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Emerging seed enhancement technologies for overcoming barriers to restoration

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Rangelands occupy over a third of global land area, and in many cases are in less than optimum condition as a result of past land use, catastrophic wildfire, and other disturbances, invasive species, or climate change. Often the only means of restoring these lands involves seeding desirable species, yet there are few cost effective-seeding technologies, especially for the more arid rangeland types. The inability to consistently establish desired plants from seed may indicate that seeding technologies being employed are not successful in addressing the primary sources of mortality in the progression from seed to established plant. Seed enhancement technologies allow for the physical manipulation and application of materials to the seed that can enhance germination, emergence, and/or early seedling growth. In this article, we examine some of the major limiting factors impairing seedling establishment in North America's sagebrush steppe ecosystem and propose seed enhancement technologies that may have the potential to overcome these restoration barriers. We discuss specific technologies for: (1) increasing soil water availability; (2) enhancing seedling emergence in crusting soil; (3) controlling the timing of seed germination; (4) improving plantability and emergence of small-seeded species; (5) enhancing seed coverage of broadcasted seeds; and (6) protecting seedlings from pre-emergent herbicide. Concepts and technologies in this article for restoring the sagebrush steppe ecosystem may apply generally to semiarid and arid rangelands around the globe.

Key words: annual grasses, restoration, revegetation, seed coating, seed technology, wildfire

Conceptual Implications

- Effort to restore rangelands with desired species has largely been based on the scaling-up of row crop agriculture technologies (e.g. seeding with seed drills), without taking the time to define specific ecological barriers to restoration success or to develop practices to overcome these barriers.
- Emerging seed enhancement technologies have the potential to improve seeding efforts by treating seed prior to sowing with amendments that are designed to mitigate identified barriers to plant establishment for the site and time the seed is sown.
- Seed enhancement technologies may significantly increase cost; however, given the typically low success rates of rangeland seedings, added costs could be offset through improved establishment success rates.

Introduction

Rangeland degradation and desertification is a global problem, with many regions of the world experiencing declines in ecosystem goods and services and biodiversity (Milton et al. 1994; Stafford Smith et al. 2007; Han et al. 2008; James et al. 2013). As an example, the sagebrush steppe ecosystem of Western North America is undergoing rapid ecological change as native perennial plant communities are displaced by exotic annual grasses and forbs (D'Antonio & Vitousek 1992). The loss of sagebrush rangelands has resulted in more than 350 sagebrush-associated animals and plants being identified as species of conservation concern (Suring et al. 2005), and is decreasing forage production and quality, reducing recreation opportunities, degrading water resources, and increasing fire frequencies (Davies et al. 2011).

Conversion from native sagebrush steppe to exotic forblands or grasslands is typically driven by severe disturbances that compromise ecological resilience and impair autogenic recovery of native species, resulting in biological vacuums that exotic species exploit (Young & Clements 2003). Catastrophic wildfires are one of the most widespread forms of disturbance and vector pathways to weed invasion (D'Antonio & Vitousek 1992).

After a disturbance, land practitioners can halt the shift to an introduced annual community by successfully seeding desired plant species (Ott et al. 2003). In the arid regions of the sagebrush steppe, success rates for seeding efforts with native

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plants are notoriously low (James et al. 2011); however, due to the underreporting of negative results in the literature, the true efficacy of seeding practices is unknown (Hardegree et al. 2011). Once a site transitions to a weed-dominated system, restoration costs increase dramatically, while the probability of restoring perennial plant dominance to the system is reduced even further (Eiswerth et al. 2009).

The inability of current restoration practices to consistently establish native plants from seed may indicate that these practices do not address the primary sources of mortality in the progression from seed to established plant (James et al. 2011). This is because much of the effort to restore rangelands with desired species has been based on the scaling-up of row crop agriculture technologies (e.g. seeding with seed drills), without taking the time to define specific ecological barriers to restoration success or practices to overcome these barriers. It is now clear that traditional interdictory-based approaches to solving the annual grass problem have not been sufficient to offset losses, despite large monetary investments (Gebert et al. 2008). In addition, the very notion of reliable establishment from seed is at odds with an ecosystem noted for extreme temporal variation in environmental conditions and sporadic recruitment events (Boyd & James 2013). To sustain the ecological integrity and productivity of Western North American rangelands, there is a substantial need to develop methodologies and technologies that result in the post disturbance establishment of functional plant communities.

The expansive, complex nature of rangeland systems produces a diverse array of abiotic and biotic factors that may limit restoration success, including: drought, soil crusting, extreme temperatures, competition from weeds, salinity, predation, and infertile soils. One consistency held among rangeland sites is that the limiting factors impairing establishment have their greatest impact during the early stages of plant development (James et al. 2011). Subsequently, restoration practices that can avoid or improve tolerance to limiting abiotic and biotic stresses during early stages of plant development should have a higher likelihood of success.

Seed enhancement technologies allow for the physical manipulation and application of materials to the seed that can influence germination, emergence, and/or early seedling growth (Taylor 2003; Halmer 2008). Film coating, encrusting, seed coating, and pelleting techniques are commonly used enhancement technologies in the seed industry for applying materials to the surface or external portions of the seed (Taylor 2003). Some of the materials being applied through these technologies include application of macro and micronutrients, soil surfactants, plant growth regulators, beneficial microorganisms, humic substances, biopolymers, hydrophilic and hydrophobic materials, and various plant protection agents including fungicides, insecticides, and predator deterrents. Seed enhancement technologies can alter the physiological status of the seed through hydration methods such as priming, steeping, hardening, soaking, and pre-germination (Gregg & Billups 2010) and break seed dormancy through such processes as chemical and mechanical scarification, stratification, and hormonal treatments (Turner et al. 2013).

