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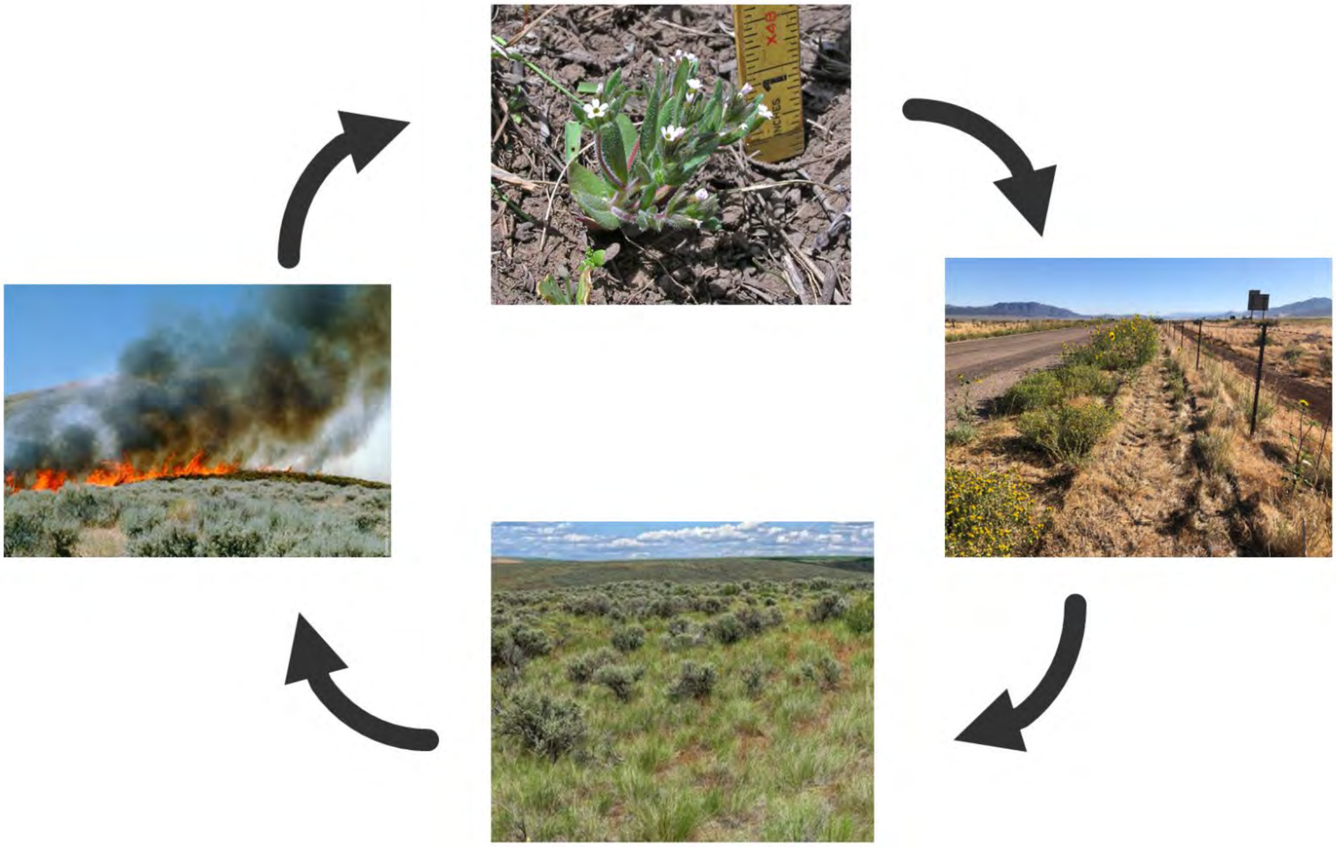
Succession Management for Rangeland Seedings



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Main Points

- Restoration practices employed in semiarid sagebrush steppe of the North American Intermountain West are typically based on objectives to restore habitat to mid- to late-seral plant communities.

- Succession management utilizes species of multiple seral stages, including early seral species, in restoration plans and seed mixes to provide temporal diversity and bridge the gap between disturbance and stable climax conditions.

- Early seral native species evolved to establish quickly and occupy disturbed soils, reduce erosion, and provide a food source for wildlife. They further alter soil chemistry and biology dynamics that favor transition to later seral phases. Additionally, many early seral natives have been shown to reduce exotic weed growth and seed production.

- Despite their benefits, early seral native species have poor representation in restoration practices largely due to cultural biases.

- Continued investigation of early seral natives in restoration practices is needed to clarify the benefits of this underused group. Likewise, plant materials developers should focus efforts on developing a broader suite of early seral germplasm sources for Intermountain restoration activities.

Introduction

When is a Weed Not a Weed?

A weed has been broadly defined as a plant that interferes with management objectives for a given area and period of time (Whitson et al., 2009). However, there may be instances when a plant is unwanted in an area only because someone else has declared it a weed. For example, in 1991, university weed scientists and extension agents from around the western U.S. published a seminal book, *Weeds of the West* (Whitson et al., 2009). In the 10th edition of *Weeds of the West*, 350 noxious, invasive, and problematic plant species are described in detail to help landowners identify and combat these pests. However, amongst the many non-native and invasive species listed, the book also contains over 100 species native to the region, several of which have no apparent liability other than not providing optimal forage to livestock. In large part because of *Weeds of the West* and other livestock and agriculture-centric publications like it, many native species have developed a stigma that has prevented them from being investigated and used for native site ecological reclamation and restoration. This stigma attached to some of these native species has kept what may be a valuable tool out of the hands of restoration practitioners, potentially hampering restoration efforts.

