Development of Native Western North American *Triticeae* Germplasm in a Restoration Context

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ABSTRACT: Restoration of native plant communities is an activity increasing in prominence in the United States. Depending on the practitioner's philosophy of restoration and circumstances of the project, there may be needs for plant materials indigenous to the restoration site (primary restoration gene pool) and for non-local materials developed through research that are available commercially (higher-order restoration gene pools). When the objective is to restore evolutionary and ecological processes, the primary restoration gene pool is emphasized. But the secondary, tertiary, and quaternary restoration gene pools may suffice when the emphasis is on restoring ecological processes. Development and use of bluebunch wheatgrass, Snake River wheatgrass, and crested wheatgrass plant material for restoration in the Intermountain Region, U.S.A. is discussed in relation to the four restoration gene pools.

Keywords: ecological restoration; functional guild; metapopulation; plant materials; restoration ecology; Restoration Gene Pool concept

Definition, origin, history, and purpose of ecological restoration

Ecological restoration, defined as the "intentional alteration of a site to establish a defined indigenous historic ecosystem" (Aronson *et al*. 1993), is being increasingly practiced on ecologically altered sites in North America to restore ecosystem structure and function and to increase biological diversity (MacMahon 1997). The objective of restoration of plant communities on disturbed sites is to restore the flora and ecological processes (and sometimes evolutionary processes) to those of the pre-disturbed ecosystem. Ecological restoration is intellectually fueled by the now full-fledged biological discipline, restoration ecology.

The origin of ecological restoration in the United States was prompted primarily by federal legislation regarding reclamation of surface-mined lands (Richards *et al*. 1998). The Surface Mining Control and Reclamation Act of 1977 (SMCRA) required establishment of "diverse, effective, and permanent vegetative cover of the same seasonal variety native to the area of land to be affected and capable of self-regeneration and plant succession". This legal requirement created a significant demand for native plant seeds and stimulated research efforts to develop native plant materials to serve industry needs. Eventually, federally administered wildlands also became significant users of native seeds (Rogers & Montalvo 2004). In recent years, large though erratic demand for native seeds has been generated by fire rehabilitation projects in the western states.

As might be surmised, a wide spectrum of philosophies can be found among restoration practitioners. One of the most contentious issues regards the use of genetically local plant materials. Aronson *et al*. (1993) distinguish between efforts to restore a historic indigenous ecosystem, termed restoration *sensu stricto*, from efforts to "redirect a disturbed ecosystem in a trajectory resembling that presumed to have prevailed prior to the onset of disturbance", termed restoration *sensu lato*. The former seeks to restore both historic ecological and evolutionary processes, while the latter emphasizes ecological processes but does not require the replication of previously existing genotypes to fuel ongoing evolutionary processes. Thus, *sensu stricto* activities emphasize genetically local plant materials, necessitating contract seed production, while *sensu lato* activities rely primarily on commercially available seed sources that are typically nonlocal.

The Restoration Gene Pool concept

The purpose of the Restoration Gene Pool (RGP) concept is to provide a framework that clarifies the issues involved in choosing and developing plant materials for restoration. The RGP concept has been explained in detail elsewhere (Jones 2003) and a flowchart has been developed to guide its pplication in restoration projects (Jones and Monaco 2006). Nevertheless, a brief explanation is in order.

Plant materials are assigned to one of four RGPs (primary to quaternary) in order of declining genetic correspondence to the indigenous population and declining preference to the restoration practitioner. The primary RGP is material of the same metapopulation as indigenous material. A comprehensive wildland collection can serve this purpose. Because primary RGP material may not be available or may be ultimately successful, material of higher-order pools may be substituted. The secondary RGP is material of the indigenous taxon but of a different metapopulation. Molecular genetic studies can define geographic boundaries of metapopulations, but in their absence ecoregion, vegetation, and/or climatic maps may identify appropriate surrogate boundaries.

In contrast to the primary and secondary RGPs, tertiary and quaternary RGPs extend beyond the boundaries of the target taxon. The tertiary RGP is material of the indigenous taxon altered by hybridization with a taxon at least partially biologically isolated from it, e.g., a different ploidy, subspecies, or species. The quaternary RGP is material of a taxon highly biologically isolated from the target, either native or introduced, that may serve as an ecological surrogate for the indigenous taxon. While quaternary RGP materials may restore ecological processes, they obviously can never replicate evolutionary processes of the pristine state. Despite a long history of reluctance to use introduced species for the purpose of ecological restoration, ecologists are increasingly seeing that their use may be desirable for particular situations (D'Antonio & Myerson 2002; Ewel & Putz 2002).

Ecological restoration in light of the RGP concept

Ecological restoration *sensu stricto* employs a conservation biology approach. The conservation biology discipline views "all of nature's diversity as important and having inherent value" and employs a stewardship ethic (Meffe & Carroll 1997). Its mission is "to retain the actors in the evolutionary play and the ecological stage on which it is performed" by preserving the diversity of genes, populations, species, habitats, ecosystems, and landscapes, as well as the associated ecological and evolutionary processes.

Central to the *sensu stricto* approach is the continued integrity of the plant metapopulation, a series of geographically continguous populations or subpopulatons that are genetically connected by gene flow (pollen and seed dispersal). Metapopulations are important because they, rather than species, are the units upon which evolutionary forces operate (Ehrlich & Raven 1969), but it is within the demes that most reproductive activity is centered (Rogers & Montalvo 2004). Metapopulations may be reconstructed by combining seed from constituent demes that have been shown experimentally to be genetically connected.

