The potential of novel native plant materials for the restoration of novel ecosystems

T.A. Jones[1*] • T.A. Monaco[1] • C.W. Rigby [1]

[1]USDA-Agricultural Research Service, Forage & Range Research Laboratory, Logan, Utah, United States

*Thomas.Jones@ars.usda.gov

Abstract

Extensive ecological change has been sustained by many dryland ecosystems throughout the world, resulting in conversion to so-called novel ecosystems. It is within such ecological contexts that native plant materials destined for ecological applications must be able to function. In the Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* [Beetle & A.M. Young] S.L. Welsh) ecosystems of the Intermountain West, for example, novel ecosystem structure and functioning are pervasive. Invasive species, particularly annual grasses, fuel repeated wildfires that drive previously stable ecosystem states across thresholds to less desirable states that are highly recalcitrant to restoration efforts. Structural changes include reductions of native flora, damage to biological soil crusts, and alterations to soil microbiota. Functional changes include altered hydrologic and nutrient cycling, leading to permanent losses of soil organic matter and nitrogen that favor the invaders. We argue that there is an important place in restoration for plant materials that are novel and/or non-local that have been developed to be more effective in the novel ecosystems for which they are intended, thus qualifying them as "ecologically appropriate." Such plant materials may be considered as an alternative to natural/local "genetically appropriate" plant materials, which are sometimes deemed best adapted due to vetting by historical evolutionary processes.

Introduction

Ecological restoration is currently defined as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SERI of Science & Policy Working Group, 2004), while restoration ecology is the scientific discipline that informs the practice of ecological restoration. The hope of restoration ecology is to discover principles that are effective on degraded lands requiring restoration, a synthetic approach, when strict adherence to principles derived from the study of pristine lands, an approach based on dissection and description, no longer apply (Aber and Jordan, 1985). While ecological restoration is sometimes envisioned as the recollection and assembly of all of the building blocks of the pristine ecosystem, Aber and Jordan (1985) and Schmitz (2012) argued that the application of such principles to disturbed lands is akin to searching for cures for disease by examining only healthy patients. In the same way, attempting to reconstruct an ecosystem from its building blocks without an understanding of ecosystem assembly may result in limited success (Temperton et al., 2004).

Local plant materials may be such building blocks. Allegiance to the *"local is best"* (terms in italics are defined in the Appendix A) paradigm, the consequent delineation of *seed transfer zones*, and the subsequent development of *"genetically appropriate" plant materials* based on naturally occurring patterns of genetic variation, have been regarded as "dogma" in some quarters (Johnson et al., 2010a). However, this model may not be optimal for the many degraded rangeland systems in need of restoration (Jones, 2013a) because they have often become modified to the point of becoming *"novel ecosystems"* (Hobbs et al. 2013). In such situations, "local is best" may be better viewed as a testable hypothesis than as dogma (Jones, 2013b). If and when local isn't best (Jones, 2013b), adjusting the restoration approach to reflect biological reality may be both justified and desirable.

If genetically appropriate plant materials are unable to achieve restoration goals in a particular circumstance, we have suggested *"ecologically appropriate" plant materials* in their place (Jones, 2013a). Such materials

exhibit *ecological fitness* on the targeted restoration site, display compatibility with other members of the plant community, and refrain from promiscuous spread (Jones, 2013a), i.e., what Callicott (2002) calls "well-behaved citizens." As long as they meet these criteria, ecologically appropriate plant materials need not be local in origin. In this paper, we limit our discussion to those ecologically appropriate plant materials that have either been subjected to genetic manipulation, i.e., the plant breeding tools of hybridization and *artificial selection*, or are non-local in origin, which we term "novel/non-local." We have suggested that genetic manipulation can be respectfully combined with conservation biology principles (Jones, 2009) to develop plant materials that are more tolerant of environmental stress and better deliver ecosystem services (Brummer et al., 2011). On the other hand, we are not suggesting the development of genetically modified organisms.

Aldo Leopold, considered by many to be the father of ecological restoration in North America, described "the land" as the embodiment of all the components of the ecosystem (Leopold, 1949). Leopold's main point was that the context of ecological restoration must always be the health of the land that is to be restored (Nash, 1987). He understood that humans are actors on the ecological stage and that humanity necessarily applies an environmental imprint of its own (Nash, 1987). Leopold (1953) also reserved a place for "intelligent tinkering," which we interpret as the development of ecologically appropriate plant material to contribute to the health of "the land." Yet, in order to service this intelligent tinkering, Leopold (1953) also emphasized the importance of precaution in keeping "every cog and wheel," which we interpret as local populations, even if their functions are not yet understood or appreciated.

The first step of restoration planning involves the detailing of project objectives to benefit "the land." We caution that developing a set of objectives is more than a matter of deciding what "I want." A conscious effort should be made to balance what is desired with what is technically feasible to achieve the desired *ecosystem state*, as well as what is ecologically sustainable over the long term. This is the essence of ecological pragmatism. Without pragmatism, a restoration plan may be unrealistic, complicating implementation and jeopardizing overall success (Shafroth et al., 2008, Step 2a).
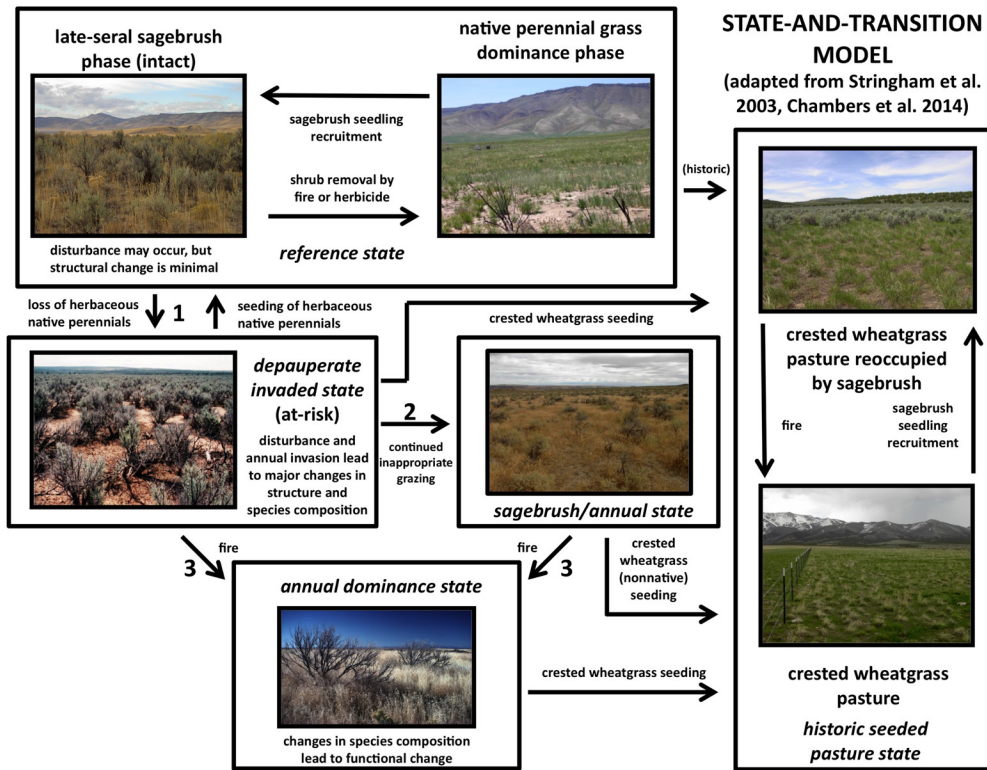
Throughout the world, drylands are susceptible to inappropriate grazing (Fleischner, 1994), invasion by exotic species (DiTomaso, 2000), conversion to alternate stable ecosystem states (Rietkerk and van de Koppel, 1997), and desertification (Dregne, 2002). As an example of a badly damaged dryland plant community in need of restoration, herein we describe the extensive structural and functional modification of Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* [Beetle & A.M. Young] S.L. Welsh) communities in the Intermountain West, USA. We describe this modification in great detail, not only to show that the manifested ecological changes are great in both degree and extent, but also to highlight the significant biotic and abiotic obstacles that must be overcome to restore such lands to a more desirable condition. While our experience is primarily with the Wyoming big sagebrush ecosystem, many other dryland ecosystems across the world display similar restoration challenges, namely dominant exotic invasive species, modified soil conditions, and altered disturbance regimes. We conclude by discussing the great need and potential for ecologically appropriate plant materials within such restoration scenarios. As a matter of ecological pragmatism, addressing the biological realities these degraded ecosystems present may need to supersede the desire to maintain "all diversity at all scales," as directly addressed by genetically appropriate plant materials. While genetically appropriate plant materials are appropriate for managing healthy lands, i.e., Aber and Jordan's (1985) "healthy patients," ecologically appropriate plant materials may be more appropriate for the recovery of highly modified ecosystems, i.e., the "sick patients."