It is our working hypothesis that the major barriers to restoration success can be alleviated by applying seed enhancements designed to address specific barriers to plant establishment for the site and time the seed is sown. Here we examine some of the major limiting factors impairing seedling establishment in North America's native sagebrush steppe ecosystem and review the progress we are making on emerging technologies for overcoming these restoration barriers. Specifically, we discuss technologies being developed for: (1) increasing soil water availability; (2) improving seedling emergence in crusting soil; (3) enhancing plantability of small-seeded species; (4) controlling the timing of seed germination; (5) providing improved seed coverage; and (6) lowering competition from weeds by improving the selectivity of pre-emergent herbicides. In general, the technologies discussed in this article diverge from the common methods employed in the seed industry and provide new conceptual ideas for improving rangeland seeding success. It should be stressed that the seed enhancements shared in this article are in their early stages of development. Additional research is needed to continue to refine these technologies and establish their utility through multiyear large-scale field trials.

Seed Enhancement Technologies

Overcoming Soil Water Repellency Using Surfactant Seed Coatings

Soil water repellency (or hydrophobicity) is one factor that may significantly limit post fire recovery in semiarid shrub and woodland plant communities where high amounts of resins, waxes, or aromatic oils, and associated thick litter layers existed prior to the fire (Doerr et al. 2000; Madsen et al. 2011, 2012*a*). Soil water repellency can led to decreased water retention in the seed zone and subsequent poor germination and seedling survival (Madsen et al. 2012*a*). Piñon (*Pinus* spp.) and juniper (*Juniperus* spp.) are examples of woody vegetation types that are strongly correlated with the presence of soil water repellency (Madsen et al. 2011; Zvirzdin 2012). Zvirzdin (2012) recorded soil water repellency persisting for over 3 years after catastrophic wildfires in Utah, U.S.A.

Because the persistence of this soil condition exceeds favorable post fire recovery time frames, it needs to be considered as land managers plan restoration treatments.

The application of soil surfactants is a best management practice for the treatment of soil water repellency in golf courses and sports fields (Kostka & Bially 2005; Throssell 2005) and is becoming more popular in various sectors of the agricultural industry (Lowery et al. 2004). Use of soil surfactants in wildland systems has also been evaluated for reducing post-fire erosion and improving reseeding success (DeBano & Conrad 1974; Madsen et al. 2012*a*). Although these wildland studies have shown soil surfactants to be effective in mitigating post fire soil water repellency, their use in wildland restoration treatments has been limited. One of the main constraints has been the method of application. In agricultural systems, irrigation water is typically used as a carrier in the delivery of soil surfactants. In wildland systems, such an approach can be

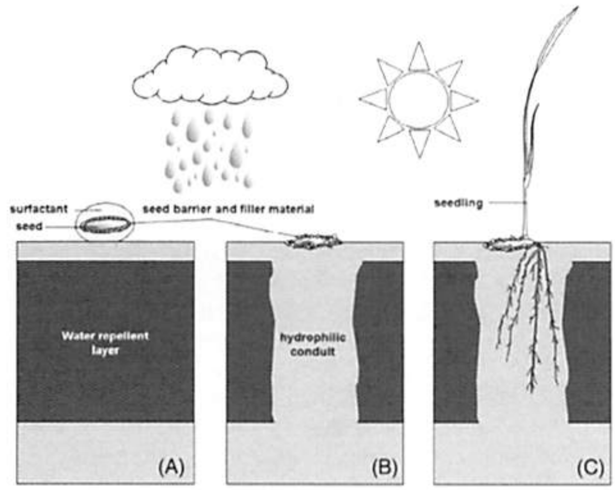

Figure 1. (A) Illustration of a seed coated with a soil surfactant to overcome hydrophobic soil conditions. (B) Precipitation releases the surfactant into the soil overcoming the water repellent layer, resulting in a hydrophilic conduit within the microsite of the seed. (C) Enhanced soil moisture promotes seed germination and seedling survival. Reproduced from Madsen et al. (2012*b*).

logistically prohibitive where the surfactant needs to be applied across large land areas with steep and rugged terrain (Rice & Osborn 1970). A potential solution to this problem was recently developed by Madsen et al. (2012*b*). In this approach, the surfactant is applied to the seed using seed coating technology (Fig. 1). Once planted, precipitation transfers the surfactant from the seed into the soil where it ameliorates water repellency at the seed microsite. In the laboratory, surfactant seed coating (SSC) technology has been shown to increase soil water infiltration, percolation, and retention in the area around the seed, improving seedling emergence and plant survival (Fig. 1). Field research by Madsen et al. (2013*a*) has shown that SSC technology can increase plant cover and density of established plants by over 2-fold. These results illustrate the potential for SSC technology to maintain ecological integrity in post fire ecosystems limited by soil water repellency.

Agglomerating Seeds to Enhance Native Seedling Emergence and Growth

In the sagebrush steppe ecosystem, seedling emergence represents a major developmental bottleneck in the progression from seed to established plant (James & Svejcar 2010; James et al. 2011; Boyd & James 2013). Nonbiotic soil-surface crusts can act as a significant barrier to seedling emergence (Awadhwal & Thierstein 1985). Intensive approaches for alleviating soil crust issues, such as irrigation, or use of equipment to mechanically break up the soil crust, are often not practical and too expensive to use in rangelands.