Restorationists in the Intermountain Region have called for species that are easily established, are drought-tolerant and are competitive against invasive weeds. For decades the Bureau of Land Management (BLM), Natural Resources Conservation Service (NRCS), and other land management agencies have answered this call with either Eurasian cultivars like crested wheatgrass (*Agropyron cristatum*) (Svejcar et al., 2017) or with long-lived native climax species like bluebunch wheatgrass (*Pseudoroegneria spicata*) and sagebrush (*Artemisia tridentata*) (Ogle et al., 2014). Introduced perennial grasses have done admirably, to the point where we now see areas of near-monocultures of crested wheatgrass that can impede native plant recruitment and limit ecological function (Hulet et al., 2010; McAdoo et al., 2017). However, establishment and restoration of native plant communities has been less successful as seeding success rates are discouraging (Kulpa & Leger, 2013; Svejcar et al., 2017; Boehm et al., 2021). Highly competitive annual invasive species like cheatgrass (*Bromus tectorum*), ventenata (*Ventenata dubia*), and medusahead (*Taeniatherum caput-medusae*) have been difficult to combat, making site conversion to persistent, healthy native ecosystems elusive. To exemplify the issue of invasive exotic species in the region, cheatgrass infestation is now a significant concern among landowners and land managers in western states because of its invasiveness and the negative impacts on the landscape. Millions of acres have already been invaded, and much of this land has reached a state of cheatgrass dominance (Stewart & Hull, 1949; Mack, 1981).

To address these issues, researchers are giving consideration to early seral natives, or native “weeds”, and seeing new restoration potential (Herron et al., 2013; Leger et al., 2014; Uselman et al., 2015). Many native early seral species possess the exact attributes that are most sought after for restoration, i.e., drought tolerance, adaptation for establishing in disturbed conditions, and the capacity to compete against true invasive species. A native weed’s ability to capture disturbed sites such as roadsides and degraded pastures can be suited for site reclamation projects like post-fire rehabilitation, oil and gas reclamation, and Conservation Reserve Program (CRP) seedings. Integrating the concepts of succession management into restoration plans may be a means of building site resilience and resistance to invasion (Pickett et al., 1987; Krueger-Mangold et al., 2006; Brown et al., 2008). In this paper, we bridge the gap between the known science of manipulating succession for rangeland restoration and practical applications for managers and plant materials developers by addressing the following questions:

1. What is the state of knowledge regarding the use of secondary succession as a restoration tool, and how is it being applied in Intermountain Western rangelands?
2. What species in the Intermountain Western region are effectively early seral for the purposes of restoration, and what is the availability of these plant materials for restoration treatments?
3. What risks and questions need to be addressed to encourage broader adoption of a succession-based approach to rangeland restoration?

Scope of Problem

A major component of ecological restoration is the removal of exotic species and their replacement with desirable native assemblages. However, this has led, in many instances, to sub-adequate results (Kulpa & Leger, 2013; Svejcar et al., 2017; Boehm et al., 2021). Exotic species may leave changes in the ecosystem after their removal, including a buried seed bank or chemical or physical alterations to the site, making long-term restoration difficult. (D’Antonio & Meyerson, 2002). For example, exotic weeds have been found to alter soil-available N compared to native vegetation (Vitousek et al., 1987; Gornish et al., 2020) while others, like cheatgrass, cause a redistribution of N within the soil profile (Sperry et al., 2006). Similarly, species such as saltcedar (*Tamarix ramosissima*) can alter soil salinity and pH in the rooting zone, restricting germination and establishment of desired species (Shafroth et al., 1995; Ladenburger et al., 2006). Many invasive species (e.g., cheatgrass) establish feedback systems that lead to their persistence on the landscape (Brooks, 2003; Brooks et al., 2004; Pilliod et al., 2017).

Cheatgrass succeeds in invading Great Basin landscapes by capitalizing on key physiological and morphological traits (Fig. 1). First, cheatgrass uses available water resources more efficiently than native plants by initiating germination and root and shoot growth at lower temperatures early in the season (Melgoza & Nowak, 1991; Knapp, 1996; Arredondo et al., 1998; Humphrey & Schupp, 2001; Norton et al., 2007; James et al., 2011). Second, cheatgrass can grow in extremely high densities, reaching as many as 10,000 plants/m^2 (Young & Evans, 1978). Cheatgrass is also highly efficient at using available N, resulting in increases in vigor and seed production (Hulbert, 1955). Cheatgrass further alters ecological functions such as soil N cycling and wildfire frequency, making conditions less suitable for native plants and more suited to its own perpetuation (McLendon & Redente, 1992; Reitstetter & Rittenhouse, 2017). Once cheatgrass has become established in a location, it is exceedingly difficult to convert the site back to its original state.

Figure 1. Cheatgrass has become a significant ecological pest in the Intermountain Region, occupying millions of hectares of western rangelands.

Despite the ecological advantages exhibited by cheatgrass and other exotic weeds in disturbed sites, some native plants have been shown to have the capacity to resist annual grass invasion and build local site resilience to invasion. One group that shows potential is the early seral native plants.

Plant Community Succession

Plant community succession is defined as a directional change in species composition or structure of a community over time (Pickett et al., 1987; Barbour, 1999) (Fig. 2). Early seral species are associated with short life spans and high seed production making them better adapted to and more competitive in severely disturbed environments. Natural succession after disturbance in the Intermountain West begins with the dominance of early seral species (mostly annual forbs) followed by establishment of perennial grasses and forbs and further transitioning to a suite of long-lived climax species (Bradshaw, 2000; Kleijn, 2003). Intermountain early seral species have evolved to capture sites following disturbance and are adapted to local soil and climatic conditions. They further fill an essential niche in space and time, reducing post-disturbance erosion and offering food sources for pollinators until later seral species become fully established (Potts et al., 2003).