Case study: The ecologically modified Wyoming big sagebrush ecosystem

The reference state

As described by Reisner et al. (2013), the intact late-seral Wyoming big sagebrush phase (Fig. 1, *reference state*, left) encompasses two native perennial communities. On coarser-textured soils with lower heat loads (a variable calculated from latitude, slope, and aspect), sandberg bluegrass (*Poa secunda* J. Presl), bluebunch wheatgrass, and/or Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth) predominate with a lower abundance of bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey). On finer-textured soils with higher heat loads, sandberg bluegrass predominates with a lower abundance of bottlebrush squirreltail, but bluebunch wheatgrass and Thurber's needlegrass representation is limited. It is this latter community that is more susceptible to invasion by downy brome (*Bromus tectorum* L.), an annual grass destined to play a nefarious role in the sagebrush communities (Reisner et al., 2013) (see Appendix B). In addition, lower-elevation sites are less *resistant* to downy brome invasion and less *resilient* in the face of disturbance (Knutson et al., 2014).

Wyoming big sagebrush is found in both the Great Basin-Colorado Plateau sagebrush semi-desert (West, 1983a) and the Western Intermountain sagebrush steppe (West, 1983b). The former is located primarily in Nevada (north of the Mojave Desert), western Utah, and northern Arizona (West 1983a, Fig. 12.2), while the latter is found further north in northwestern Nevada, eastern and central Oregon, the Columbia Plateau and Basin of Washington, southern Idaho, and the southwestern corner and the central third of Wyoming (West, 1983b, Fig. 13.2). While these two provinces are often not distinguished and the boundary separating

them is indistinct, the former province is more arid, has a lower abundance of perennial herbaceous species, is lower in productivity, displays less ecological resilience to stress and disturbance (Chambers et al., 2014a), is less responsive to restoration treatments, and features somewhat different allied species (West, 1983a, 1983b).

The Wyoming subspecies of big sagebrush has long been recognized as inhabiting sites that are drier than those occupied by the basin subspecies (*A. tridentata* ssp. *tridentata*) and lower in elevation than those occupied by the mountain subspecies (*A. tridentata* ssp. *vaseyana* [Rydb.] Beetle) (West, 1983a). Recently, it been discovered that ssp. *wyomingensis* originates via the hybridization of these two parental subspecies (Richardson et al., 2012). Furthermore, ssp. *wyomingensis* is polyphyletic, meaning such hybridization events have occurred independently at multiple times and places (Richardson et al., 2012).

Here we describe and emphasize the extensive structural and functional modifications to the Wyoming sagebrush ecosystem with the aid of a *state-and-transition model* (Fig. 1) based on the treatments of Stringham et al. (2003) and Chambers et al. (2014b). This starts with the *reference* (pristine) *state*, which consists of two *community phases*, either of which may be present at a particular ecological site at any particular time. These are the intact phase (Fig. 1, reference state, left) and the native perennial grass dominance phase (Fig. 1, reference state, right). A phase shift from the first to the second may result from naturally occurring wildfire, prescribed burning, or herbicide application. The latter two causes are historic management practices that have been applied to reduce sagebrush density in order to improve forage availability or wildlife habitat. For example, sandberg bluegrass and squirreltail displayed an increase in cover percentage in response to sagebrush-removal treatments in Wyoming big sagebrush communities (Chambers et al., 2014b). This phase shift is reversible, as the native perennial grass dominance phase may revert to the intact phase upon reoccupation by sagebrush.

The "at-risk" state

Of greater consequence than a phase shift is the conversion of the reference state to an altered state upon disturbance. Disturbance is important in all ecosystems, yet due to ecological resilience, it does not always result in significant ecosystem change (Chambers et al., 2014a). For example, mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* [Rydb.] B. Boivin) communities, found at moister sites at higher elevations, are relatively resistant to downy brome invasion, particularly in face of fire (Seefeldt et al., 2007; Chambers et al., 2014b). Wyoming big sagebrush communities, however, display low ecological resilience to disturbance (Chambers et al., 2014a).

The first *transition* toward degradation is characterized by changes in the Wyoming big sagebrush community structure, e.g., loss of herbaceous perennials, arrival of exotic annual grasses and perennial forbs, increased patchiness of vegetation, and increased bare ground, which are driven by disturbance (see Appendix C). The result of Transition 1 is an "at-risk" (Bestelmeyer et al., 2010) depauperate invaded state (Fig. 1,

center left). The initial presence of annual grasses that characterizes this state may be facilitated by a history of inappropriate grazing (Brotherson and Brotherson, 1981; Allen-Diaz and Bartolome, 1998) or triggered by a high-severity fire following a history of grazing exclusion (Davies et al., 2009). Either way, an *ecosystem threshold* has been crossed from the reference state (Transition 1), and reversal requires human intervention. Today, this usually involves the seeding of native species. Historically, however, crested wheatgrass was widely seeded on these sites specifically to provide forage for livestock grazing (seeded pasture state).

The at-risk state typically features a severely reduced component of the grazing-susceptible bluebunch wheatgrass and a much larger component of downy brome, co-occurring with native bunchgrasses such as sandberg bluegrass, Thurber's needlegrass, and/or bottlebrush squirreltail (Reisner et al., 2013). The potential for reestablishment of desirable herbaceous species without human intervention is limited due to depletion of their seed bank. However, as stated above, there may be an opportunity at this point to return to the reference state with a seeding of native herbaceous perennials. For this reason, the at-risk state may be regarded as a *hybrid ecosystem*, as Transition 1 is potentially reversible (Hobbs et al., 2013; Fig. 3.2). Stated restoration objectives would be to reduce wildfire propensity, increase resilience, increase forage production, and/or improve wildlife habitat. However, it should be noted that risk is involved, particularly if the seeding fails. Disturbance of the soil surface by mechanical seeding operations can damage existing native vegetation (Knutson et al., 2014; see sandberg bluegrass data) or create microsite disturbances that facilitate downy brome invasion (Lavin et al., 2013).

If another threshold is crossed, to either the sagebrush/annual state (Transition 2) or the annual dominance state (Transition 3), reversal becomes much more difficult. Either of these two states may be considered a novel (as opposed to a hybrid) ecosystem. A novel ecosystem is one that results from intentional or inadvertent human activity, assembles and maintains itself without human intervention, manifests novel structural and/or functional attributes, and is not normally reversible (Hobbs et al., 2013).

The sagebrush/annual state

Once downy brome is present, continued inappropriate grazing can lead to the crossing of a second threshold (Transition 2) to the sagebrush/annual state (Fig. 1, center), which displays increasingly impaired *ecosystem functioning* over time. This state is highly susceptible to wildfire, and fire further reduces resistance to downy brome expansion (Chambers et al., 2014b). These authors estimate that about 20% cover of herbaceous perennials is required to resist increases in invasive annuals.

The annual dominance state

From the at-risk state, one or more wildfire events may trigger Transition 3, the crossing of another threshold (Friedel, 1991; Laycock, 1991; Bestelmeyer, 2006; Briske et al., 2006). Transition 3 may proceed from either the at-risk state or the sagebrush/annual state. In the resulting annual dominance state (Fig. 1, bottom center), undesirable exotic, early-maturing, annual grasses and biennial forbs may become increasingly dominant if their seed banks can be replenished prior to the onset of each fire season. The annual dominance state is both undesirable and stable due to high seed production of the annuals and recurring disturbances that favor them (Hassan and West, 1986; Humphrey and Schupp, 2001). This state features greatly increased frequency, size, and duration of wildfire (Balch et al., 2013), with the fire-return interval contracting from 107 years for the reference state and 75 years for the at-risk state to nine years for the annual dominance state (Weltz et al., 2014). Abundance of native species is sharply reduced, and desirable shrubs, particularly sagebrush, are extirpated due to their inability to resprout following fire (Britton and Ralphs, 1979).

Plant-soil feedbacks (PSF) may affect the stability of ecosystem states. A plant species' PSFs, i.e., soil-borne effects on plant growth such as the species' root exudates or accumulated pathogens, are a legacy of the soil's previous exposure to that species, and they may impact that species' growth either positively or negatively (Kulmatiski et al., 2008). Grasses, in particular, display highly negative PSFs, i.e., ones that hinder themselves, while exotic invasive species display less negative PSFs. These authors have suggested that this may explain why grasslands are particularly susceptible to exotic invasions. The less negative PSFs of exotic invasives may also explain the high stability of the annual dominance state.