Madsen et al. (2012*c*) developed a new coating method that alters the traditional approach to seed coating to promote the clumping of seeds into agglomerates (Fig. 2). Agglomerated seeds may have improved seedling emergence because the

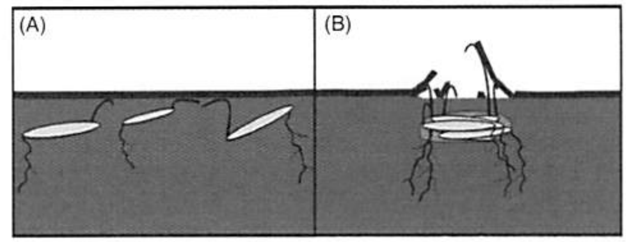

Figure 2. (A) Illustration of seedling emergence impeded by a soil crust layer, and (B) agglomerate pellet with multiple seedlings collectively generating sufficient force to penetrate through the soil crust. Reproduced from Madsen et al. (2012).

penetration force of emerging seedlings increases with the number of seeds sown in the same location (Awadhwal & Thierstein 1985; Fig. 2). Greenhouse evaluations of this technology showed that in a crusting heavy clay soil, agglomerated seeds emerged earlier and over a longer period of time than did non agglomerated seeds (Madsen et al. 2012*c*). Seedling emergence at the conclusion of the study was 2-fold higher with the agglomeration treatment compared to non treated seeds. This study also suggests that facilitation associated with clustered plant growth extended beyond seedling emergence. Seedlings growing in clusters had higher biomass than those from non agglomerated seeds, which may indicate that facilitation plays a more important role than intraspecific competition. These results indicate that current seeding practices that evenly space grass seeds may not be the most effective technique for seeding rangelands with crusting soils.

Extruded Seed Pellets to Facilitate Planting of Small, Low Vigor, or Difficult to Germinate Seeds

Seeding depth is one of the most critical factors for successfully establishing native plant materials from seed (Ott et al. 2003; Monson et al. 2004; James & Svejcar 2010). Depending on species and seed size, seedling emergence can be curtailed as a result of improper seed placement in the soil (i.e. seeds planted either too deep or shallow). As an example, James and Svejcar (2010) found that seedling density was more than 7-fold higher when sown at the proper depth, in comparison to seeding with a rangeland drill, which has only minimal control on seed placement.

Small or low vigor species can be especially susceptible to being planted at depths that prevent seedling emergence. For example, big sagebrush (*Artemisia tridentata* Nutt. spp.) produces seeds that are approximately 0.5 mm in size. When drill seeding big sagebrush, strict attention must be paid so that the drilling depth does not exceed 3 mm (Jensen et al. 2001). Due to the depth restrictions of big sagebrush, land managers typically will use broadcast seeding methods to apply the seed.

Our research group is seeking to improve seedling emergence of small-seeded species by using what we have coined "seed extrusion technology" to produce pellets that encapsulate seeds within an environment that is engineered to enhance seedling emergence and plant growth (Fig. 3). The extruded pellets are formed with equipment that is similar to what is used in the food

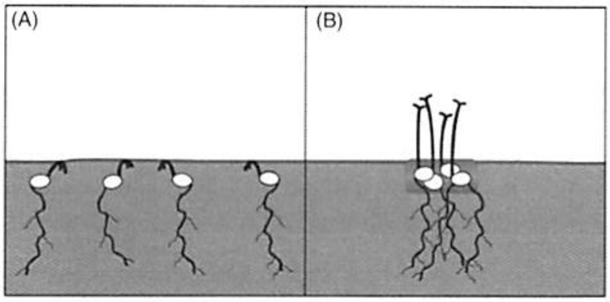

Figure 3. (A) Illustration of seedling emergence being impeded by a physical soil crust layer, and (B) seeds in an extruded seed pellet that are able to bypass the soil crust layer and emerge from the soil.

industry to produce pastas. In the process of producing extruded pellets, a seed dough mixture is extruded through a circular die, cut into pellets, and then dried. In addition to seed, there is a host of materials that can be incorporated within the "dough"; including water sensitive binders, hydrophilic filler materials, super-absorbent-polymers, fungicides, plant growth regulators, humates, fertilizers, inoculates, deterrents, and soil surfactants.

Through this technology, when the pellets are drill seeded with the top of the pellet near the soil surface, the emerging seedlings bypass restrictive near surface soil layers (such as soil physical crust; Fig. 3). The high water absorbency of the materials used also causes the pellet to swell, which pushes seeds to the surface and creates small voids or conduits for the emerging seedlings to follow.

In the laboratory, we evaluated the effect of extruded seed pellets on seedling emergence and early planting growth of Wyoming big sagebrush (*A. tridentata* Nutt. ssp. *wyomingensis*) over a range of seeding depths (5, 10, and 15 mm), within silt-loam and sandy-loam soil in a randomized block split-plot design with 10 blocks. The study was split by soil type. Ten 16 L wooden boxes (50×40 cm on a side, with a depth of 8 cm) were filled with each soil type. Within a wooden box, seed of each treatment was planted in rows, with the location of the row randomly assigned. Rows were 40 cm long and contained approximately 120 pure live seeds. Soil was watered to field capacity directly after planting and to approximately 70% of field capacity twice a week during the remainder of the study. Sagebrush density was recorded 10 weeks after planting. Data were analyzed using a mixed-model analysis (SAS Version 9.2 (2006); SAS Institute, Cary, NC, U.S.A.). Seed treatment × planting depth interactions and seed treatment × soil type interactions were significant (Table S1, Supporting Information); therefore, the LSMEANS procedure was used to compare seed treatment means within a planting depth and soil type using the SLICE option with a Bonferroni adjustment.