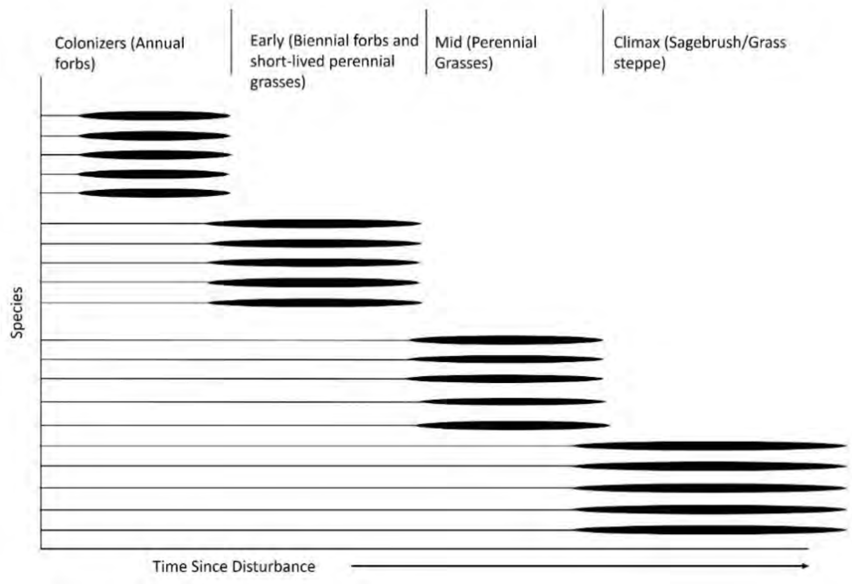

Figure 2. Conceptualization of plant community succession as it applies to Intermountain Western rangelands. Modified from Egler (1954) to include plant functional groups common to successional stages in the Intermountain West.

Early seral species have been shown to alter soil biology and nutrient cycling in ways that ultimately favor later-successional species (Weintraub and Schimel, 2003; Busby et al., 2011; Kieffer Stube, 2012). In a study examining the interactions between native annual plants and arbuscular mycorrhizal fungi (AMF), Busby et al. (2011) found that certain early seral species produced a more rapid increase in AMF compared to late seral species. Kieffer Stube (2012) further found a significant effect on AMF richness or abundance from native early seral species. Understanding these relationships may be necessary in restoring soil biology and facilitating full site recovery.

Early seral species have also been shown to manipulate soil chemical properties. They hold dominance over the plant community until available N is depleted to the point where they no longer have a competitive advantage, resulting in the successional transition toward mid- and late-seral species (McLendon & Redente, 1992; Paschke et al., 2000; Vasquez et al., 2008; Reitstetter & Rittenhouse, 2017) (Fig. 3). In contrast, invasive exotic species typically alter soil N dynamics in ways foreign to the naturally evolved community. In Intermountain shrublands, high levels of N produced in disturbance regimes have been linked to supporting the persistence of invasive weeds over native species (Mooney & Drake 1986; Brooks 2003; Reitstetter & Rittenhouse 2017). The differential capacity of each species to acquire resources and nutrients drives succession. Therefore, rebuilding soil biology and chemistry can have a significant impact on progressing from a disturbed state to the desired plant community (Stevenson et al., 2000).

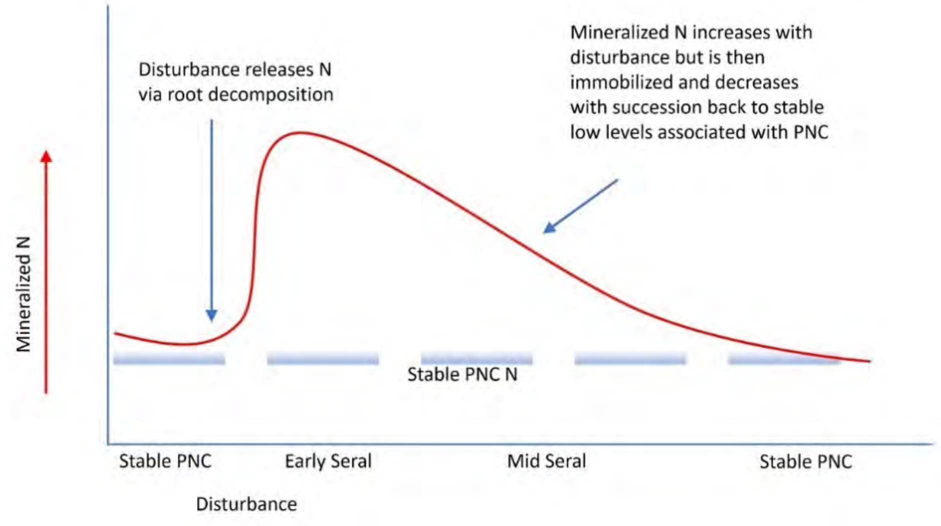

Figure 3. Plant mortality following disturbance creates high levels of mineralized N. Natural plant succession lowers N levels back to those suited for the potential natural community (PNC). Based on Rietstetter and Rittenhouse (2017).

Because succession in semiarid communities of the Intermountain West occurs slowly - decades to centuries if not interrupted (Rottler et al., 2018), - the current practice of seeding mid- to late-seral seed mixes in post-disturbance landscapes may create a temporal lag between the removal or control of exotics and the actualization of the desired native plant community (D'Antonio and Meyerson, 2002; Ott et al., 2019). Tilley et al. (2021) reported that four years after reseeding, many native grasses, especially long-lived rhizomatous perennials, had not reached their full expression and that only after ten years did they reach high densities due to underground spreading. Similarly, mean cover of the late seral rhizomatous grass species western wheatgrass (*Pascopyrum smithii*) seeded into post-fire locations in western Utah increased 14-fold between 3 years post-fire and 16 years post-fire (Ott et al., 2019). Likewise, in a long-term succession study in southeastern Idaho, the dominant shrub Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) did not regain a significant onsite presence for over 15 years after fire (Humphrey, 1984), leading the authors to conclude that some conditions of a more mature community may be required for later seral species to become established.

This temporal niche creates a vacuum in which invasive species may quickly colonize or re-establish themselves where they once were. Utilizing species of additional seral stages with properties more similar to those expressed by invasive weeds could help bridge that gap. Research is needed to help us understand which aspects of the plant community build resistance to invasion and how local scale mechanisms translate to larger-scale management (D'Antonio & Meyerson, 2002; Pokorny et al., 2005; Krueger-Mangold et al., 2006; Rinella et al., 2007).

