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OPINION ARTICLE

A new perspective and approach to ecosystem restoration: a seed enhancement technology guide and case study

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Restoration efforts in dryland systems are often limited by a complex range of environmental variables and chronically low establishment of seeded native species. Methods for restoring large tracts of degraded drylands in the western United States and southwestern Australia have not advanced substantially since the early 1900s despite continuous efforts to improve success. Historic agricultural practices used in large-scale restoration efforts are often unsuccessful. A multidisciplinary approach toward problem resolution is necessary for future advancements in restoration applications and methods. Specifically, agricultural technologies such as seed enhancements should be applied to native restoration approaches. Seed enhancement technologies, such as activated carbon coating and extruded pelleting, are novel in the restoration context. However, their use is increasingly recognized as an opportunity to overcome current limitations to restoration efforts. At this early juncture in the development of seed enhancement technologies within restoration, we reflect on the need to tailor current agricultural technologies in light of the differences between agricultural and restoration contexts and reconceptualize our approach to seed enhancement technologies. In this paper, we provide a guide for the development of seed enhancement technologies in ecological restoration.

Key words: Banksia woodlands, extruded pelleting, Great Basin, inter-disciplinary approach, revegetation, seed coating

Conceptual Implications

- Novel approaches to seed-based restoration are needed to account for restoration failures globally.
- Recent development of seed enhancement technologies that are activated carbon-based show promise, however; there is a need to develop other technologies to overcome remaining restoration barriers that affect degraded ecosystems.
- Looking beyond agricultural technologies may be necessary for effective, efficient methods of overcoming limitations to native ecosystem restoration.

Introduction

Ecosystem degradation and fragmentation is one of the major global threats of the 21st century (Millennium Ecosystem Assessment 2005). Levels of degradation have become so great that conservation alone is not enough to preserve biodiversity in many systems (Volis 2019; Ritchie et al. 2021) and an intense need for advances in both the science and practice of ecosystem restoration are highlighted by the UN Decade on Ecosystem Restoration 2021–2030 (United Nations General Assembly 2019). How we proceed with restoration efforts has become an increasingly critical issue with forecasts of climate change and biological invasions (Hardegree et al. 2017; IPCC 2021). As climatic conditions become more erratic in many regions globally (IPCC 2021), years for optimal restoration conditions may become more limited. For example, historic 10-year heatwave events are forecast to occur three times more often at our current 1°C state (IPCC 2021). Biological invasion is a common disturbance that drives a need for ecosystem restoration (Shackelford et al. 2021). Invasive exotic plant species can create hostile conditions for desired species establishment due to competition for limited resources (Rafferty & Young 2002). Altering climatic conditions (e.g. more frequent heatwaves, floods, and droughts) and increasing competition from exotic plants will create ever greater challenges for an already difficult task, reestablishing desirable species. As such, there is a need to reevaluate current restoration practices and develop novel approaches to ecosystem restoration.

One of the most common restoration practices involves seeding native species into degraded landscapes (i.e. seed-based

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restoration). Billions of dollars are spent annually on native restoration seeding efforts around the world (Pilliod et al. 2017; Stevens & Dixon 2017), with typically low success (Cao et al. 2011; James et al. 2011). Alternatives to seeding, such as planting nursery grown plants, may hold greater success in plant establishment in some ecosystems, especially ecosystems with woody plants (Davies et al. 2020). However, the large expanses of degraded lands in many ecosystems (1000s of hectares), the geographic variability, species diversity, and financial limitations can make planting nursery grown plants logistically impossible for achieving restoration objectives (Shackelford et al. 2021). This necessitates a need to evaluate current seeding practices and explore novel methodologies for improving native species seeding outcomes (Copeland et al. 2021).