In the silt-loam soil, pellets improved seedling emergence between 2.3-fold and 10.0-fold (Fig. S1). In the sandy-loam soil, there was no treatment effect at the 5 and 15 mm depths, but pellets enhanced emergence at the 10 mm depth by 3.1-fold (Fig. S1). Overall, these results indicate that extruded seed pellet technology may improve sagebrush seeding efforts and may also aid in emergence of other small-seeded species.

Time-Delay Seed Coatings to Prevent Early-Germination of Fall-Sown Seeds

In the cold desert regions of North America, seeds are typically planted in late fall, which allows seed dormancy to be released and insures that seeds are in place in the spring when soil temperature and moisture are more favorable for seed germination and plant establishment (Monson et al. 2004). However, many of the cool season bunchgrasses, which are often planted in sagebrush steppe restoration projects, exhibit minimal to no dormancy at the time of seeding (e.g. bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) and bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey). Research indicates that when seeds are planted during the fall period, germination is often rapid and may reach 70% prior to winter onset (James et al. 2011; Boyd & James 2013). However, these seedlings may not survive through the winter. Laboratory results by Boyd and Lemos (2013) have shown that freezing, even for short durations, can cause significant mortality to young seedlings. Seeds planted in the fall may also experience high mortality from pathogens (Gornish et al. 2015). For example, fungal disease organisms can cause seed and seedling mortality through seed rot, damping-off, seedling blights, and root rot.

Our research group is developing time-delay coatings for fall planted seeds that contain hydrophobic polymers that are designed to prevent seed imbibition until spring. Hydrophobic seed coatings have had some use for controlling the timing of seed imbibition and germination for agricultural crops (Johnson et al. 2004). We hypothesized that delaying seed germination of fall planted seeds until spring with a hydrophobic seed coating would minimize seed and seedling mortality over the winter period and increase seedling emergence in the spring. We tested this hypothesis in a preliminary study at a site located on the Northern Great Basin Experimental Range operated by the USDA-Agricultural Research Service, which is approximately 50 km west of Burns, Oregon.

Research plots were established on a south-west facing hillside (slope 12.5 %) at an elevation of 1,460 m, which contained a Carryback gravelly loam soil and a plant community dominated by Wyoming big sagebrush and Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth). The site was sprayed in May 2014 with 11.7 L/ha of glyphosate and then burned. Within a randomized complete block design, with five blocks, non treated seed and time-delay coated seeds were sown in October 2014. Plots were 8.75 m^2 ($2.5\,m \times 3.5\,m$). Anatone bluebunch wheatgrass was used as the test species and sown at a rate of 500 seeds/m^2. To determine if the seed coating was delaying germination, we used the buried seed bag technique (Abbott & Roundy 2003). At the time of planting, two nylon mesh bags (S-10648W, Uline, Chicago, IL, U.S.A.) containing field soil and 50 seeds were planted in each plot. One bag was pulled in December and the second bag was pulled in May. After removing the bags from the plot, soil was separated from the seed through washing over a 0.5-mm mesh screen and seeds with visible radicle development were considered germinated. At the same time, seed germination bags were removed in May and seedling density was also determined within eight 0.25 m^2 quadrats per plot.

Data were analyzed in SAS (Version 9.3; SAS Institute, Cary, NC, U.S.A.) using a randomized complete block analysis of variance (ANOVA; Proc Mixed). Block was considered a random factor. In the analysis of seed germination, effects tested included: sampling period, seed treatment, and their interaction. Mean values were separated using the Tukey–Kramer honestly significant difference multiple comparison method. Significance was determined at $p \leq 0.05$.

The proportion of non treated seeds that had germinated in seed bags pulled in December was 75%, whereas seed bags pulled in May for the same treatment had 74% germination (Table S2; Fig. S2). Germination of time-delay coated seed in December and May was 14 and 60%, respectively (Fig. S2). These results imply that all of the non treated seeds germinated in fall or early winter, while the majority of the coated seeds germinated in late winter or spring. Measurements of plant density showed that plots seeded with time-delay coatings had 2.2-fold more plants than plots seeded with non treated seed (Fig. S3). Based on these preliminary results, it appears that time-release coatings may be a viable tool for reducing seedling mortality during winter, subsequently increasing the number of viable seeds available to capture essential early spring moisture. Future research is needed to refine time-release coating methods and to evaluate the technology at different sites and planting times.

Seed Pillows for Enhancing Seed Coverage of Broadcast Seed

In many situations, it is not possible to use ground-based equipment, such as seed drills, due to a host of logistical constraints, such as the site being too steep and/or rocky, high densities of tree skeletons, lack of financial or logistical resources, and cultural constraints (Vallentine 1989; Bryan et al. 2011). Under these conditions, land managers are limited to using broadcast aerial seeding (Monson et al. 2004). With this method, successful germination and establishment are highly dependent on the seed falling within a safe site that contains adequate nutrients and moisture and is protected from predation (Harper et al. 1965; Chambers 2000). Particularly within arid low elevations sites, where the seed bed has not been prepared, studies have shown that aerial seeding alone is not a reliable restoration approach (Ott et al. 2003; Lysne & Pellant 2004). For example, Lysne and Pellant (2004) found that aerially seeded big sagebrush failed to establish on 23 of 35 post fire rehabilitation projects.