Succession as a Management Tool – the Value of Early seral Species

The implications of succession management in restoration are promising. Species and functional group diversity can be equated with competition for limited resources above and below ground. Species of the same functional group compete directly against one another for water and nutrient demands (Emery, 2007). They often share similarities in root structure, leaf morphology and placement, and nutrient requirements. Grime (2006) described early seral species as those better adapted to conditions in transient and temporary habitats. Those species often are small in stature, have increased seed production rates, decreased generation time, and are better adapted to direct sunlight (Grime, 1977). One sees these traits commonly expressed in invasive non-native weeds, and they are the same traits found in many native early seral species. Therefore, one way to “even the playing field” against undesirable weedy species like cheatgrass is to include “home-grown” weedy species in restoration strategies (Leger, 2008; Brown et al., 2008; Perry et al., 2009; Herron et al., 2013).

The notion of increasing resilience through species diversity is well understood. Several studies have shown that increasing functional group diversity can translate to increased resistance against invasion (Sheley & Carpinelli, 2005; Urza et al., 2019) (Fig. 4). For example, an increase in perennial herbaceous cover after wildfire in a mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) community led to improved resistance to cheatgrass invasion (Condon et al., 2011). Similarly, high functional group diversity was positively correlated with decreased densities of spotted knapweed (*Centaurea maculosa*) (Pokorny et al., 2005). In a study of Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) community restoration, cheatgrass cover and density were shown to be inhibited by the presence of diverse native bunchgrass communities. Similarly, cheatgrass declines were attributed to native bunchgrass establishment success and population growth (Bowman-Prideuax, 2019). Summarizing, Chambers et al. (2007) and Urza et al. (2019) concluded that invasibility of sagebrush communities by cheatgrass is lowest on sites with relatively high cover of perennial herbaceous species.

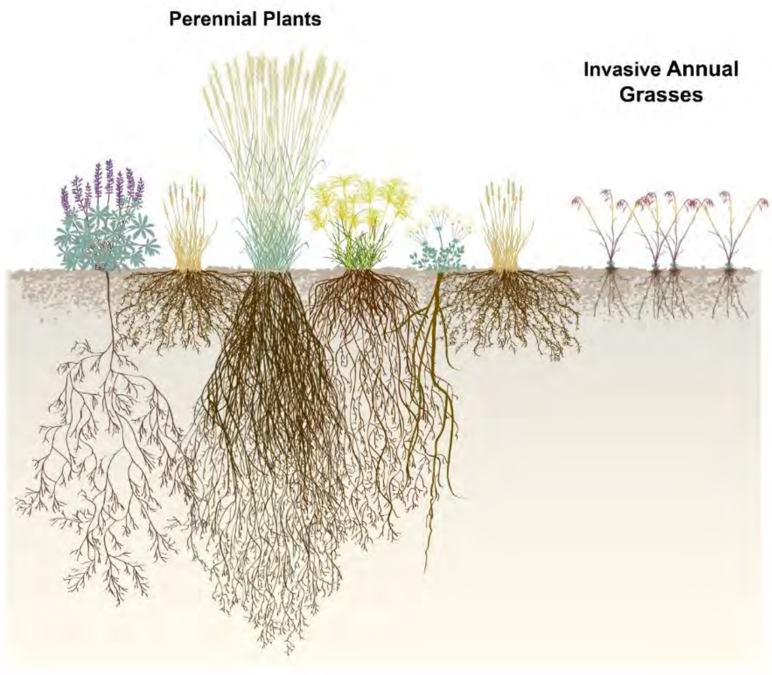

Figure 4. Above and below ground diversity of growth forms and root structures fills spatial niches and increase resilience against invasion. Image courtesy of Jeremy Maestas and Maja Smith, Sage Grouse Initiative. Used with permission.

Similar to the resilience gained from a healthy, diverse mature plant community, numerous greenhouse and field studies have shown early seral species to be more effective at competing against, and even suppressing, exotic species than late seral species. This trait could be especially valuable to restoration efforts during the critical first years of establishment following seeding treatments. Several native annual Intermountain forbs were found to be highly competitive against cheatgrass in controlled studies (Leger et al., 2014). Bristly fiddleneck (*Amsinckia tessellata*) significantly reduced cheatgrass biomass, while fiddleneck and western tansymustard (*Descurainia pinnata*) reduced cheatgrass seed production by greater than 79%. In a similar greenhouse study, Perry et al. (2009) found the annual native forbs, annual ragweed (*Ambrosia artemisiifolia*), and common sunflower (*Helianthus annuus*), reduced biomass of several weeds, including cheatgrass, Japanese brome (*Bromus arvensis*), Canada thistle (*Cirsium arvense*) and whitetop (*Cardaria draba*). Herron et al. (2013) likewise found a significant reduction in weed cover in plots seeded with early seral native annuals compared to mid and late seral perennials. Kieffer Stube (2012) found early seral native species reduced cheatgrass biomass and density during establishment, and Uselman et al. (2015) showed early seral natives generally had earlier germination and better survival than late seral natives, implying that they fill a more similar functional group to cheatgrass.

Application in Intermountain Rangelands

It has been demonstrated that early seral species, especially annuals and short-lived perennials, occupy an ecological niche similar to many of the region's exotic grass invaders and that these can be more capable of competing against potential invaders than the more dissimilar late seral species (Emery, 2007; Hu et al., 2021). Therefore, it may be beneficial to include site-adapted, early seral species that have evolved to colonize a site following disturbance in restoration seed mixes to promote the establishment of the target plant community and build site resiliency (Leger, 2008; Herron et al., 2013; Uselman et al., 2015). Developing restoration strategies that include species diversity in space *and time* can increase resiliency throughout the successional stages of the plant community, eliminating temporal niches of low resilience (Fig. 5).