Historic seeded pasture state

The original introduction of crested wheatgrass into the United States was in the northern Great Plains, and it was not until 1932 that the first known seedings in the Intermountain Region were planted in southeastern Idaho (Young and Evans, 1986). There, enthusiasm among ranchers for this grass grew quickly (Conner, 2008, ch. 3). After World War II, seedings of crested wheatgrass (*Agropyron* Gaertn. spp.) became widespread in the Intermountain West, particularly due to its forage value and grazing tolerance (Gunnell et al., 2011) (Figs. 2, 3). The native bunchgrasses of the sagebrush communities are relatively susceptible to grazing in comparison (Caldwell et al., 1981; Richards, 1984; Richards et al., 1988). Thus, for economic reasons, the
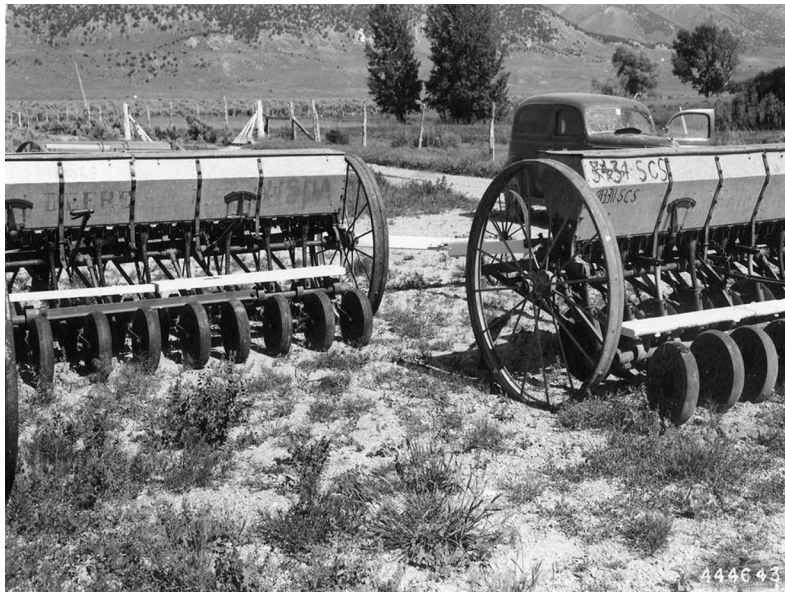
intentional conversion of reference state sites to seeded crested wheatgrass pastures became commonplace (Fig. 1). To displace sagebrush for crested wheatgrass seedings, 2,4-D was employed initially (Hull et al., 1952), but later tebuthiuron came to be widely used as well (Britton and Sneva, 1983).

By the late 1940s, crested wheatgrass had become recognized as a perennial grass capable of competing with downy brome, by then recognized as an invasive species (Hull and Stewart, 1948). Crested wheatgrass made possible the conversion of the depauperate invaded state and the sagebrush/annual state to the more stable seeded pasture state (Fig. 1). Seedings of crested wheatgrass were further encouraged by the Halogeton Control Act of 1952, leading to a 'Golden Age' of rangeland seedings that encompassed the decade between the mid-1950s and mid-1960s (Young and Evans, 1986).

Crested wheatgrass has been criticized for its lack of biological diversity when sown in monoculture (Marlette and Anderson, 1986). Nevertheless, when a sagebrush seed source is proximally located, big sagebrush may reoccupy crested wheatgrass stands (Fig. 1, state 3) (Johnson, 1958), leading to the return of native non-game bird populations (McAdoo et al., 1989). Crested wheatgrass can also serve as an effective firebreak to protect remnant pristine areas (Conner, 2008, ch. 4). Today, native bunchgrasses, particularly bluebunch wheatgrass and Snake River wheatgrass (*Elymus wawawaiensis* J. Carlson & Barkworth), are widely seeded in the region, though they are generally less effective than crested wheatgrass for reversing the dominance of invasive annual greases (Davies et al., 2015). Thus, as a form of insurance, crested wheatgrass is commonly

seeded together with native perennial grasses (Davies et al., 2015). However, in seeding mixtures that include both crested wheatgrass and native perennial grasses, the more vigorous crested wheatgrass seedlings negatively impact native grass seedling establishment (Knutson et al., 2014).

Plant materials for Wyoming big sagebrush communities

Considerations for plant materials for modified sites

Today, the use of native species may seem like the obvious choice for rangeland restoration. However, early attempts to seed native species met largely with failure, especially relative to the recently introduced crested wheatgrasses. For example, Hull (1974) summarized the results of 60 seeding experiments across southern Idaho that evaluated a total of 90 species. At least partial success was achieved with 42 of these species, while total failure was experienced for all attempts at seeding the remaining 48. Of the 42 species, the crested wheatgrasses (*Agropyron* spp.) had at least a 97% success rate in stand establishment, while the best native species were considerably lower: sandberg bluegrass (75%), western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve) (58%), beardless bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve ssp. *inerme*) (54%), thickspike wheatgrass (*Elymus lanceolatus* [Scribn. & J.G. Smith] Gould) (33%), awned bluebunch wheatgrass (*P. spicata* ssp. *spicata*) (29%), and big bluegrass (*Poa ampla* Merr.) (27%). More recently, across 34 trials involving 18 grass species, Robins et al. (2013) found that thickspike wheatgrass was the only native species comparable to introduced species for establishment at low-precipitation (< 310 mm annually) sites, though many others performed better at more mesic sites. These data help explain the greater interest in crested wheatgrass relative to native species for many years, as well as the necessity to develop more effective plant materials of native species, particularly for lower-precipitation regions. In previous work (Jones, 2003), we have suggested the use of the plant material that is most closely phylogenetically related to the indigenous material currently or previously present, yet is still able to establish and function on the often-modified site.

For at-risk sites threatened by the stresses and impacts of ecological change, use of genetically appropriate plant materials in combination with improved management may be preferred by many restoration practitioners. However, rates of restoration success are much lower for the sagebrush/annual state and especially for the annual dominance state than for the relatively tractable at-risk state (Davies and Johnson, 2011). Indeed, Transition 3 is often considered irreversible (Fig. 1) (Stringham et al., 2003). When modification beyond the historic range of variation has occurred, Kessler and Thomas (2006) have suggested a prescriptive approach, namely managing for a biological community with enhanced ecological resilience, even if differs from the reference state.

Perennial plant materials intentionally developed for tolerance to common stresses resulting from intentional or inadvertent human activities are key to such efforts (Hull and Stewart, 1948; Robins et al., 2013). Over the past several decades, novel/non-local native plant materials have been developed by 1) choosing among large numbers of wildland-collected populations evaluated in common gardens, 2) hybridization among particular populations to expand genetic variation or combine desired traits, 3) artificial selection for critical functional traits, or 4) some combination of the above (Jones and Robins, 2011). More recently, a second approach toward plant material development has gained favor. Natural/local native plant materials that are representative of geographically defined seed transfer zones defined for a given species can be generated based on the quantitative expression of adaptive traits by a series of wildland-collected populations evaluated in common gardens (Erickson et al., 2004; Johnson et al., 2010b, 2012, 2013; Parsons et al., 2011; St. Clair et al., 2013). This second approach has long been employed for timber species, but only recently has been extended to herbaceous species (Johnson et al., 2004). Regardless of the approach employed, a critical need exists for native plant materials that increase the probability of reversing Transitions 1 and 2. Plant materials must be able to establish, grow, reproduce, and recruit new generations of propagules on the modified sites that are commonly targeted for restoration.

We have employed the first approach (novel/non-local) to develop ecologically appropriate plant materials that feature greater genetic variation, better abiotic stress tolerance, and greater competitive ability against downy brome. Their seedlings should be more vigorous, and they should be able to rebuild the native seed bank. Our objective, over time, is to increase viable native plant material options for the restoration practitioner. This is an iterative process that we hope will yield incremental gains in plant adaptation across multiple generations of native plant materials. As more plant materials of individual species become available, within-species genetic diversity within and among the available plant materials will increase. The second (natural/local) approach involves hybridization or bulking of populations within a seed transfer zone, creating genetically appropriate plant materials. To date, this approach has not encompassed the practice of artificial selection, but such a combination of the two approaches has intuitive appeal. The advantages of the natural/local approach are that it provides good adaptation to typical environments within the seed transfer zone and that it is representative of naturally occurring genetic patterns resulting from past evolutionary processes.

Objections to the novel/non–local approach and a brief rebuttal

The principle ecological objection to novel/non-local plant materials relies on the presumption that they are unlikely to be ecologically adapted to local conditions because they did not evolve within their context. However, due to the advent of novel ecosystems and altered ecosystem states, there is only limited reason to believe that local genotypes that are presumably products of natural selection are particularly well adapted to the new conditions. Thus, the ecological grounds for the exclusive use of local plant materials in restoration are weak (Jones, 2013b). The principal genetic objection to novel/non-local plant materials involves the claim that such plant materials may introduce unadapted genes that may display undesirable genetic interactions upon hybridization with remnant local plant material on the restoration site. However, this genetic objection understates the ability of natural selection to ameliorate such circumstances.

This leaves the preservation of evolutionary patterns as seemingly the most legitimate scientific argument against novel/non-local plant materials (Sackville Hamilton, 2001). Yet with the preservation argument, what remains are values-based motivations rooted in a latent belief in a balance-of-nature. This belief quickly becomes a dilemma in a rapidly changing world, and such justifications will be increasingly difficult to sustain in the Anthropocene. Such a preservation ethic reflects a desire to do whatever can be done to preclude, or at least to control and direct, evolutionary change. Yet, whether humanity exerts an influence or not, evolutionary patterns come and go, hence the term "evolution." While the intention of the preservation ethic may be to free nature from humanity, the actual consequence is to hinder the ordinary operation of evolutionary processes, making humankind itself the author of evolution. Ironically, this is the ultimate expression of the Anthropocene.