To improve broadcast-seeding success, we are developing the "seed pillow," which is comprised of a pillow-shaped agglomeration of absorbent materials and other beneficial additives, with seeds attached either within or on the underside of the pillow (Madsen & Svejcar 2013; Fig. 4). To increase the probability that the pillow lands upright (i.e. seed side down), the seed side of the pillow is weighted. The shape of the pillow is also designed to improve coverage by having a flat bottom and convex top (Fig. 4). With this shape, a broadcasted seed pillow tumbling along the soil surface is more likely to come to arrest with the bottom of the pillow toward the ground. During a precipitation event, the pillow material breaks down over the seeds, thus providing seed coverage and enhanced conditions for seed germination and growth. For more rapid germination, seeds can be primed using solid matrix techniques in the medium used to form the seed pillows (Madsen & Hulet 2015). Laboratory emergence trials conducted on muttongrass (*Poa fendleriana* (Steud.) Vasey) and bluebunch wheatgrass showed that days to 50% emergence was between 66.2 and 82.4% faster (5.2–14.5 days less) for seeds in pillows than for non treated seed, depending on species and soil type they were sown within (Madsen & Hulet 2015).

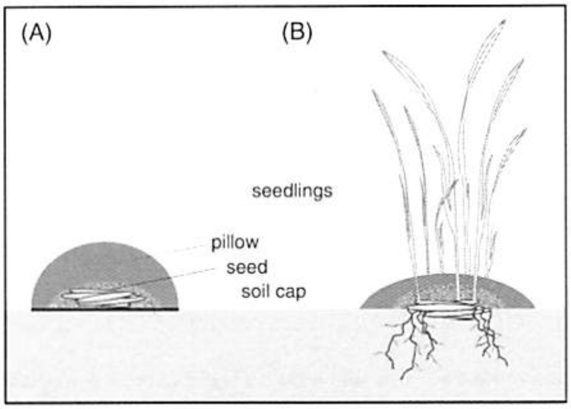

Figure 4. (A) Illustration of seeds attached to a seed pillow. (B) Precipitation melts the pillow material over the seeds and enhances seed soil contact.

This technology has the potential to be applied to a variety of seed sizes and types, which allows for seeding a diversity of native plant species. Because seeding with seed pillows does not require the use of disks or other mechanical equipment to plant the seed, the technology may be used to increase abundance of limiting species without disturbing native species that are already present on the site.

Improving Herbicide Selectivity through Herbicide Protection Pod Technology

Cost-effective strategies are limited for successfully reestablishing native perennial sagebrush-steppe species in areas dominated by exotic annual grasses (Eiswerth et al. 2009). This is because native perennial seedlings do not compete effectively with exotic annual grass seedlings; these annual grasses have higher plant and seed bank densities, faster germination velocity and growth rates, and greater germination potential (Chambers et al. 2007). The superior competitive ability of exotic annuals necessitates the need for removal or reduction of these weeds prior to reseeding native or desired non-native perennial species (Monson et al. 2004).

The most effective control of exotic annual grasses has been achieved with pre-emergent, that is soil active, herbicides (Monaco et al. 2005; Davies 2010). Imazapic is one such herbicide that has been shown to effectively control exotic annual grasses when applied appropriately (Davies & Sheley 2011). Often, seeding efforts are postponed for up to a year following imazapic application to allow herbicide activity to decline to a level that minimizes non target plant injury (Davies 2010;

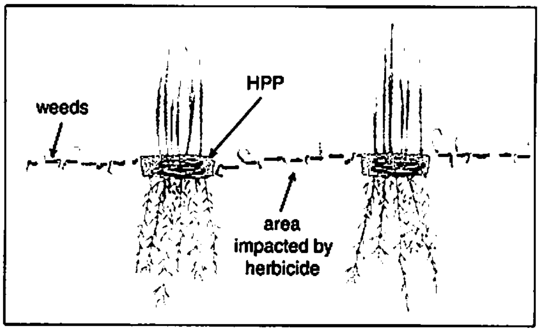

Figure 5. Illustration of a weed infested area that was planted with seed that was incorporated within herbicide protection pods (HPPs). The site was treated with pre-emergent herbicide, which controlled weed species whereas activated carbon in the HPPs deactivates herbicide in the immediate vicinity of the sown seed and allows for plant growth. Reproduced from Madsen et al. (2013*b*).

Davies et al. 2014). However, when seeding is delayed, the exotic species targeted for control may reestablish (Sheley et al. 1996). Not only does this reestablishment limit seeding success but also restoration that requires multiple steps is typically more expensive and energy demanding than single step approaches (Sheley et al. 2001).

Herbicide selectivity has been improved in row crops through "banding," applying a band of activated carbon to deactivate herbicide over the seed row (Lee 1973). A limitation of banding is that the technique does not provide complete control because weed seed within the band will also be protected from herbicide (Lee 1973).

It has been proposed that the selectivity of a range of herbicides for weeds can be further improved by coating crop seeds with activated carbon (Hagon 1977; Cook & O'Grady 1978). Commercial seed coatings are typically applied using rotary and drum coaters; through these technologies the coating forms thin layers around the seed 1–2 mm thick (Gregg & Billups 2010). Unlike banding, an activated carbon seed coating only provides protection to the seed and potentially a thin layer around the seed. We assume that protection from herbicide is decreased as the radical from the germinated seed extends into the soil and is subject to herbicide uptake.