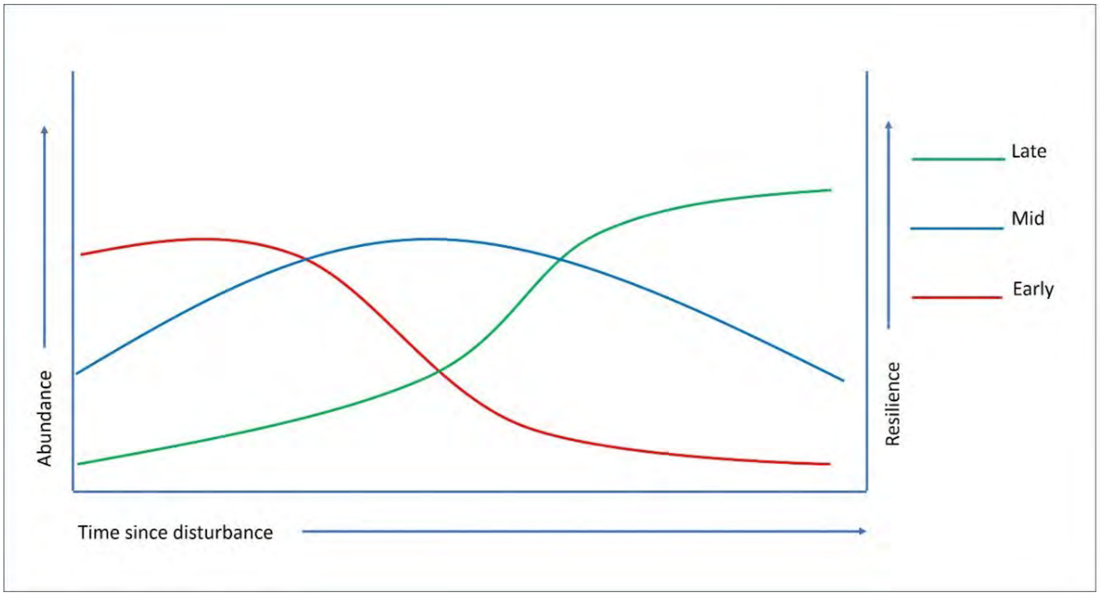

Figure 5. Generalized conceptualization of seral stage progression and site resilience. Following disturbance, early seral species quickly establish providing initial resilience. The early seral species then decrease in abundance as mid-seral perennial species increase. The ultimate "climax" community in the Intermountain West is often a mixture of late-seral shrubs and long-lived perennial grasses. Developing restoration strategies that include species temporal and spatial diversity can increase resilience throughout the life of the plant community.

Restorationists have largely excluded early seral species as an element of restorative seed mixture components (Bugg et al., 1997; Sheley & Carpinelli, 2005; Brown et al., 2008; Rottler et al., 2018). Seed mix designs are usually based on efforts to duplicate the pre-disturbance plant community. Historically, State and Transition Models in the NRCS' Ecological Site Descriptions (ESDs) have been recommended for information on species' relative abundance to develop seed mixtures for sagebrush steppe restoration (Tilley et al., 2014). However, while these resources provide valuable information regarding the potential natural community and other phases and successional trajectories, they do not include comprehensive information concerning early and mid-successional species.

Current seeding guides and recommendations for Intermountain rangelands overlook principles of plant community succession (Monsen et al., 2004; Rottler et al., 2018). For example, NRCS Idaho seeding guide Technical Note 24 (Ogle et al., 2014) mentions succession only once, in the description for fern bush (*Chamaebatiaria millefolium*). However, it does mention several species as being “short-lived” and likely to be replaced over time by longer-lived species. Some of these “temporary” species include squirreltail (*Elymus elymoides* and *E. multisetus*), slender wheatgrass (*E. trachycaulus*), and smoothstem blazingstar (*Mentzelia laevicaulus*). Several other species, including blue and Lewis flax (*Linum perenne* and *L. lewisii*), and several beardtongue species (*Penstemon* spp.) are noted as short-lived, but this information is provided largely as a production factor for seed producers and not as a guiding principle for restorationists. Information provided by Lambert (2005) follows a similar pattern. Similarly, Jensen et al. (1997) exclude succession theory in their planting guide but do include short-lived perennial grasses like slender wheatgrass in many of their seed mixture recommendations. Finally, Monsen et al. (2004) mention succession and warn against planting species that might inhibit the natural successional pathways. They also suggest using a combination of species to “initiate natural successional processes” but do not go so far as to make recommendations based on the successional status of the species.

Seeding recommendations developed by some researchers do implicitly follow successional theory by employing the practice of using nurse crops to assist in site capture and reducing soil erosion (Perry et al., 2009). Recommended species, especially for post-fire erosion control, can include non-native grasses like common wheat (*Triticum aestivum*) and sterile triticale (*xTriticosecale*) (USDA NRCS, 2020), and annual ryegrass (Robichaud et al., 2000). Krueger-Mangold et al. (2006) recommend using cover crops (i.e., nurse crops) to push competition in favor of native species. The assumption is that these species will provide quick cover, die before reproducing, and not present a nuisance or obstacle to restoration goals. However, experience suggests an inherent risk with using exotic species in a novel environment (Beyers, 2004). Additionally, these non-native species may lack characteristics critical to the establishment and health of succeeding late-seral plant populations.

A few short-lived native perennial grasses have found their way into restoration protocols and are accepted within the commercial market. Slender wheatgrass and bottlebrush squirreltail are currently recommended and used as nurse crops (Robichaud et al., 2000; Ogle et al., 2014; Staub et al., 2016). Mooney & Drake (1986) argued that the potential of native species as nurse crops has not been fully explored and that more research in the field is required. Thus, a more extensive palette, inclusive of early seral forb species, is needed to capitalize on successional habitat characteristics fully.

Going Forward

Land managers should consider succession when developing restoration plans and seed mixtures. Traditional approaches to restoration typically fall into three strategies: 1) matching pre-disturbance species as closely as possible with local ecotypes; 2) approximating pre-disturbance plant functional groups (grasses, forbs and shrubs) with mostly non-local, adapted germplasms and cultivars; or 3) capturing the site and increasing forage with introduced forage species. The first approach, while closest in similarity to the existing community in composition and genetic makeup, is expensive and often unachievable due to limitations in seed availability. This approach may also lack the temporal diversity needed for maximum resilience against invasion. The second approach is becoming more common in the West but may have low inherent resilience due to low temporal species diversity and limited genetic diversity due to the reliance on non-local cultivars. The third is the common reclamation mixture often consisting of one or two introduced forage grasses. This option is cheap but is least similar to the natural plant community.