The *sensu lato* approach is acceptable when restoration of the ecological stage takes precedence over replication of a particular evolutionary play. It is unnecessary and undesirable to eschew higher-order RGPs solely on ecological grounds, the matter of concern to the *sensu lato* restorationist. This is especially true when the indigenous gene pool is already in a compromised state (Moritz 1999).

An approach for development of the secondary RGP for *sensu lato* restoration is to develop widely adapted material by amalgamating high-performing materials from multiple locations within the region targeted for the plant material. For example, P-7 bluebunch wheatgrass germplasm, generated by hybridization among 25 sources, has 10% more genetic variation than existing cultivars (Larson *et al*. 2000), giving natural selection more raw material on which to operate.

Tertiary RGP material is developed with a thorough knowledge of phylogenetic relationships among species. It involves overcoming sterility barriers to permit the introduction of desirable traits from one ploidy or taxon to another. While this sort of work obviously isn't undertaken with a large number of species, it can increase establishment, vigor, and persistence of critical keystone species, particularly when their adaptation has been compromised by a modified environment.

Adoption of the quaternary RGP is facilitated by the functional guild concept. Functional guilds are used to condense species lists into groups consisting of individual species with similar characteristics of ecological structure and function (Naeem & Wright 2003; Brown 2004). Species within a guild are said to be ecologically redundant in form or function (Walker 1992).

Application of the RGP concept to bluebunch wheatgrass in the Intermountain Region

Bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) is a perennial allogamous bunchgrass common in the Intermountain Region, bounded on the east by the Rocky Mountains and on the west by the Sierra Nevada and Cascade Mountains. Bluebunch wheatgrass is found in the Western Great Plains as well. There are about fifteen *Pseudoroegneria* species, with bluebunch wheatgrass being one of two native to the western hemisphere. To service primary RGP needs, we hold 184 accessions collected in nine states and two Canadian provinces. We enter our collections into the National Plant Germplasm System (Bretting 2004), a seed repository that perpetuates the accessions and distributes them to scientists worldwide. These accessions are overwhelmingly diploid ($2n = 14$), with a few autotetraploids ($2n = 28$). To service the secondary RGP, we currently conduct artificial selection in eight breeding populations, seven diploid and one tetraploid. These populations trace to both single and multiple sites of origin, mostly, but not exclusively, from the eastern parts of the states of Washington and Oregon and adjacent portions of Idaho. We believe this region is a center of diversity for bluebunch wheatgrass because several metapopulations converge there (Larson *et al.* 2004). Furthermore, this region's bluebunch wheatgrass germplasm is generally agronomically superior to that found elsewhere.

The tetraploid race is relatively infrequent, being found mostly in the northwestern portion of the species' distribution, but it may be used to generate interploidy hybrids for the tertiary RGP. We have used colchicine-doubling, as verified by flow cytometry, to induce tetraploids, which we have artificially selected both directly and as hybrids with natural tetraploids. Seed mass of induced tetraploids is about 50% greater than diploid material, yet interestingly there is little difference in seed mass between diploid and natural tetraploid populations. We are investigating whether the larger induced tetraploid seed results in better seedling establishment. We have seen that interploidy hybrids in the natural tetraploid cytoplasm are considerably more vigorous than the reciprocal cross.

Snake River wheatgrass (*Elymus wawawaiensis* J.R. Carlson & Barkworth) is a relatively recently recognized allogamous allotetraploid ($2n = 28$) taxon (Carlson & Barkworth 1997) that is native to the vicinity of the lower Snake River and its tributaries. Snake River wheatgrass was long confused with bluebunch wheatgrass, with which it shares a superficial resemblance. Functionally, Snake River wheatgrass and bluebunch wheatgrass are similar. They have in common a caespitose habit, C-3 metabolism, semi-arid climatic adaptation, similar phenology, and a long-lived perennial life history. The distribution of Snake River wheatgrass is much more restricted than that of bluebunch wheatgrass, but the former possesses excellent agronomic properties in general while agronomic suitability of the latter is highly variable. We hold 51 accessions from Washington, Idaho, and Oregon, many of which were collected by others as bluebunch wheatgrass that we later identified as Snake River wheatgrass. These may be employed for the primary RGP for Snake River wheatgrass. But the primary application of this species is as the quaternary RGP for bluebunch wheatgrass, simply because of the restricted natural distribution of Snake River wheatgrass.

Another quaternary RGP surrogate for bluebunch wheatgrass that has been extensively used for several decades is the Asian introduction, crested wheatgrass (*Agropyron desertorum* [Fisch. ex Link] Schult.). Crested wheatgrass was first introduced into the northern Great Plains of the U.S.A. in 1898 (Lorenz 1986), but it is not known to have been planted in the Intermountain Region before 1932 (Young & Evans 1986). Beginning in the mid-1950s, large hectareages were seeded to control *Halogeton glomeratus*, an introduced weed toxic to sheep. This "Golden Age" of seeding lasted approximately 10 years. Compared to bluebunch wheatgrass, crested wheatgrass greens up earlier in the spring, yet is later phenologically. Another attribute is its high tolerance for grazing, a feature that bluebunch wheatgrass does not share (Richards & Caldwell 1985). Thus, crested wheatgrass has been an excellent surrogate in terms of providing forage for the livestock industry.

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