Madsen et al. (2013*b*) have developed a new seed enhancement technology designed to combine the protective ability of activated carbon banding with the selectivity of seed coating. Designated as "herbicide protection pods" (HPPs), the technology uses the same extrusion equipment as described previously to pass a dough mixture containing seed, water sensitive binders, activated carbon, and other additives through a rectangular die. The extruded material is then cut into short strips and dried. In the field, HPPs are sown flat with the top of the pod level with or just below the soil surface (Fig. 5). This seeding method is anticipated to provide sufficient coverage of activated carbon for the seeded species to neutralize herbicide uptake while minimizing herbicide protection to weed species.

Activated carbon-coated seeds and HPP technology have been evaluated in a laboratory grow-room study with bluebunch wheatgrass as the model-seeded species and cheatgrass (*Bromus tectorum* L.) as the exotic invasive (Madsen et al. 2013*b*). In this study, bluebunch wheatgrass was either left uncoated, coated with activated carbon or incorporated into HPPs. Cheatgrass was sown in all treatments at equal densities. After planting, growing pots were sprayed with 70, 105, 140, or 210 g active ingredient (ai)/ha of imazapic or left unsprayed. Cheatgrass biomass dominated the growing space in the unsprayed treatments. Imazapic effectively prevented establishment of cheatgrass and untreated bluebunch wheatgrass. Seeds coated with activated carbon showed increased herbicide protection when imazapic was applied at its lowest rate, 70 g ai/ha. Seeds incorporated into HPPs were protected from imazapic regardless of herbicide application rate. When averaged across the four imazapic applications rates (excluding the unsprayed control), the HPP treatment had 4.8-, 3.8-, and 19.0-fold higher bluebunch wheatgrass density, height, and biomass respectively, compared to the uncoated seed treatment. These results indicate that HPPs and, to a lesser extent, activated carbon seed coatings, may make it possible for land managers to use a single entry system to plant desired species while simultaneously applying imazapic at rates necessary for weed control.

Economic Savings Associated with Improved Restoration Success

One of the greatest economic impacts associated with the invasion of exotic annual grasses in the sagebrush steppe ecosystem is the subsequent increase in wildfire suppression costs (Gebert et al. 2007, 2008; Taylor et al. 2013). For example, the exotic annual grass cheatgrass has significantly increased fire frequency and is disproportionately represented in the largest wildfires in the Western United States (Balch et al. 2013). Gebert et al. (2008) showed that wildfire suppression expenditures by the largest U.S. land management agencies (i.e. Forest Service and Bureau of Land Management), can exceed $1 billion dollars per year.

The successful establishment of perennial grasses can slow or halt the spread of exotic annuals (Davies et al. 2011). Therefore, seeding of desired species into degraded sagebrush steppe could result in considerable savings in wildfire suppression costs. However, economic analysis by Taylor et al. (2013) demonstrated that for degraded Wyoming big sagebrush sites (which represent the more arid but dominant portions of the sagebrush steppe) it is typically not feasible to seed because there is a low probability that restoration efforts will be successful. Subsequently, Taylor et al. (2013) suggested that treatment success rates have to be improved, treatment cost lowered, or some combination of the two, for restoration treatments to be economically efficient.

Seed enhancement technologies may significantly increase the cost of the seeds planted; however, given the typically low success rates of rangeland seedings, we anticipate that these costs can be offset through improved establishment success rates. Our conversations with regional land managers suggest that the probability of successfully restoring a diverse community of native species in the sagebrush steppe may be less than 10%. In other words, 90% or more of the funds used to seed native species are without positive return. The actual cost of a successful restoration treatment on a unit area basis can be thought of as the cost of the treatment divided by the probability of success (Boyd & Davies 2012). If we assume a rehabilitation cost of $250 per hectare and a 10% probability of success, the cost outlay for every successfully rehabilitated hectare is $2,500. If the success rate is increased to 50% using precision seed enhancement technologies, then cost per successful hectare drops to $500 (potential savings of $2,000 for each successfully rehabilitated hectare). If seed enhancement technologies increase the success rates of individual seeds, it is also conceivable that direct cost savings could be made because less seed may be required to complete the restoration project. Furthermore, matching individual seed enhancement technologies with spatial and temporal predictions of barriers to seedling establishment (i.e. "precision seeding") will further improve the cost-effectiveness of arid land restoration. Indirect savings may also be realized by maintaining functioning ecosystems through lowering wildfire suppression costs and maintaining landscapes that support both anthropogenic activities and a diversity of wildlife habitats.