We propose two novel strategies for semi-arid rangeland restoration seed mixtures. The first is a mixed-seral species mixture that includes representation from all functional groups and multiple successional phases. This approach should maximize spatial and temporal diversity and provide the greatest resilience against invasion by noxious weeds. The second is a mixture consisting of only early seral species. This mix design could have application in post-fire sites or other scenarios where quick establishment and protection against invasion and erosion is needed, but a seed bank of later seral species is known to be present to allow later transition and recovery.

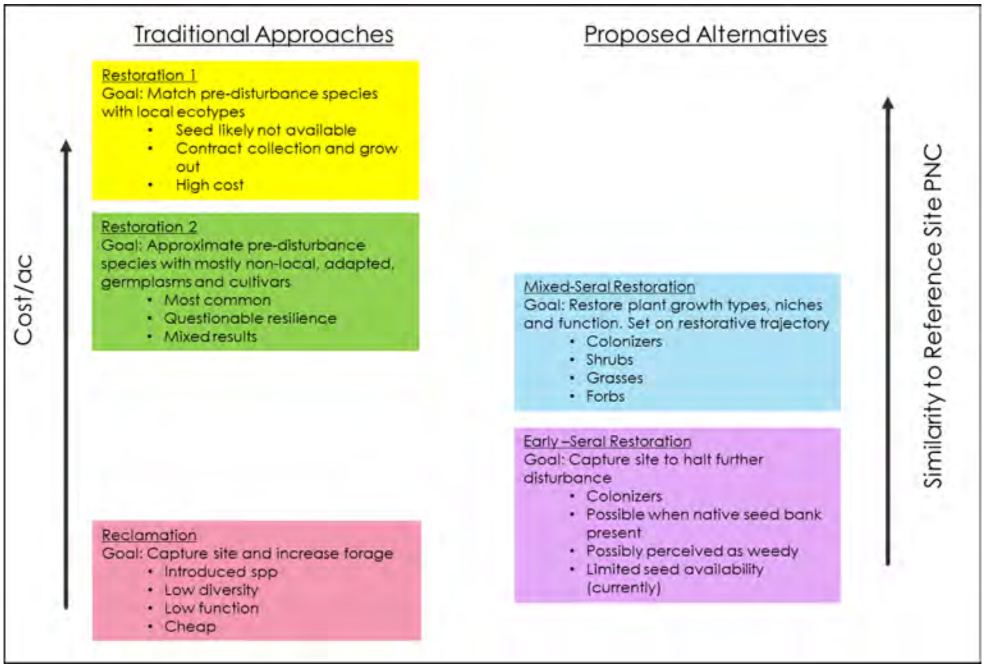

Figure 6. Rangeland restoration and reclamation seed mixes traditionally attempt to approximate pre-disturbance climax plant communities or include introduced forage species. A mixed seral alternative would include representation from multiple seral phases to add temporal resilience. An all-early seral mix option might be useful in burned areas where quick establishment for erosion control is needed while the site recovers.

A hypothetical mixed seral seed mix for a semi-arid rangeland site is shown in Table 1. All functional groups are represented as are two broadly defined seral phases (early and late). Seeding rates shown in lb/ac and pure live seeds (PLS)/ft are based on recommendations found in Ogle et al. (2014) where small seeded species (>500,000 seeds/lb) are seeded at a target rate of 50 PLS/ft, and large seeded species (<500,000 seeds/lb) are seeded at a target rate of approximately 25 PLS/ft. Not all species shown may be suitable for all situations.

Table 1. A hypothetical seed mixture for a 9-12 inch precipitation site with loamy soils in the Intermountain West containing representation from all plant functional groups and seral phases. Seed rates are based on Ogle et al. (2014) drill seeding recommendations wherein a seed rate of 45-50 pure live seeds (PLS) per m ft2 is recommended for small-seeded species (species with >500,000 seeds/lb) and 25-30 PLS/ft2 is targeted for large-seeded species (species with <500,000/lb). Some species shown may not be readily available commercially.

				Full rate	Full rate	Applied rate	Applied rate
		Functional group	% of mix	lb/ac	pls/ft	lb/ac	pls/ft
Curlycup gumweed		early forb	7	4	25	0.28	1.75
Hoary tansyaster		early forb	7	1	50	0.07	3.5
Menzie’s fiddleneck		early forb	7	9	25	0.63	1.75
Common sunflower		early forb	7	18	25	1.26	1.75
Bottlebrush squirreltail		early grass	7	6	25	0.42	1.75
Sand dropseed		early grass	7	1	50	0.07	3.5
Purple threeawn		early grass	7	4	25	0.14	0.875
Rubber rabbitbrush		early shrub	7	0.5	50	0.04	3.5
Bluebunch wheatgrass		late grass	7	8	25	0.56	1.75
Sandberg’s bluegrass		late grass	7	2	50	0.14	3.5
Thickspike wheatgrass		late grass	7	8	25	0.56	1.75
Western yarrow		late forb	7	2	50	0.14	3.5
Munro’s globemallow		late forb	7	2	25	0.14	1.75
Perennial flax		late forb	7	4	25	0.28	1.75
Big sagebrush		late shrub	7	0.5	50	0.02	1.75
						4.74	34.13

What Species are Effectively Early Seral for Restoration Purposes?

Determining which species are of potential worth in succession-based restoration is problematic. Which species are present following disturbance is generally understood, and at least a partial understanding of common traits shared by early seral species exists. In some cases, additional information can be found in regional floras (Cronquist, 1994; Welsh, 2003) and other sources with species descriptions. However, no comprehensive lists exist that group Intermountain species by seral category, and there are few long-term analyses tracking successional phases from which to draw conclusions.

