River drainages rather than southern Idaho, but it is fairly easy to establish, vigorous, and a consistently better seed producer than bluebunch wheatgrass. Snake River wheatgrass bears a strong superficial resemblance to bluebunch wheatgrass. Only after release of Secar did genetic studies reveal that this cultivar was different enough from bluebunch wheatgrass to merit its placement in a separate genus. Subsequently, many morphological characters have been found distinguishing the two taxa (Jones et al. 1991). Here, a species of the same life form that originates in the same continent but does not happen to be part of the target flora has been substituted for the target taxon. This would be a natural course of action rather than using material introduced from another continent, particularly if no introduced material has been screened for adaptation or invasive potential.

Third, crested wheatgrass has long been used as a corollary to bluebunch wheatgrass in the Intermountain Region because it is adapted to similar climatic regimes and exhibits a caespitose growth habit but is more competitive and tolerant of grazing (Caldwell et al. 1981, 1983). Crested wheatgrass very ably demonstrates the concept that genetic identity, which declines in higher order RGPs, is not necessarily related to adaptation to the target environment. Its genetic identity is dissimilar to bluebunch wheatgrass, but its adaptation is very high in the Lower Snake River Plain ecosystem, particularly as perturbed by annual weed invasion and unnaturally high fire frequency (Shaw & Monsen 2000). In fact, adaptation of crested wheatgrass exceeds that of the native populations of bluebunch wheatgrass in this perturbed ecosystem.

These three examples are successful or potentially successful substitutes for bluebunch wheatgrass in the target region. Bridgewater (1990) justified the role of plant communities composed of exotic, naturalized, and native species, which he terms "synthetic vegetation." Such vegetation is anthropogenic, either intentional or accidental, and may show enhanced resilience, particularly in environments not historically subject to disturbance. He argued for management of synthetic communities in and of themselves.

Potential invasiveness is an issue when unfamiliar material is a candidate for the quaternary RGP, so such material is to be avoided. Many invasive weed species were introduced to this continent because of potential commercial importance but were never screened for invasive potential. However, the problem remains as to how potential invasiveness is to be predicted (Gordon & Thomas 1997). These workers were generally pessimistic about the accuracy of making such predictions on the basis of taxonomic status or ecophysiological traits. They suggested that the best approach is to document invasive characteristics in regions of similar climate, including the native region in areas where disturbance has perturbed the ecosystem.

I am not advocating the indiscriminate introduction of plant material to this continent. But it cannot be denied that many introductions of the past have proven economically useful without an invasive tendency. The recommendation of crested wheatgrass above is appropriate because this species has already been introduced and has been in wide use for over 60 years in the Intermountain West (Young & Evans 1986) without an invasive tendency. Crested wheatgrass has been criticized as impervious to invasion by native vegetation (Marlette & Anderson 1986), but this is a result of the past practice of planting it in extensive monocultures for forage production rather than any flaw in the species itself.

These three examples are successful or potentially successful introductions from this or other continents. Their genes for adaptation to the perturbed ecosystem are directly responsible for their success. I conclude that there can be a place for introduced plants in restoration, and it is in the quaternary RGP. This is not to say that I favor genes for adaptation over genes for identity. Rather, I favor genes for adaptation when genes for identity are unable, for whatever reason, to meet the restoration challenge. When options offered by lower level RGPs have been exhausted or eliminated, the quaternary RGP should be implemented.

Many restoration ecologists would consider only primary and secondary RGP materials as appropriate for restoration. But they would argue that whereas use of tertiary and quaternary RGP materials are philosophically inconsistent with restoration, they may be appropriate for "reclamation" or "rehabilitation." Preferences in terminology and objectives among projects may differ, but the higher order RGPs can still be viewed as the most appropriate alternatives when primary and secondary RGPs have been deemed infeasible. Hopefully the RGP concept provides a framework that transcends the chasm between purist and pragmatist points of view.