Thus, evolution is stood on its head. Evolution becomes viewed wrongly as an optimizing and inerrant force (Gould, 1998) that must be preserved, thus contradicting its own living and ever-changing nature. This has the unfortunate and unintended result of turning the term "evolutionary change" into an oxymoron, as the preservation of evolutionary patterns of the past takes precedence over providing for evolutionary processes to guide the future (Broadhurst et al., 2008). It should be remembered that evolutionary processes beget evolutionary patterns, not the other way around. Thus the question is raised, "is restoration merely about perpetuating a museum of relics and artifacts?" If this is even partly true, it calls into question the exclusive use of local plant materials as an *ecosystem management* practice, which ostensibly benefits the entire ecosystem and not just one or a few of its components.

In contrast to the genetically appropriate approach, our assisted evolution approach (Jones and Monaco, 2009) emphasizes evolutionary processes, and it proposes to feed these processes with significant quantities of genetic variation using ecologically appropriate plant materials. To the person with an intrinsic interest in the genetic integrity of native plants and who looks to the past as a restoration target, the arguments for novel/non-local plant materials are less than convincing. But to the person who is interested in restoring the health of the land, i.e., the functioning of the ecosystem as a whole, and who looks to the future fully cognizant of the difficulties that must be overcome to achieve restoration goals, not only are these arguments convincing, they are also liberating.

More effective native plant materials for functional restoration

According to the state-and-transition model (Fig. 1), two primary problematic states in the Wyoming sagebrush ecosystem may occur. First, increased shrub density and/or suboptimal forage production for ranching operations and wildlife habitat, combined with depletion of the herbaceous understory, lead to replacement by annual grasses. Second, shrubs become locally extinct and wildfire maintains annual grass dominance, limiting the seasonality of forage production, ecosystem capture of solar energy, and cycling of water and nutrients. Missed opportunities or failed attempts to reestablish the herbaceous understory often result in increased functional change, e.g., more frequent wildfires, further cheatgrass dominance, and continued soil/site degradation. However, changes in species composition that result in repair of specific ecological processes (Stringham et al., 2003; Monaco et al., 2012) may increase ecosystem functioning.

Plant materials are needed that address these two problematic states. Ecologically appropriate plant materials can conceivably play a role in their repair by virtue of specific *functional traits* they possess (Jones et al., 2010). Indeed, plant functional traits are increasingly being used to inform restoration (Funk et al., 2008; Roberts et al., 2010; Clark et al., 2012; Larson et al., 2014). If functional traits that confer ecological fitness, i.e., the ability to establish, grow, and reproduce, can be identified, artificial selection for these traits may potentially lead to plant materials that are able to restore a degree of ecosystem functioning (Jones and Monaco, 2009; Jones et al., 2010). As *feedback switches* are modified, e.g., by diminishing the annual grass-fuel-fire feedback loop, or are replaced with feedbacks that rebuild desirable species populations and ecosystem functioning, ecosystems may eventually regain desirable structural components and build resilience that hinders reversion to the undesired state. Recently, trait-based models have been used to determine traits, trait values, and species assemblages that contribute to effective ecosystem functioning (Laughlin, 2014). In this case, native

species were identified that collectively display similar trait values to an exotic invader, Dalmatian toadflax (*Linaria dalmatica* [L.] Mill.), thereby providing an opportunity to competitively exclude it (Laughlin, 2014).

When managing for functional diversity, a key question faced by restoration practitioners is whether local native genotypes are best suited to initiate self-recovery in highly modified ecosystems. More specifically, if interventions create windows of opportunity for reintroducing local genotypes, are they the best adapted to the site simply because they exist(ed) locally? Furthermore, using the terminology of Walker (1992), do local genotypes have the capacity to function as drivers of ecological processes as opposed to merely occupying the site as ecological passengers? We suggest that the answers to these questions may first depend on post-disturbance native-species abundance, i.e., whether the remnant populations are sufficiently large to rebound demographically, e.g., Grime (1998), particularly given the superior competitive ability of downy brome. Alternatively, a threshold may have been crossed whereas populations continue their decline. Second, the answers may depend on whether native-species abundance is closely associated with measurable effects on the ecological processes needed to reverse degradation and initiate sustainable ecosystem dynamics at a particular site. The basis for these suggestions arises from the recognition that plant-community composition is capable of regulating important ecological processes (Luck et al., 2009) and the independent effects of individual species on these processes (Eviner and Chapin, 2003).

Improved seedling recruitment

The ability of herbaceous perennials, particularly grasses, to recruit seedlings in modified Wyoming big sagebrush ecosystems is critical to the restoration of these systems. The most important reason that an exotic, crested wheatgrass, has been so widely used and continues to be used is its much better seedling recruitment relative to native grasses under a variety of environmental conditions. A great deal of the effort invested in native plant material development for these ecosystems has been and will continue to be directed towards increasing the numbers of seed produced and the frequency that those seeds become established seedlings, the two components of seedling recruitment. The four key life transitions that make up seedling recruitment are germination, seedling emergence, seedling establishment to an autotrophic state, and seedling survival through the end of the first growing season (Fenner and Thompson, 2005). Of these, emergence has been shown to be the most important for rangeland species (James et al., 2011; Larson et al., 2014). Thus, native plant materials with an improved ability to emerge, particularly in unfavorable soil environments, may increase the probability of successful seedling recruitment. Low coleoptile tissue density, i.e., dry-matter percentage, is a functional trait associated with high emergence (Larson et al., 2014).

Several native grass plant materials have been *released* for use on Intermountain rangelands based on their improved ability to emerge and establish (Robins et al., 2013). 'Recovery' western wheatgrass, in particular, was developed by artificial selection for improved rate of seedling emergence from deep seeding (Waldron et al., 2011). Significant advances in seedling establishment have been made in bluebunch wheatgrass (since 1946) and Snake River wheatgrass (since 1980), mirroring the progress made in crested wheatgrass (Fig. 4). Likewise, progress in seedling establishment has been made in Indian ricegrass (*Achnatherum hymenoides* [Roem & Schult.] Barkworth) (Robins et al., 2013). Also, while squirreltail plant material work has only been conducted over a short time, with the earliest release (Sand Hollow Germplasm) made in 1996, materials are now available that, in some cases, rival 'Hycrest' crested wheatgrass for seedling establishment (Fig. 5). This squirreltail trial (Fig. 5) is of particular interest, as seedlings emerged in a loamy clay despite soil crusting. Our
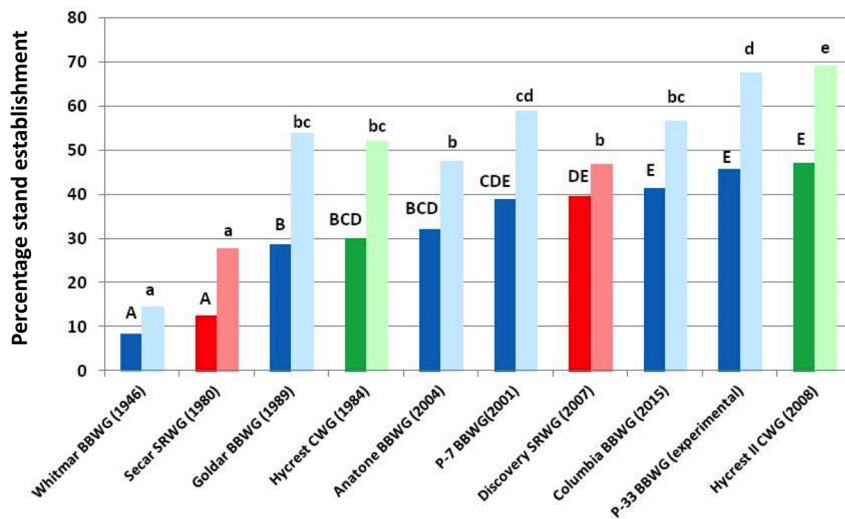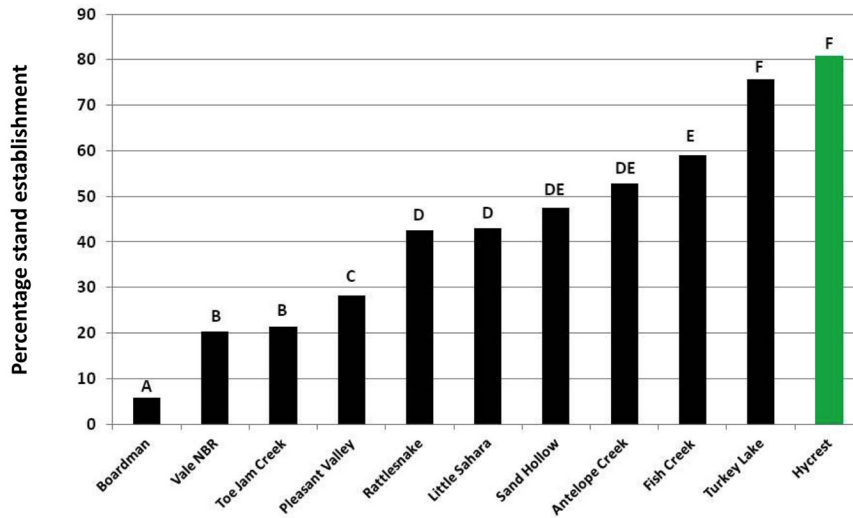

Figure 4

First- and second-year seedling establishment percentage in a dormant seeding planted at Nephi, Utah on November 6, 2012.