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LITERATURE CITED

Abbott LB, Roundy BA (2003) Available water influences field germination and recruitment of seeded grasses. Journal of Range Management 56:56–64

Awadhwal NK, Thierstein GE (1985) Soil crust and its impact on crop establishment: a review. Soil & Tillage Research 5:289–302

Balch JK, Bradley BA, D'Antonio CM, Gómez-Dans J (2013) Introduced annual grass increases regional fire activity across the arid western U.S.A. (1980–2009). Global Change Biology 19:173–183

Boyd CS, Davies KW (2012) Spatial variability in cost and success of revegetation in a Wyoming big sagebrush community. Environmental Management 50:441–450

Boyd CS, James JJ (2013) Variation in timing of planting influences bluebunch wheatgrass demography in an arid system. Rangeland Ecology & Management 66:117–126

Boyd CS, Lemos JA (2013) Freezing stress influences emergence of germinated perennial grass seeds. Rangeland Ecology & Management 66:136–142

Bryan NM, Anderson VJ, Fugal RA (2011) Disturbance to surface lithic components of archaeological sites by drill seeding. Rangeland Ecology & Management 64:171–177

Chambers JC (2000) Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. Ecological Applications 10:1400–1413

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

Cook BG, O'Grady R (1978) Atrazine in kikuyu grass establishment: a preliminary study. Tropical Grasslands 12:184–187

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Reviews in Ecology and Systematics 23:63–87

Davies KW (2010) Revegetation of medusahead-invaded sagebrush steppe. Rangeland Ecology & Management 63:564–571

Davies KW, Boyd CS, Beck JL, Bates JD, Svejcar TJ, Gregg MA (2011) Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biological Conservation 144:2573–2584

Davies KW, Madsen MD, Nafus AM, Boyd CS, Johnson DD (2014) Can imazapic and seeding be applied simultaneously to rehabilitate medusahead-invaded rangeland? Single vs. multiple entry. Rangeland Ecology & Management 67:650–656

Davies KW, Sheley RL (2011) Promoting native vegetation and diversity in exotic annual grass infestations. Restoration Ecology 19:159–165

DeBano LF, Conrad CE (1974) Effect of a wetting agent and nitrogen fertilizer on establishment of ryegrass and mustard on a burned watershed. Journal of Range Management 27:57–60

Doerr SH, Shakesby RA, Walsh RPD (2000) Soil water repellency, its characteristics, causes and hydro-geomorphological consequences. Earth-Science Reviews 51:33–65

Eiswerth ME, Krauter K, Swanson SR, Zielinski M (2009) Post-fire seeding on Wyoming big sagebrush ecological sites: regression analyses of seeded nonnative and native species densities. Journal of Environmental Management 90:1320–1325

Gebert KM, Calkin DE, Huggett RJ, Abt KL (2008) Economic analysis of federal wildfire management programs. Pages 295–322. In: Holmes TP, Prestemon JP, Abt KL (eds) The economics of forest disturbances. Vol 79. Springer, Netherlands, Bethesda, Maryland

Gebert KA, Calkin DE, Yoder J (2007) Estimating suppression expenditures for individual large wildland fires. Western Journal of Applied Forestry 22:188–196

Gornish ES, Aanderud ZT, Sheley RL, Rinella MJ, Svejcar T, Englund SD, James JJ (2015) Altered snowfall and soil disturbance influence the early life stage transitions and recruitment of a native and invasive grass in a cold desert. Oecologia 177:595–606

Gregg BR, Billups GL (2010) Seed conditioning. Pages 818–834. In: Technology-Part A. Vol 2. Science Publishers, Enfield, New Hampshire

Hagon MW (1977) Effects of competition, herbicides and activated carbon on establishment of Australian grasses. Weed Research 17:297–301

Halmer P (2008) Seed technology and seed enhancement. Acta Horticulturae 771:17–26

Han JG, Zhang YJ, Wang CJ, Bai WM, Wang YR, Han GD, Li LH (2008) Rangeland degradation and restoration management in China. The Rangeland Journal 30:233–239

Hardegree SP, Jones TA, Roundy BA, Shaw NL, Monaco TA (2011) Assessment of range planting as a conservation practice (chapter 4). Pages 171–212. In: Briske DD (ed) Conservation benefits of rangeland practices: assessment, recommendations, and knowledge gaps. US Department of Agriculture, Natural Resources Conservation Service, Washington D.C.

Harper JK, Williams JT, Sagar GR (1965) The behavior of seeds in soil: I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. Journal of Ecology 53:273–286

James JJ, Sheley RL, Erickson T, Rollins KS, Taylor MH, Dixon KW (2013) A systems approach to restoring degraded drylands. Journal of Applied Ecology 50:730–739

James JJ, Svejcar TJ (2010) Limitations to postfire seedling establishment: the role of seeding technology, water availability, and invasive plant abundance. Rangeland Ecology & Management 63:491–495

James JJ, Svejcar TJ, Rinella MJ (2011) Demographic processes limiting seedling recruitment in aridland restoration. Journal of Applied Ecology 48:961–969

Jensen K, Horton H, Reed R, Whitesides R, USDA-ARS-FRRL (2001) Intermountain planting guide. Utah State University, Logan, AG 510

Johnson EN, Miller PR, Blackshaw RE, Gan Y, Harker KN, Clayton GW, Kephart KD, Wichman DM, Topinka K, Kirkland KJ (2004) Seeding date and polymer seed coating effects on plant establishment and yield of fall-seeded canola in the Northern Great Plains. Canadian Journal of Plant Science 84:955–963

Kostka SJ, Bially PT (2005) Synergistic surfactant interactions for enhancement of hydrophilicity in water repellent soils. International Turfgrass Society Research Journal 10:108–114

Lee WO (1973) Clean grass seed crops established with activated carbon bands and herbicides. Weed Science 21:537–541

Lowery B, Jordan M, Kelling K, Speth P (2004) Use of surfactants to improve water and nitrate use efficiency and decrease leaching. Pages 123–125. Vol. XVIII. Proceedings of 2004 Wisconsin's Annual Potato Meetings