While studies tracking temporal succession are scarce, opportunities for successional observations under disturbed conditions are abundant. Along any stretch of highway in the Intermountain Region, identification of early seral native species is easily accomplished by observing those persisting and thriving in cyclically disturbed conditions in the presence of invasive annuals. Indeed, Intermountain roadsides may be ideal collection sites for adapted plant materials to restore severely degraded lands (Leger, 2008). Highway corridors often experience heavy traffic, soil compaction, and repeated mowing treatments, as well as periodic fire. Often a distinct plant community occupies the first few meters of the roadside (Fig. 7). There is typically a high presence of invasive weeds like cheatgrass and tumble mustard (*Sisymbrium altissimum*), but the same space also hosts native species. Rubber rabbitbrush often makes up the overstory, especially further from the road where mowing is less frequent. Grasses can include sand dropseed (*Sporobolus cryptandrus*) and purple threeawn (*Aristida purpurea*). Upright native biennial and annual forbs consist of curlycup gumweed (*Grindelia squarrosa)*, common sunflower and bristly fiddleneck, and there may be a component of prostrate forbs like bigbract verbena (*Verbena bracteata*). Moving further away from the roadside, the plant community transitions, sometimes very distinctly, to a late seral, perennial-dominated system. Table 2 summarizes many species that have been suggested as early seral in Intermountain Western rangelands.

Figure 7. Many Intermountain roadways provide a continuous demonstration of plant community succession. Early seral members commonly include curlycup gumweed, common sunflower, rubber rabbitbrush, and sand dropseed. Further away from the disturbed roadside, the plant community transitions into more longer-lived perennial species.

Table 2. Some of the native semiarid Intermountain species presented as short-lived, early seral colonizers in various publications. Species are grouped by family and then alphabetically within families.

Family	Scientific Name	Common Name	Life span
Amaranthaceae	*Amaranthus retroflexus*[1]	Redroot pigweed	Annual
Asteraceae	*Ambrosia artemisiifolia*[1, 2]		Annual
Asteraceae	*Chrysothamnus viscidiflorus*[3]	Yellow rabbitbrush	Perennial
Asteraceae	*Coreopsis tinctoria*[1]	Golden tickseed	Annual
Asteraceae	*Ericameria nauseosa* [3, 4]	Rubber rabbitbrush	Perennial
Asteraceae	*Grindelia squarrosa*[5]	Curlycup gumweed	Biennial
Asteraceae	*Gutierrezia sarothrae*[3]	Broom snakeweed	Perennial
Asteraceae	*Helianthus annuus*[1, 2]	Common sunflower	Annual
Asteraceae	*Machaeranthera canescens*[6, 8]	Hoary tansyaster	Biennial
Asteraceae	*M. tanacetifolia*[8, 9]	Tansyleaf tansyaster	Biennial
Asteraceae	*Senecio multilobatus*[3, 6]	Multilobed groundsel	Biennial
Boraginaceae	*Amsinckia tessellata*[10]	Bristly fiddleneck	Annual
Boraginaceae	*Lappula occidentalis*[6]	Flatspine stickseed	Annual
Brassicaceae	*Descurainia pinnata*[6, 10]	Western tansymustard	Annual
Capparaceae	*Cleome serrulata*[1]	Rocky Mountain beeplant	Annual
Chenopodiaceae	*Chenopodium album*[1]	Lambsquarters	Annual
Fabaceae	*Lotus humistratus*[9]	Foothill deervetch	Annual
Loasaceae	*Mentzelia albicaulis*[6, 7]	Whitestem blazingstar	Annual
Loasaceae	*M. laevicaulis*[11]	Smoothstem blazingstar	Annual
Loasaceae	*M. veatchiana*[4]	Veatch’s blazingstar	Annual
Malvaceae	*Sphaeralcea coccinea*[3, 6]	Scarlet globemallow	Perennial
Papaveraceae	*Argemone munita*[6]	Prickly poppy	Perennial
Poaceae	*Aristida purpurea*[12]	Purple threeawn	Perennial
Poaceae	*Elymus elymoides*[3, 4, 11, 13]	Bottlebrush squirreltail	Perennial
Poaceae	*Elymus multisetus*[10]	Big squirreltail	Perennial
Poaceae	*Elymus trachycaulus*[11, 13]	Slender wheatgrass	Perennial
Poaceae	*Sporobolus cryptandrus*[14]	Sand dropseed	Perennial
Poaceae	*Vulpia microstachys*[1]	Small fescue	Annual
Poaceae	*Vulpia octoflora*[1]	Sixweeks fescue	Annual
Polemoniaceae	*Microsteris gracilis*[6, 15]	Slender phlox	Annual
Scrophulariaceae	*Collinsia parviflora*[15]	Maiden blue eyed Mary	Annual
Solanaceae	*Nicotiana attenuata*[6]	Coyote tobacco	Annual
Verbenaceae	*Verbena bracteata*[1]	Bigbract verbena	Annual

1=Herron et al. (2013); 2= Perry et al. (2009); 3=Hoelzle et al. (2012); 4= Uselman et al. (2015); 5= Tilley & Pickett (2019); 6= Ott et al. (2003); 7= Morris & Leger (2016); 8=Tilley (2015a); 9= Barak et al. (2015); 10= Leger et al. (2014); 11= Ogle et al. (2014); 12= Abella et al. (2012); 13=Tilley et al. (2021); 14= Welsh et al. (2003); 15= de Quieroz et al., 2021

Plant Materials

While wildland-collected seed of Intermountain West early seral species may be available in limited quantities, few released germplasm sources from this group exist. Several cultivars of slender wheatgrass have been developed and released. For example, 'Pryor' was released by the NRCS Plant Materials Center in Bridger, Montana and the Montana and Wyoming Agricultural Experiment Stations in 1988, and 'San Luis' was released in 1984 by Colorado, and New Mexico Agricultural Experiment Stations, NRCS, and the Upper Colorado Environmental Plant Center (Tilley et al., 2006). More recently, 'First Strike' was released cooperatively in 2006 by the Agricultural Research Service (USDA-ARS) and the U.S. Army (Staub et al., 2016). Likewise, the USDA-ARS Forage and Range Research Laboratory (FRRL) has made several germplasm source releases of squirreltail, including 'Toe Jam Creek,' 'Pleasant Valley,' 'Antelope Creek,' 'Fish Creek,' and 'Rattlesnake' bottlebrush squirreltail, as well as, 'Sand Hollow' big squirreltail (*Elymus multisetus*) (Staub et al., 2016).