Data collected on May 30, 2013 (dark bars; means separated by upper-case letters) and April 3, 2014 (light bars; means separated by lower-case letters). Included are six bluebunch wheatgrass (BBWG; native; blue bars), two Snake River wheatgrass (SRWG; native; red bars), and two crested wheatgrass (CWG; exotic; green bars) plant materials, each released in the year indicated within parentheses. The absence of a letter in common indicates significant differences among plant materials (*P* < 0.05).

doi: 10.12952/journal.elementa.000047.f004

trials, which are initiated annually, have not included genetically appropriate plant materials for comparison to date because they are not yet available. However, our intention is to include them in these trials as they are released (Johnson et al., 2010a).

Conclusion

When restoration is directed toward highly modified ecosystems, the ecological context required to assemble a functioning ecosystem must be considered. Here we have detailed the extensive and intensive ecological modification of the Wyoming big sagebrush ecosystems in order to highlight the intensity of the obstacles that native plant materials must overcome. This is the ecological context within which these plant materials must function. It would be a great mistake to miss, underappreciate, or misunderstand this context. It is this ecological context that often dictates what is technically feasible. In this vein, we suggest the utility of ecologically appropriate plant materials that are novel/non-local as pragmatic alternatives to genetically appropriate plant materials when the latter are insufficient for correction of recalcitrant modified states. Specifically, we propose that novel/non-local plant materials that exhibit improved stress tolerance, enhanced ecological fitness, greater contributions to ecosystem functioning, and improved delivery of ecosystem services in the substantially modified novel ecosystems that increasingly predominate in our world have potential merit for ecological restoration.

Appendix A

Glossary of terms italicized upon first mention in the text

artificial selection	The modification of a population's genotype by culling undesired individuals.
community phase	One of multiple approximated seral stages of vegetation development within an ecosystem state (Bestelmeyer et al., 2003).
ecological fitness	The ability of a plant or population to persist and propagate itself on a site.
ecosystem management	Natural resource management based on the welfare of the ecosystem as a whole rather than on one or a few components of the ecosystem.
ecosystem state	One of multiple possible soil/plant community combinations for an ecological site (lands with similar soils/landform/ climate), separated from others by threshold boundaries and irreversible without significant management input.
ecologically appropriate plant materials	Plant materials that exhibit ecological fitness on their intended site, demonstrate compatibility with other desirable species in the ecological community, and do not display a tendency to invade adjacent sites; may encompass hybridization (to augment genetic variation to fuel natural selection) or artificial selection (to improve general adaptation and stress tolerance) if necessary to reach restoration objectives, particularly for widespread, cross-pollinating generalist species (Jones, 2013a); may be natural/local, natural/non-local, novel/local, or novel/non-local.
ecosystem functioning	Key processes or properties of the whole ecosystem that are used to compare ecosystems or assess the performance of whole ecosystems (Jax, 2010).

feedback switch	A point when negative feedbacks that maintain ecosystem resilience switch to positive feedbacks that decrease ecosystem resilience; feedback switches may contribute to a state change via a threshold (Briske et al., 2008).
functional traits	Plant traits that impact ecological fitness.
genetically appropriate plant materials	Plant materials that are locally adapted, regionally appropriate, and genetically diverse, being developed without artificial selection for specific traits or hybridization among genetically disparate populations, i.e., natural/local (Johnson et al., 2010).
hybrid ecosystem	An altered ecosystem derived from the reference state that may be returned to the reference state by ecological restoration.
land-use legacy	Changes in basic ecosystem processes that persist for years to millennia due to human utilization of lands (Morris and Rowe, 2014).
"local is best"	The assumption that a local population is best adapted to its indigenous site relative to other populations of the same species.
natural plant material	A plant material developed without artificial selection and without involving hybridization with a distant genotype.
novel ecosystem	An ecosystem characterized by novel species assemblages or ecosystem functioning and resulting from intentional or inadvertent human action, though not requiring human activity for its continued existence (Hobbs et al., 2009).
novel plant material	A plant material developed by artificial selection or involving hybridization with a distant genotype.
plant material	Seeds or other propagules of a cultivar, germplasm, population, or genotype.
release	An administrative action making a new plant material available to the public, e.g., seed growers, nurseries, and restoration practitioners.
reference state	The ecological state that supports the most potential ecosystem services; the reference state is used to derive the condition or status of all other states and phases within a state-and-transition model; this state is regarded as representing the historical or natural range of variability for or ecosystem functioning most preferred by a society (Bestelmeyer et al., 2009).
resilience	The ability of ecological processes, structure, and functioning to recover from stress and disturbance (Chambers et al., 2014a).
resistance	The ability of an ecosystem to preclude or minimize the invasion of exotic species.
seed transfer zone	A geographically defined zone within which plant material of an individual species may be translocated without adverse adaptation; boundaries determined by measurement of plant traits in a variety of populations in common gardens.
state-and-transition model	A model consisting of ecosystem states connected by transitions across ecosystem thresholds.
thresholds	Boundaries between alternative stable vegetation states that may be crossed upon biotic and abiotic changes in a system, requiring human intervention to repair (Whisenant, 1999).
transition	A trajectory from one ecological state to another caused by external and internal feedback mechanisms; transitions are generally viewed as irreversible without active restoration inputs (Whisenant, 1999; Bestelmeyer et al., 2003).

doi: 10.12952/journal.elementa.000047.t001

Appendix B

Downy brome invasion and its impacts

Downy brome (*Bromus tectorum* L.) was introduced to the West in multiple events, either inadvertently or, in some cases, intentionally (Novak and Mack, 2001). The earliest known record of this species in western North America was in British Columbia in 1889, but by 1902, downy brome was present in Washington, Utah, Colorado, and Oregon (Novak and Mack, 2001). Downy brome quickly became a dominant weed on both degraded rangeland and on land newly cultivated by homesteaders for wheat production in the Pacific Northwest (Mack, 1981). By 1930, downy brome had already occupied much of its current distribution in British Columbia, Washington, Oregon, Idaho, Nevada, and Utah (Mack, 1981). As of 10 years ago, downy brome and another invasive annual grass, medusahead wildrye (*Taeniatherum caput-medusae* [L.] Nevski), had infested 22 and 1 million hectares of rangeland, respectively, in the 17 western states (Duncan et al., 2004). Introduced ruderal biennial forbs, such as Russian thistle (*Salsola kali* L.), flixweed (*Descurainia sophia* [L.] Webb), and tumble mustard (*Sysimbrium altissimum* L.), also became prominent (Piemeisel, 1951).

Initially, the decrease in native perennial grass cover due to historical mismanagement allowed sagebrush to increase (Brooks and Chambers, 2011). But once downy brome arrived, its high plasticity, particularly its ability to produce copious amounts of seed when conditions are favorable (Young and Evans, 1978), allowed

it to spread rapidly into depleted understories (Fig. 6). Increased fine fuels led to increased wildfire frequency and ultimately to the removal of the fire-sensitive Wyoming big sagebrush from plant communities (Brooks and Chambers, 2011) (Figs. 7, 8). High wildfire incidence has also increased the severity of runoff and wind (Fig. 9) and water erosion (Wilcox et al., 2012; Weltz et al., 2014) (Fig. 10).

Downy brome displays a superior ability to extract soil resources, both generally (James et al., 2009) and specifically in the cooler months, making it competitive against natives that do not initiate root growth until spring (Harris, 1967; Kulmatiski et al., 2006a). Downy brome is less dependent on soil mycorrhizal associations than native perennial grasses for nutrient extraction, possibly because of its high root-surface area (Owen et al., 2013). As native perennials are reduced, soil water and nitrogen that were previously utilized by them become available for production of downy brome biomass and seed (Blank et al., 1996; Stubbs and Pyke, 2005; Leffler and Ryel, 2012). When native-species loss is combined with wildfire, they generate a synergistic effect on resource availability (Chambers et al., 2007). Excess or unused resources may also facilitate the invasion of additional undesirable species if resource availability coincides with propagule availability of the invaders (Davis et al., 2000).

Downy brome has a remarkable impact on soil microbes and soil functioning. Unlike sagebrush, downy brome is a poor host for arbuscular mycorrhizal fungi (Weber et al., 2015). These fungi facilitate nutrient uptake in their hosts and generate soil macroaggregates that sequester soil carbon. Thus, downy brome-dominated

soils sequester less carbon and favor species of soil fungi that are saprophytic or pathogenic relative to sagebrush-dominated soils (Weber et al., 2015). Downy brome also reduces the vertical stratification of phylogenetic diversity of soil bacteria across soil depth relative to sagebrush-dominated soils, which display more homogeneous soil bacterial communities that are more homogeneous across soil depth (Weber, 2015). Thus, dominance by downy brome likely impacts carbon cycling and plant-soil fungi interactions.