Comparison of the Four Restoration Gene Pools

The four RGPs can be compared for genetic identity, genetic variation, and adaptation (Table 1). Genetic identity relative to the target population is very high (nearly identical) for primary RGP examples A and B and slightly lower for example C, where selection pressure may have increased the frequency of alleles adapted to a distinct microhabitat. Note here that the primary RGP corresponds to Aronson et al.'s (1993) restoration *sensu stricto* and to the Society for Ecological Restoration's definition of restoration as "the intentional alteration of a site to establish a defined indigenous, historic ecosystem."

Secondary and higher order RGPs represent successive deviations from restoration *sensu stricto* in the direction of Aronson's restoration *sensu lato*. An MOPX (secondary RGP, example D) is lower in genetic identity than the primary RGP but higher than the typical cultivar (secondary RGP, example E). This is because it is likely that some of

the MOPX component accessions would be genetically more similar to the target population than others, whereas cultivars derived from single-site populations would most often be disconnected from the target population. Of course this would be the reverse if the cultivar happened to originate from near the target site and was genetically connected to the target population. Genetic identity relative to the target of the tertiary and quaternary RGPs is much lower than the primary or secondary RGPs because of their greater taxonomic distance from the target. Thus genetic identity declines from the top to bottom of Table 1.

Notice that this trend does not correspond to the trend for adaptation (Table 1). Adaptation is high for the primary RGP but only moderate for the MOPX (secondary RGP, example D). Adaptation for any cultivar should be determined by field testing; therefore it is stated to be "variable" pending conclusive test results. In contrast, the tertiary and quaternary RGPs are always very highly adapted and noninvasive by definition; otherwise, their use would or should never be considered.

Finally, consider genetic variation for the various RGPs (Table 1). The MPPX (example B) has greater genetic variation than the other primary RGP examples because of its inclusion of more subpopulations. Genetic variation of cultivars would be of a similar order of magnitude because they too originate from a single population. But genetic variation of the MOPX would be much higher because of the inclusion of many accessions from across a region or across the species' distribution. The naturally occurring genetic variation of the primary and secondary RGPs, however, is much lower than material originating from an artificially constructed wide-cross (e.g., doubled diploid X tetraploid) (tertiary RGP). Genetic variation of successful natives from other ecosystems or introductions from other continents (quaternary RGP) would depend on how the specific material was developed.

I have discussed the four RGPs as if they are discrete categories for sake of convenience, but their distribution may be more continuous than implied. For example, consider the placement of *P. strigosa* ssp. *aegilopoides*. One could argue that it belongs in the tertiary RGP rather than the quaternary RGP, as I previously stated. Genomically, it is very closely related to the native North American bluebunch wheatgrass, which supports a tertiary position, yet their hybrids are totally sterile, supporting a quaternary position. Obviously, assignment to a particular gene pool in these ambiguous cases is not as important as the restorationist's understanding of the trend from primary to quaternary.

For many examples all four RGPs will not be applicable. The tertiary RGP, in particular, will often be nonexistent. In other cases there will be no genuine quaternary RGP. In fact, in many examples there will be no need for a tertiary or quaternary RGP because users are able to contract with seed producers for production of primary RGP seed and/or secondary RGP seed sources are suitable for most applications. But there will be cases, as in this blue-

bunch wheatgrass example, where all four RGPs have merit, at least at the present time.

Point of origin data are all that are necessary for differentiation between primary and secondary RGPs. However, additional specialized genetic information is required for differentiation between secondary and tertiary RGPs. This information is generally available, at least in a cursory way, for “flagship” species, which attract considerable human attention because of their charisma or visibility (Noss 1991). And an incentive is present for obtaining such information for species of particular conservation significance. These include “vulnerable” species, because of their legal status, and “umbrella” species (e.g., large carnivores), whose protection necessitates the conservation of large contiguous geographical areas that in turn provides habitat for many other species. The need for such information is greatest for “keystone” species, those that play a pivotal role in ecosystem structure or function. Chapin et al. (1992) described a keystone species as a functional group without redundancy within the ecosystem. The presence or absence of these species triggers massive changes in ecosystem structure and function (either favorable or unfavorable); thus their identification as keystone species is critical. In many cases genetic information is simply unavailable for ephemeral or nonvascular organisms.