Lysne C, Pellant M (2004) Establishment of aerially seeded big sagebrush following southern Idaho wildfires. Technical Bulletin No. 2004-01. U.S. Department of the Interior, Bureau of Land Management, Idaho State Office, Boise, Idaho, 14 p

Madsen MD, Davies KW, Mummey DL, Svejcar TJ (2013*b*) Improving imazapic selectivity through activated carbon seed enhancement technologies. Rangeland Ecology & Management 67:61–67

Madsen MD, Davies KW, Williams CJ, Svejcar TJ (2012*a*) Agglomerating seeds to enhance native seedling emergence and growth. Journal of Applied Ecology 49:431–438

Madsen MD, Hulet A (2015) Primed seed matrix composition and method of making extruded seed pellets. U.S. Patent Application No. 62/111,451

Madsen MD, Kostka SJ, Inouye AL, Zvirzdin DL (2012*b*) Innovative use of seed coating technology for the restoration of soil hydrology and wildland vegetation in post-fire water repellent soil. Rangeland Ecology & Management 65:253–259

Madsen MD, Petersen SL, Fernelius KJ, Roundy BA, Taylor AG, Hopkins BG (2012*a*) Influence of soil water repellency on seedling emergence and plant survival in a burned semi-arid woodland. Arid Land Research and Management 26:236–249

Madsen MD, Svejcar TJ (2013) Development and application of "Seed Pillow" technology for overcoming the limiting factors controlling rangeland reseeding success. U.S. Patent Application No. 14/039,873

Madsen MD, Zvirzdin DL, Petersen SL, Roundy BA, Hopkins BG, Chandler DG (2011) Soil water repellency within a burned piñon-juniper woodland: spatial distribution, severity, and ecohydrologic implications. Soil Science Society of America Journal 75:1543–1553

Madsen MD, Zvirzdin DL, Kostka SJ (2013*a*) Improving reseeding success after catastrophic wildfire with surfactant seed coating technology. ASTM International 1569:44–55

Milton SJ, Dean WRJ, du Plessis MA, Siegfried WR (1994) A conceptual model of arid rangeland degradation. BioScience 44:70–76

Monaco TA, Osmond TM, Dewey SA (2005) Medusahead control with fall-and spring-applied herbicides on northern Utah foothills. Weed Technology 19:653–658

Monson SB, Stevens R, Shaw NL (2004) Restoring western ranges and wildlands. Pages 699–866. Vol. III. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado. General Technical Report RMRS-GTR-136-Vol-3.

Ott JE, McArthur ED, Roundy BA (2003) Vegetation of chained and non-chained seedings after wildfire in Utah. Journal of Range Management 56:81–91

Rice RM, Osborn JF (1970) Wetting agent fails to curb erosion from burned watershed. U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experimental Station, Berkeley, California. USDA Forest Service Research Note PSW-219

Sheley RL, Jacobs JS, Lucas DE (2001) Revegetating spotted knapweed infested rangeland in a single-entry. Journal of Range Management 54: 576–583

Sheley RL, Svejcar TJ, Maxwell BD (1996) A theoretical framework for developing successional weed management strategies on rangeland. Weed Technology 10:712–720

Stafford Smith DM, McKeon GM, Watson IW, Henry BK, Stone GS, Hall WB, Howden SM (2007) Learning from episodes of degradation and recovery in variable Australian rangelands. Proceedings of the National Academy of Sciences 104:20690–20695

Suring LH, Rowland MM, Wisdom MJ (2005) Identifying species of conservation concern. Pages 150–162. In: Wisdom MJ, Rowland MM, Suring LH (eds) Habitat threats in the sagebrush ecosystem—methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, Kansas

Taylor AG (2003) Seed treatments. Pages 1291–1298. In: Thomas B, Murphy DJ, Murray BG (eds) Encyclopedia of applied plant sciences. Elsevier Academic Press, Philadelphia, Pennsylvania

Taylor M, Rollins HK, Kobayashi M, Tausch R (2013) The economics of fuel management: wildfire, invasive plants, and the evolution of sagebrush rangelands in the western United States. Journal of Environmental Management 126:157–173

Throssell C (2005) GCSAA-USGA wetting agent evaluation. Golf Course Management 73:52–83

Turner SR, Steadman KJ, Vlahos S, Koch JM, Dixon KW (2013) Seed treatment optimizes benefits of seed bank storage for restoration-ready seeds: the feasibility of prestorage dormancy alleviation for mine-site revegetation. Restoration Ecology 21:186–192

Vallentine JF (1989) Range development and improvements. 3rd edition. California Academic Press, San Diego, 524 p

Young JA, Clements CD (2003) Rangeland monitoring and invasive weeds. Arid Land Research and Management 17:439–447

Zvirzdin DL (2012) Post-fire soil water repellency: extent, severity and thickness relative to ecological site characteristics within piñon-juniper woodlands. MSc Thesis. Brigham Young University, Provo, Utah

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Mixed-model ANOVA results for the effect of seed technology, soil type, planting depth, and their interactions on plant density.
Table S2. Mixed-model ANOVA results on seed germination responses.
Figure S1. Plant density, height, biomass per plant, and total biomass (mean ± SE) produced from untreated seed versus seed in an extruded pellet, sown at 5, 10, and 15 mm planting depths in silt-loam and sandy-loam soil.
Figure S2. Seed germination (±SE) recorded in germination bags pulled in December and May for non treated seed (control) and seed treated with a time-delay seed coating.
Figure S3. Plant density (±SE) produced from non treated seed (control) and seed coated with a time-delay coating.

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