Invasive annual grasses increase soil nitrogen mineralization rates (Ryel et al., 2010) but senesce by early summer, generating large pools of nitrate in the fall (Booth et al., 2003). Presumably, this fall spike of nitrogen may be available for growth of downy invasive annual seedlings, allowing them to escape competition from already senesced perennial species. Once established, invasive annual grasses may further drive mineralization of soil nutrients to inorganic mineral forms of nitrogen and carbon, thus perpetuating mineralized soil environments (Booth et al., 2003; Norton et al., 2007) that increasingly favor annual grasses over time (Norton et al., 2004a; Kulmatiski and Beard, 2008). Changes in associated soil fungal populations also favor fast-growing annuals over perennial species (Kulmatiski et al., 2006b). Increased soil porosity, due to annual grasses' fine roots, enhances microbial decomposition near the soil surface by increasing exposure to air and water, reduces soil organic-matter content, negatively impacts soil structure, and increases turnover of carbon and nitrogen pools (Norton et al., 2004a, 2004b). These modified nutrient pools can be described as "leaky," meaning that nutrients are now susceptible to being permanently lost from the ecosystem via denitrification

(gaseous loss to the atmosphere) or leaching (Schimel, 1986; Evans et al., 2001; Norton et al., 2012). Consequently, exotic species may be 'drivers' as well as 'passengers' of ecological change (McDougall and Turkington, 2005; Kulmatiski and Beard, 2008).

Downy brome's ability to increase wildfire frequency, to complete its life cycle prior to summer drought, to reproduce prolifically, and to manipulate the ecosystem to its advantage, explains its tendency to displace native vegetation. In addition to these indirect effects of invasive species on desirable plants, the existence of direct effects has also been documented. Sequestering soil organic compounds by adding activated charcoal to soils dominated by exotic species reduces growth of downy brome and diffuse knapweed, while increasing native grass growth (Kulmatiski and Beard, 2006; Kulmatiski, 2011). This suggests that these exotic species produce organic compounds, sequestered by the activated charcoal, that either encourage their own growth or discourage the growth of their competitors, i.e., allelopathy.

Appendix C

Disturbance and ecological legacies

Historical disturbances in the late 19th and early 20th centuries included inappropriate grazing, cultivation, and shrub removal. Between time of settlement and the passage of the 1936 Taylor Grazing Act, excessive grazing of Wyoming big sagebrush communities was pervasive. During the spring, when reproductive tillers are elongating, grazing damages native perennial bunchgrasses, particularly bluebunch wheatgrass (Mueggler, 1972; Busso and Richards, 1995; Jones and Nielson, 1997; Mukherjee et al., 2013). The susceptibility of native bunchgrasses to inappropriate grazing has been attributed to an evolutionary history of minimal grazing pressure due to small populations of native ungulates west of the Rocky Mountains (Mack and Thompson, 1982). Reduction of native bunchgrass density and damage to biological soil crusts by hoof action of large herbivores increases the size and connectivity of gaps between perennial vegetation, thus increasing the opportunities for weed invasion (Peterson, 2013; Reisner et al., 2013).

Besides inappropriate grazing, other intentional disturbances have altered the Wyoming sagebrush ecosystems. During a historical period of high grain prices and high natural rainfall (the early 1910s to the early 1920s), shrubs were mechanically removed to facilitate dry-farming (cultivation without irrigation) of newly homesteaded lands (Morris et al., 2011) (Fig. 11). Also, promiscuous burning of shrubs was practiced in the early 20th century to stimulate herbaceous growth for livestock grazing (Pickford, 1932). Later, mechanical (Fig. 12, 13) and chemical removal of sagebrush became widely used to improve productivity of herbaceous species for grazing livestock (Eckert and Evans, 1968) and wildlife habitat (Dahlgren et al., 2006). Such activities have generated *ecological legacies* that have persisted long after the original disturbance abated (Kulmatiski and Beard, 2008, 2011; Morris et al., 2011, 2013). These ecological legacies and the continuing presence of exotic plants can contribute to a loss of abundance and diversity of soil microbes and fungi (Kulmatiski and Beard, 2008).

Figure 11
Abandoned farmland with farmhouse and fencing remaining.

Photo courtesy of the Utah State Historical Society.

doi: 10.12952/journal.elementa.000047.f011

Figure 12
Removal of native rangeland vegetation by disking.

Photo courtesy of the Utah State Historical Society.

doi: 10.12952/journal.elementa.000047.f012

Figure 13
Removal of native rangeland vegetation by railing and simultaneous seeding by two men using broadcast seeders.

Photo courtesy of the Utah State Historical Society.

doi: 10.12952/journal.elementa.000047.f013

Novel plant materials for novel ecosystems

References

Aber JD, Jordan WR III. 1985. Restoration ecology: an environmental middle ground. *BioScience* **35**: 399.

Allen-Diaz B, Bartolome JW. 1998. Sagebrush-grass vegetation dynamics: comparing classical and state-transition models. *Ecol Appl* **8**: 795–804.

Balch JK, Bradley BA, D'Antonio CM, Gomez-Dans J. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Glob Change Biol* **19**: 173–183.

Bestelmeyer BT. 2006. Threshold concepts and their use in rangeland management and restoration: the good, the bad, and the insidious. *Restor Ecol* **14**: 325–329.

Bestelmeyer BT, Brown JR, Havstad KM, Alexander R, Chavez G, et al. 2003. Development and use of state-and-transition models for rangelands. *J Range Manage* **56**: 114–126.

Bestelmeyer BT, Moseley K, Shaver PL, Sanchez H, Briske DD, et al. 2010. Practical guidance for developing state-and-transition models. *Rangelands* **32**: 23–30.

Bestelmeyer BT, Tugel AJ, Peacock GL, Robinett DG, Shaver PL, et al. 2009. State and transition models for heterogeneous landscapes: a strategy for development and application. *Rangel Ecol Manage* **62**: 1–15.

Blank RR, Allen FL, Young JA. 1996. Influence of simulated burning of soil litter from low sagebrush, squirreltail, cheatgrass, and medusahead sites on water-soluble anions and cations. *Int J Wildland Fire* **6**: 137–143.

Booth MS, Stark JM, Caldwell MM. 2003. Inorganic N turnover and availability in annual- and perennial-dominated soils in a northern Utah shrub-steppe ecosystem. *Biogeochemistry* **66**: 311–330.

Briske DD, Bestelmeyer BT, Stringham TK, Shaver PL. 2008. Recommendations for development of resilience-based state-and-transition models. *Rangel Ecol Manage* **61**: 359–367.

Briske DD, Fuhlendorf SD, Smeins FE. 2006. A unified framework for assessment and application of ecological thresholds. *Rangel Ecol Manage* **59**: 225–236.

Britton CM, Ralphs MH. 1979. Use of fire as a management tool in sagebrush ecosystems, in, The Sagebrush Ecosystem: a Symposium. Logan, Utah: Utah State University, College of Natural Resources: pp. 101–109.

Britton CM, Sneva FA. 1983. Big sagebrush control with tebuthiuron. *J Range Manage* **36**: 707–708.

Broadhurst LM, Lowe A, Coates DJ, Cunningham SA, McDonald M, et al. 2008. Seed supply for broadscale restoration: maximizing evolutionary potential. *Evol Appl* **1**: 587–597.

Brooks ML, Chambers JC. 2011. Resistance to invasion and resilience to fire in desert shrublands of North America. *Rangeland Ecol Manage* **64**: 431–438.

Brotherson JD, Brotherson WT. 1981. Grazing impacts on the sagebrush communities of central Utah. *Great Basin Nat* **41**: 335–340.

Brummer EC, Barber WT, Collier SM, Cox TS, Johnson R, et al. 2011. Plant breeding for harmony between agriculture and the environment. *Frontiers Ecol Environ* **9**: 561–568.

Busso CA, Richards JH. 1995. Drought and clipping effects on tiller demography and growth of two tussock grasses in Utah. *J Arid Environ* **29**: 239–251.

Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* **50**: 14–24.

Callicott JB. 2002. Choosing appropriate temporal and spatial scales for ecological restoration. *J Bioscience* **27** (Supplement 2): 409–420.

Chambers JC, Bradley BA, Brown CS, D'Antonio C, Germino MG, et al. 2014a. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. *Ecosystems* **17**: 360–375.

Chambers JC, Miller RF, Board DI, Pyke DA, Roundy BA, et al. 2014b. Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. *Rangel Ecol Manage* **67**: 440–454.

Chambers JC, Roundy BA, Blank RR, Meyer SE, Whittaker A. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? *Ecol Monogr* **77**: 117–145.

Clark DL, Wilson M, Roberts R, Dunwiddie PW, Stanley A, et al. 2012. Plant traits - a tool for restoration? *Appl Veg Sci* **15**: 449–458.

Conner L. 2008. Growing wild: crested wheatgrass and the landscape of belonging [thesis]. Logan, Utah: Utah State University.

Dahlgren DK, Chi R, Messmer TA. 2006. Greater sage-grouse response to sagebrush management in Utah. *Wildlife Soc B* **34**: 975–985.

Davies KW, Johnson DD. 2011. Are we "missing the boat" on preventing the spread of invasive plants in rangelands? *Invasive Plant Sci Manage* **4**: 166–172.

Davies KW, Boyd CS, Johnson DD, Nafus AM, Madsen MD. 2015. Success of seeding native compared with introduced perennial vegetation for revegetating medusahead-invaded sagebrush rangeland. *Rangel Ecol Manage* **68** (in press). http://dx.doi.org/10.1016/j.rama.2015.03.004

Davies KW, Svejcar TJ, Bates JD. 2009. Interaction of historical and nonhistorical disturbances maintains native plant communities. *Ecol Appl* **19**: 1536–1545.