A comprehensive ecological understanding of the flora is needed to determine whether taxa qualify for the quaternary RGP. If there is a great need to use the quaternary RGP, the greatest research challenge lies in understanding ecological redundancy so the options in this gene pool may be effective and appropriate. The degree to which redundancy occurs is the degree to which the candidates for the quaternary RGP can satisfactorily substitute for missing component taxa. Walker (1992) provided a procedure to characterize redundancy. The first step is to divide the ecosystem's species into guilds based on biotic regulation of dominant or limiting ecosystem processes. The second step is to determine the number of species in each guild. The third step is to determine whether remaining species exhibit density compensation when one species in the guild is removed. (If so, they are redundant.) The fourth step is to examine how a change in abundance of a functional group affects ecosystem and community processes. Finally, remember that, by definition, less than perfect redundancy is anticipated for the quaternary RGP because its most effective taxa are expected to be more tolerant of the disturbance-induced ecosystem perturbations than the target taxon.

Extension to a Self-Pollinated Taxon

The grass bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey) provides an opportunity to show how the self-pollinated example contrasts with the cross-pollinated example of bluebunch wheatgrass described above. The differences are found primarily in the primary RGP (examples A and B) and the secondary RGP (example D).

The polycross of examples B and D is replaced with a composite, the term for a mixture of self-pollinating lines or populations. Hence, the appropriate terms are metapopulation composite or multiple-origin composite. The metapopulation composite is genetically connected mostly by seed dispersal rather than by pollen transfer. The concern over deleterious inbreeding in remnant plants or among relatives for the primary RGP is moot in bottlebrush squirreltail because homozygosity is the natural condition and self-incompatibility mechanisms are not present.

Similar to the bluebunch wheatgrass MOPX, the bottlebrush squirreltail multiple-origin composite retains its advantages of greater likelihood of adaptation and more efficient natural selection. However, the concern of loss of linkage disequilibrium over generations of seed increase is of relatively little concern for a bottlebrush squirreltail multiple-origin composite. Instead, the concern is that genetic shift will discriminate against some of the more or less intact component lines and favor others. This was less of a concern in bluebunch wheatgrass because the components were never intact in the polycross.

Placing the RGP Concept in a Larger Framework

In contrast to the traditional native/non-native either/or dichotomy, the RGP concept recognizes that the genetic similarity and adaptation of plant materials can be separate and often do not correspond. By defining these attributes they may be discussed on their own merit without eliciting inflammatory emotions regarding the geographical origin of the plant material. This should allow plant materials decisions to be made in the scientific context that ecosystem management demands (Jones & Johnson 1998).

The RGP concept can be implemented within the larger context of planning seedings. First, components of the *initial strategy*, including seeding objective, site potential and desired landscape, and genetic integrity of the plant material, are delineated. Second, *feasibility factors*, such as community seral status, weed invasion, and economic limitations, are used to refine the initial strategy.

Once the initial strategy has been reconciled with the feasibility factors, the planning process may proceed to examine available plant materials that meet the needs of the plan (see *ecological adaptation and genetic variation*, Fig. 1, in Jones & Johnson 1998). Although the practitioner of restoration ecology may initially prefer the primary RGP for all species in his or her flora list, a higher order RGP may be more successful because of enhanced adaptation. A mix of RGPs among the various species will often prove to be the most pragmatic solution. Knowledge of ecological adaptation and genetic variation of plant materials is necessary to meet plan specifications. The RGP concept, which encompasses both ecological adaptation and genetic variation, provides a workable framework to find the most appropriate plant material to successfully implement the project.

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