Regional early seral forb releases are poorly represented in the plant materials catalog. Most early seral research to date for the western U.S. has been conducted on native annuals, few of which are well-suited for commercial seed production. See de Queiroz et al. (2021) for a discussion on Great Basin annual forb seed increase. Many species, such as foothill deervetch (*Lotus humistratus*), bigbract verbena, and sixweeks fescue (*Vulpia octoflora*) (Herron et al., 2013; Barak et al., 2015), are low-statured or prostrate in growth habit, making seed harvest difficult (Fig. 8). Still others such as blazingstar (*Mentzelia* spp.) and slender phlox (*Microsteris gracilis*) (Leger et al., 2014) produce limited quantities of seed, making them economically unsustainable and prohibitively costly for most restoration projects. Development and release of early seral species that serve the same function while having better seed production attributes would be both beneficial for restoration and more likely sustainable amid market forces.

Figure 8. Bigbract verbena is a common Intermountain early seral forb. Despite its colonizing abilities, its prostrate growth habit does not lend to seed production. Selecting early seral species with suitable seed production attributes can keep costs down and facilitate their adoption into restoration practices.

Another native species currently in the evaluation and selection process at IDPMC is curlycup gumweed, a common native forb found along roadsides and disturbed sites throughout the west (Tilley & Pickett, 2019) (Fig. 9). This forb exhibits tremendous benefits for pollinators (Tilley & Pickett 2019) and has been documented as a dietary component of greater sage-grouse (Peterson, 1970). Recent studies have also indicated curlycup gumweed possesses fire-retarding capabilities that may make it a valuable component of fuel break greenstrips in the west (Tilley & Wolf, 2020). Despite these benefits, only minimal acceptance of gumweed is prevalent with regard to use in rangeland restoration. On the contrary, this species has been designated as a weed by several counties in Wyoming (Wyoming Weed and Pest Council, 2018), where it is actively sprayed by county weed crews despite its being a native species (Welsh, 2003).

Figure 9. Curlycup gumweed, a native, early seral forb, is being investigated for plant germplasm release by the NRCS Aberdeen Plant Materials Center. Its attractiveness to native pollinators, seed production attributes, and ability to establish in disturbed soils make it a worthy candidate for succession management in the Intermountain West.

Risks and Questions

Ultimately the acceptance of early seral native weeds for use in restoration necessitates answers to two questions: 1) will early seral natives migrate outside of the restoration site and degrade communities where they are not wanted? And 2) will the addition of early seral native species facilitate a transition to the desired plant community, or will they hinder successional processes and ultimate climax species composition?

Intuitively, the answer to the first question is “no.” Early seral species are, by definition, not likely to invade and persist in a healthy climax community (Grime, 1977) and should only establish when a site has become degraded. For example, non-local germplasms of curlycup gumweed (Moore, 2010) and common sunflower, both North American native species, are becoming more and more common along roadsides and in disturbed areas around the west leading some to conclude that they are invasive. However, there is no evidence of these species becoming a problem in healthy, species-rich landscapes. Long-term monitoring is advisable, but it seems likely their apparent increase results from increased disturbance.

Answering the second question is more complicated. It is conceivable that overloading a restoration seed mixture with highly competitive early seral species could prevent or delay the longer-lived perennial species from fully establishing. In some instances, early seral species could simply be too competitive to be useful. Using early seral native species for assisted succession may not lead to a full transition back to the climax community or may send succession on an unwanted path (Ambrose & Wilson, 2003; Cox and Anderson, 2004; Brown et al., 2008; Hoelzle et al., 2012). It is also possible that the inclusion of early seral species might not provide enough benefit to warrant the added cost and that seeding a late-seral mix is adequate depending on the existing propagule bank and site conditions.

The next steps in developing succession management protocols for the Intermountain West should include field trials to evaluate the role, benefits, and risks of early seral native species. Field-scale trials of varying seed mixtures are also needed to compare ratios of seed representing various successional and functional groups to determine the best mix compositions. Long-term monitoring, as opposed to standard 2 to 4-year studies, will also be needed to observe successional change on a meaningful time scale.

Conclusions

Early successional species, especially annuals and short-lived perennials, represent an integral component of the plant community. Evolution and selection over the lifetime of the ecosystem have produced these species with traits to fill a functional niche that may be unwise to ignore. As has been noted, many of these species are similar in morphology and function to some of the region's most troublesome exotic invaders. Early seral species are well adapted to establish in disturbed sites under difficult conditions. While these traits can be viewed as weedy, this should be seen as an advantage and not a detriment as species with similar ecological attributes are better equipped to compete against invasion from exotics and conserve native site dynamics (Emery, 2007). Unfortunately, many of these species have been branded as unfit for restoration purposes.

Succession management is a tool that has been underutilized in the western sagebrush steppe. While the benefits of morphological diversity have been widely accepted, the temporal diversity of successional groups has yet to be fully incorporated into practice. By integrating the ideas of plant community succession in restoration plans, restorationists can naturally and more successfully alter site conditions and guide succession towards the desired state. One obstacle to achieving this goal is the limited number of early seral plant materials currently available.

The BLM, NRCS, US Fish and Wildlife Service (FWS), and other agencies have recently put forth a Native Plant Strategy with the mantra to "use the right plant at the right time" (Plant Conservation Alliance, 2015). Conservation practitioners should strive to use the right plant to meet resource objectives, whether forage production, disturbed site reclamation, or native habitat restoration. The right choice could be an introduced cultivar, a long-lived, local, perennial ecotype, or it might just be an ugly, short-lived native with little forage value that has evolved over millennia to capture disturbed sites and pave the way for climax species. Just because a species has found its way onto a weed list does not mean it should be automatically excluded from consideration in reclamation and restoration seedings. Weeds have evolved, for good and bad, to quickly invade and colonize sites that have been opened by disturbance. This is a trait that restorationists could be exploiting rather than resisting. Successional management and early seral natives are tools at the disposal of ecologists, which, if properly utilized, could help make meaningful strides in restoration outcomes. Plant Materials developers should continue to evaluate new species for conservation practices, including those considered native weeds, because sometimes a weed *IS* the right plant at the right time.

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