Davis MA, Grime JP, Thompson K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* **88**: 528–534.

DiTomaso JM. 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Sci* **48**: 255–265.

Dregne HE. 2002. Land degradation in the drylands. *Arid Land Res Manage* **16**: 99–132.

Duncan CA, Jachetta JJ, Brown ML, Carrithers VF, Clark JK, et al. 2004. Assessing the economic, environmental, and societal losses from invasive plants on rangeland and wildlands. *Weed Technol* **18**: 1411–1416.

Eckert RE Jr, Evans RA. 1968. Chemical control of low sagebrush and associated green rabbitbrush. *J Range Manage* **21**: 325–328.

Erickson VJ, Mandel NL, Sorensen FC. 2004. Landscape patterns of phenotypic variation and population structuring in a selfing grass, *Elymus glaucus* (blue wildrye). *Can J Bot* **82**: 1776–1789.

Evans RD, Rimer R, Sperry L, Belnap J. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecol Appl* **11**: 1301–1310.

Eviner VT, Chapin RS III. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annu Rev Ecol Evol Syst* **34**: 455–485.

Fenner M, Thompson K. 2005. *The Biology of Seeds*. Cambridge, U.K.: Cambridge University Press.

Fleischner TL. 1994. Ecological costs of livestock grazing in western North America. *Conserv Biol* **8**: 629–644.

Friedel MH. 1991. Range condition assessment and the concept of thresholds: a viewpoint. *J Range Manage* **44**: 422–426.

Funk JL, Cleland EE, Suding KN, Zavaleta RS. 2008. Restoration through reassembly: plant traits and invasion resistance. *Trends Ecol Evol* **23**: 695–703.

Gould S.J. 1998. An evolutionary perspective on strengths, fallacies, and confusions in the concept of native plants. *Arnoldia* **58**: 11–19.

Grime JP. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J Ecol* **86**: 902–910.

Gunnell KL, Williams JR, Monaco TA. 2011. Clarifying potential successional trajectories in sagebrush communities historically seeded with crested wheatgrass. *Natur Resources Environ Issues* **16**: article 17.

Harris GA. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecol Monogr* **37**: 89–111.

Hassan MA, West NE. 1986. Dynamics of soil seeds pools in burned and unburned sagebrush semi-deserts. *Ecology* **67**: 269–272.

Hobbs RJ, Higgs ES, Hall CM. 2013. *Novel Ecosystems – Intervening in the New Ecological World Order*. Chichester, U.K.: John Wiley & Sons.

Hull AC Jr. 1974. Species for seeding arid rangeland in southern Idaho. *J Range Manage* **27**: 216–218.

Hull AC, Kissinger NA Jr., Vaughan WT. 1952. Chemical control of big sagebrush in Wyoming. *J Range Manage* **5**: 398–402.

Hull AC Jr, Stewart G. 1948. Replacing cheatgrass by reseeding with perennial grass on southern Idaho ranges. *J Am Soc Agron* **40**: 694–703.

Humphrey LD, Schupp EW. 2001. Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. *West N Am Naturalist* **61**: 85–92.

James JJ, Mangold JM, Sheley RL, Svejcar T. 2009. Root plasticity of native and invasive Great Basin species in response to soil nitrogen heterogeneity. *Plant Ecol* **202**: 211–220.

James JJ, Svejcar TJ, Rinella MJ. 2011. Demographic processes limiting seedling recruitment in arid grassland restoration. *J Appl Ecol* **48**: 961–969.

Jax K. 2010. *Ecosystem functioning*. Cambridge, U.K.: Cambridge University Press.

Johnson GR, Sorenson FC, Clair JBS, Cronn RC. 2004. Pacific Northwest forest tree seed zones - a template for native plants? *Native Plants J* **5**: 131–140.

Johnson R, Stritch L, Olwell P, Lambert S, Horning ME, et al. 2010a. What are the best seed sources for ecosystem restoration on BLM and USFS lands? *Native Plants J* **11**: 117–131.

Johnson RC, Erickson VJ, Mandel NL, St. Clair JB, Vance-Borland KW. 2010b. Mapping genetic variation and seed zones for *Bromus carinatus* in the Blue Mountains of eastern Oregon, USA. *Botany* **88**: 725–736.

Johnson RC, Cashman MJ, Vance-Borland K. 2012. Genecology and seed zones for Indian ricegrass collected in the southwestern United States. *Rangel Ecol Manage* **65**: 523–532.

Johnson RC, Hellier BC, Vance-Borland KW. 2013. Genecology and seed zones for tapertip onion in the US Great Basin. *Botany* **91**: 686–694.

Johnson WM. 1958. Reinvasion of big sagebrush following chemical control. *J Range Manage* **11**: 169–172.

Jones TA. 2003. The Restoration Gene Pool concept: beyond the native versus non-native debate. *Restor Ecol* **11**: 281–290.

Jones TA. 2009. Conservation biology and plant breeding: special considerations for the development of native plant materials for use in restoration. *Ecol Restor* **27**: 8–11.

Jones TA. 2013a. Ecologically appropriate plant materials for restoration applications. *BioScience* **63**: 211–219.

Jones TA. 2013b. When local isn't best. *Evol Appl* **6**: 1109–1118.

Jones TA, Monaco TA. 2009. A role for assisted evolution in designing native plant materials. *Frontiers Ecol Environ* **7**: 541–547.

Jones TA, Monaco TA, James JJ. 2010. Launching the counterattack: interdisciplinary deployment of native-plant functional traits for repair of rangelands dominated by invasive annual grasses. *Rangelands* **32**: 38–42.

Jones TA, Nielson DC. 1997. Defoliation tolerance of bluebunch and Snake River wheatgrasses. *Agron J* **89**: 270–274.

Jones TA, Robins JG. 2011. Appropriate use of genetic manipulation for the development of restoration plant materials. *Prog Bot* **72**: 249–264.

Kessler WB, Thomas JW. 2006. Conservation biology from the perspective of natural resource management disciplines. *Conserv Biol* **20**: 670–673.

Knutson KC, Pyke DA, Wirth TA, Arkle RS, Pilliod DS, et al. 2014. Long-term effects of seeding after wildfire on vegetation in Great Basin shrubland ecosystems. *J Appl Ecol* **51**: 1414–1424.

Kulmatiski A. 2011. Changing soils to manage plant communities: activated carbon as a restoration tool in ex-arable fields. *Restor Ecol* **19**: 102–110.

Kulmatiski A, Beard KH. 2006. Activated carbon as a restoration tool: potential for control of invasive plants in abandoned agricultural fields. *Restor Ecol* **14**: 251–257.

Kulmatiski A, Beard KH. 2008. Decoupling plant-growth from land-use legacies in soil microbial communities. *Soil Biol Biochem* **40**: 1059–1068.

Kulmatiski A, Beard KH. 2011. Long-term plant growth legacies overwhelm short-term plant growth effects on soil microbial community structure. *Soil Biol Biochem* **43**: 823–830.

Kulmatiski A, Beard KH, Cobbold SM, Stark JM. 2008. Plant-soil feedbacks: a meta-analytical review. *Ecol Lett* **11**: 980–992.

Kulmatiski A, Beard KH, Stark JM. 2006a. Exotic plant communities shift water-use timing in a shrub-steppe ecosystem. *Plant Soil* **288**: 271–284.

Kulmatiski A, Beard KH, Stark JM. 2006b. Soil history as a primary control on plant invasion in abandoned agricultural fields. *J Appl Ecol* **43**: 868–876.

Novel plant materials for novel ecosystems

Larson JE, Sheley RL, Hardegree SP, Doescher PS, James JJ. 2014. Seed and seedling traits affecting critical life stage transitions and recruitment outcomes in dryland grasses. *J Appl Ecol* **52**: 199–209.

Laughlin DC. 2014. Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecol Lett* **17**: 771–784.

Lavin M, Brummer TJ, Quire R, Maxwell BD, Rew LJ. 2013. Physical disturbance shapes vascular plant diversity more profoundly than fire in the sagebrush steppe of southeastern Idaho, U.S.A. *Ecol Evol* **3**: 1626–1641.

Laycock WA. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *J Range Manage* **44**: 427–433.

Leffler AJ, Ryel RJ. 2012. Resource pool dynamics: conditions that regulate species interactions and dominance, in Monaco TA, Sheley RL, eds., *Invasive Plant Ecology and Management: Linking Processes to Practice*. Wallingford, U.K.: CAB International: pp. 57–78.

Leopold A. 1949. The land ethic, in, *A Sand County Almanac: Sketches Here and There*. New York: Oxford University Press: pp. 201–226.

Leopold LB. 1953. *Round River, from the Journals of Aldo Leopold*. New York: Oxford University Press.

Luck GW, Harrington R, Harrison PA, Kremen C, Berry PM, et al. 2009. Quantifying the contribution of organisms to the provision of ecosystem services. *Bioscience* **59**: 223–235.

Mack RN. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. *Agro-ecosystems* **7**: 145–165.

Mack RN, Thompson JN. 1982. Evolution in steppe with few large, hooved mammals. *Am Nat* **119**: 757–773.

Marlette GM, Anderson JE. 1986. Seed banks and propagule dispersal in crested-wheatgrass stands. *J Appl Ecol* **23**: 161–175.

McAdoo JK, Longland WS, Evans RA. 1989. Nongame bird community responses to sagebrush invasion of crested wheatgrass seedings. *J Wildl Manage* **53**: 494–502.

McDougall AS, Turkington R. 2005. Are invasive species the drivers of passengers of change in degraded ecosystems? *Ecology* **86**: 42–55.

Monaco TA, Call C, Hirsch MC, Fowers B. 2012. Repairing ecological processes to direct ecosystem state changes. *Rangelands* **34**: 23–26.

Morris LR, Monaco TA, Sheley RL. 2011. Land-use legacies and vegetation recovery 90 years after cultivation in Great Basin ecosystems. *Rangel Ecol Manage* **64**: 488–497.

Morris LR, Monaco TA, Leger EA, Blank R, Sheley RL. 2013. Cultivation legacies alter soil nutrients and differentially affect plant species performance nearly a century after abandonment. *Plant Ecol* **214**: 831–844.

Morris LR, Rowe RJ. 2014. Historical land use and altered habitats in the Great Basin. *J Mammal* **95**: 1144–1156.

Mueggler WF. 1972. Influence of competition on the response of bluebunch wheatgrass to clipping. *J Range Manage* **25**: 88–92.

Mukherjee JR, Jones TA, Monaco TA. 2013. Biomass and defoliation tolerance of 12 populations of *Pseudoroegneria spicata* at two densities. *Rangel Ecol Manage* **66**: 706–713.

Nash R. 1987. Aldo Leopold's intellectual heritage, in, Callicott JB, ed., *A Companion to a Sand County Almanac*. Madison, Wisconsin: University of Wisconsin Press: pp. 63–88.

Norton JB, Monaco TA, Norton U. 2007. Mediterranean annual grasses in western North America: kids in a candy store. *Plant Soil* **298**: 1–5.

Norton JB, Monaco TA, Norton JM, Johnson DA, Jones TA. 2004a. Cheatgrass invasion alters soil morphology and organic matter dynamics in big sagebrush-steppe rangelands, in, Seed and Soil Dynamics in Shrubland Ecosystems: *Proceedings (RMRSP-31)*. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: pp. 57–63.

Norton JB, Monaco TA, Norton JM, Johnson DA, Jones TA. 2004b. Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. *J Arid Environ* **57**: 445–466.

Norton U, Saetre P, Hooker TD, Stark JM. 2012. Vegetation and moisture controls on soil carbon mineralization in semiarid environments. *Soil Sci Soc Am J* **76**: 1038–1047.

Novak SJ, Mack RN. 2001. Tracing plant introduction and spread: genetic evidence from *Bromus tectorum* (Cheatgrass). *Bioscience* **51**: 114–122.

Owen SM, Sieg CH, Johnson NC, Gehring CA. 2013. Exotic cheatgrass and loss of soil biota decrease the performance of a native grass. *Biol Invasions* **15**: 2503–2517.

Parsons MC, Jones TA, Larson SR, Mott IW, Monaco TA. 2011. Ecotypic variation in *Elymus elymoides* ssp. *brevifolius* in the northern Intermountain West. *Rangel Ecol Manage* **64**: 649–658.

Peterson EB. 2013. Regional-scale relationships among biological soil crusts, invasive annual grasses, and disturbance. *Ecol Processes* **2**: Article 8.

Pickford GD. 1932. The influence of continued heavy grazing and of promiscuous burning on spring-fall ranges in Utah. *Ecology* **13**: 159–171.

Piemeisel RL. 1951. Causes affecting change and rate of change in a vegetation of annuals in Idaho. *Ecology* **32**: 53–72.

Reisner MD, Grace JB, Pyke DA, Doescher PS. 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. *J Appl Ecol* **50**: 1039–1049.

Richards JH. 1984. Root growth response to defoliation in two *Agropyron* bunchgrasses: field observations with an improved root periscope. *Oecologia* **64**: 21–25.

Richards JH, Mueller RJ, Mott JJ. 1988. Tillering in tussock grasses in relation to defoliation and apical bud removal. *Ann Bot* **62**: 173–179.

Richardson BA, Page JT, Bajgain P, Sanderson SC, Udall JA. 2012. Deep sequencing of amplicons reveals widespread intraspecific hybridization and multiple origins of polyploidy in big sagebrush (*Artemisia tridentata*; Asteraceae). *Am J Bot* **99**: 1962–1975.

Rietkerk M, van de Koppel J. 1997. Alternate stable states and threshold effects in semi-arid grazing systems. *Oikos* **79**: 69–76.

Roberts RE, Clark DL, Wilson MV. 2010. Traits, neighbors, and species performance in prairie restoration. *Appl Veg Sci* **13**: 270–279.

Robins JG, Jensen KB, Jones TA, Waldron BL, Peel MD, et al. 2013. Stand establishment and persistence of perennial cool-season grasses in the Intermountain West and Central and Northern Great Plains. *Rangel Ecol Manage* **66**: 181–190.

Ryel RJ, Leffler AJ, Ivans C, Peek MS, Caldwell MM. 2010. Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. *Vadose Zone J* **9**: 548–560.

Sackville Hamilton NR. 2001. Is local provenance important in habitat creation? A reply. *J Appl Ecol* **38**: 1374–1376.

Schimel DS. 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. *Biogeochemistry* **2**: 345–357.

Schmitz OJ. 2012. Restoration of ailing wetlands. *PLoS ONE Biol* **10**: e1001248.

Seefeldt SS, Germino M, DiCristina K. 2007. Prescribed fires in *Artemisia tridentata* ssp. *vaseyana* steppe have minor and transient effects on vegetation cover and composition. *Appl Veg Sci* **10**: 249–256.

SERI or Society for Ecological Restoration International Science & Policy Working Group. 2004. The SER International Primer on Ecological Restoration. Tucson, Arizona: Society for Ecological Restoration International.

Shafroth PB, Beauchamp VB, Briggs MK, Lair K, Scott ML, et al. 2008. Planning riparian restoration in the context of *Tamarix* control in western North America. *Restor Ecol* **16**: 97–112.

St. Clair JB, Kilkenny FF, Johnson RC, Shaw NL, Weaver G. 2013. Genetic variation in adaptive traits and seed transfer zones for *Pseudoroegneria spicata* (bluebunch wheatgrass) in the northwestern United States. *Evol Appl* **6**: 933–948.

Stringham TK, Krueger WC, Shaver PL. 2003. State and transition modeling: an ecological process approach. *J Range Manage* **56**: 106–113.

Stubbs MM, Pyke DA. 2005. Available nitrogen: a time-based study of manipulated resource islands. *Plant Soil* **270**: 123–133.

Temperton VM, Hobbs RJ, Nuttle T, Halle S. 2004. *Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice*. Washington, D.C.: Island Press.

Waldron BL, Jensen KB, Palazzo AJ, Cary TJ, Robins JG, et al. 2011. 'Recovery', a new western wheatgrass cultivar with improved seedling establishment on rangelands. *J Plant Registrations* **5**: 367–373.

Walker BH. 1992. Biodiversity and ecological redundancy. *Conserv Biol* **6**: 18–23.

Weber CF. 2015. Reduced vertical stratification of soil bacterial community structure and composition is associated with *Bromus tectorum* invasion of sagebrush steppe. *J Arid Environ* **115**: 90–99.

Weber CF, King GM, Aho K. 2015. Relative abundance of and composition within fungal orders differ between cheatgrass (*Bromus tectorum*) and sagebrush (*Artemisia tridentata*)-associated soils. *PLoS ONE* **10**: e0117026.

Weltz MA, Spaeth K, Taylor MH, Rollins K, Pierson F, et al. 2014. Cheatgrass invasion and woody species encroachment in the Great Basin: benefits of conservation. *J Soil Water Conserv* **69**: 39A–44A.

West NE. 1983a. Great Basin-Colorado Plateau sagebrush semi-desert, in West NE, ed., *Temperate Deserts and Semi-deserts*. Amsterdam, The Netherlands: Elsevier Scientific Publishing Company: pp. 331–349.

West NE. 1983b. Western Intermountain sagebrush steppe, in West NE, ed., *Temperate Deserts and Semi-deserts*. Amsterdam, The Netherlands: Elsevier Scientific Publishing Company: pp. 351–374.

Whisenant SG. 1999. *Repairing damaged wildlands: a process-orientated, landscape-scale approach*. Cambridge, UK: Cambridge University Press. 328 p.

Wilcox BP, Turnbull L, Young MH, Williams CJ, Ravi S, et al. 2012. Invasion of shrublands by exotic grasses: ecohydrological consequences in cold versus warm deserts. *Ecohydrology* **5**: 160–173.

Young JA, Evans RA. 1978. Population dynamics after wildfires in sagebrush grasslands. *J Range Manage* **31**: 283–289.

Young JA, Evans RA. 1986. History of crested wheatgrass in the Intermountain area, in Johnson KL, ed., *Crested Wheatgrass – its Values, Problems, and Myths*. Logan, Utah: Utah State University: pp. 21–25.