Recently, research has begun reevaluating agricultural technology transfer to seed-based ecosystem restoration applications with robust efforts in two floristically unique regions facing similar restoration challenges: the Great Basin of the western United States (Madsen et al. 2013; Davies et al. 2018) and Banksia Woodlands of south-western Australia (Brown et al. 2019; Ritchie et al. 2020). Seed enhancement technologies are defined as "a post-harvest treatment, technique or technology that is applied to seeds that protects seeds, improves germination, vigour or emergence, allows for precision delivery and/or increases the tolerance to, or avoidance of, seeds and seedlings to environmental stress" (Brown et al. 2021). The science of seed enhancement technologies in native plant restoration is becoming more widely used and many novel advances are being made. However, the development of seed enhancement technologies still requires further research (Brown et al. 2021), especially before technologies go into production and are broadly applied for management purposes to ensure efficacy of product. For example, coating and pelleting technologies should focus on improving germination, emergence or establishment while taking into consideration species-specific variables, such as seed size, shape, and morphology (Brown et al. 2021). Similarly, optimal coating or extruded pelleting formulations need to be developed with consideration of the major barriers to seedling establishment such as surface soil repellency (Ritchie et al. 2020), predation by granivores (Taylor et al. 2020), and competition by exotic plants (Davies et al. 2018). In this article, we focus on seed enhancement technologies that have been developed to overcome competition from exotic plants. Given the infancy of seed enhancement technologies in restoration ecology, we feel this is an opportune time to create a guide for future developments based on work to date. Specifically, a detailed understanding of the limitations posed on native plant establishment and the technologies available to overcome those barriers is necessary for successful implementation (Copeland et al. 2021). In this paper, we utilize the precision restoration framework concept (Copeland et al. 2021) to create a guide for seed enhancement technology development and use a successful technology, carbon-based coatings and extruded pellets in the Great Basin and Banksia Woodlands, as a case study.

A Guide for Seed Enhancement Technology Development

The complexity of native ecosystem restoration requires a more holistic understanding of the conditions required for successfully establishing native plant species (Copeland et al. 2021). The use of seed enhancement technologies has the potential to improve restoration success and become a major component of precision restoration plans. However, while the desire to proceed quickly into producing these technologies at large-scales exists, careful consideration in the development of seed enhancement technologies is needed before they are mass produced. The first step to take when considering seed enhancement development is characterizing the degree of and processes driving degradation at both small (meters) and large (kilometers) scales (Table 1, step 1). Once the processes driving degradation are identified, then barriers to native seedling establishment need to be identified (Table 1, step 2). For example, if an area is degraded due to invasion from exotic plants and it is determined that herbicide is the best management practice for controlling their proliferation, then consideration of the impact herbicides have on native or desirable species needs to be made.

After barriers to native or desirable seed establishment are determined, then consideration of potential solutions to those barriers may be explored (Table 1, step 3). Solutions to seedling establishment barriers may be derived from any number of alternative disciplines, such as agriculture, engineering, chemistry, and medicine. To date, the majority of seed enhancements have been derived from technologies in agriculture (Brown et al. 2021). However, a direct transfer of agricultural technologies to ecosystem restoration is not recommended as cropped and native systems differ substantially (Box 1). Thus, a nuanced approach to the application of those technologies is required (Table 1, step 4). In particular, the seed physical and

Table 1. A seed enhancement technology (SET) guide and its application.

Steps	*Example*
1. Characterize current degree of degradation	• Invasion of exotic species that trigger positive feedback loop with fire • Large scale: high overall risk of exotic species spread • Small scale: sites may vary in degree of invasion
2. Targeting barriers to native seedling establishment following degradation (Copeland et al. 2021)	• Reduce the impact of high summer mortality of native seedlings by targeting exotic species competition • No resistance to herbicides in native species
3. Identify potential solutions to barriers to seedling establishment (Copeland et al. 2021)	• Use activated carbon in SET for improved herbicide avoidance to native seeds when controlling exotic species
4. Determine what materials and species to use in SET: dose, germination timing, establishment, survival (see Fig. 1)	• Activated carbon: how much activated carbon should be used? Is activated carbon base material locally sourced? • Test all species to be used in SET

Box 1 Cropped and native system differences and similarities.

Agricultural technologies used to improve seeded crop species may be used to enhance establishment success of native plant species, but direct transfer of these technologies per se is not recommended for ecological restoration due to vast differences between cropped and native systems (Table S1). In general, cropping systems are relatively homogeneous while native systems are highly heterogeneous. Crop systems attempt to minimize variation within a species and environment through biotic and abiotic manipulations, such as precision irrigation systems. Relative to cropping systems, native systems often experience variability in both biotic and abiotic conditions. For example, one of the major limitations of native plant restoration in dryland systems is interannual climatic variation (Sheley et al. 2011). Natural variability in precipitation and temperature can mean the difference between success and failure of a native seeding project (Boyd & James 2013) and physical manipulation of abiotic conditions, such as watering via irrigation, are logistically and economically unfeasible in most situations.

Biotic and abiotic conditions are more frequently altered in order to develop uniform plant emergence, establishment and maturity in cropping systems to ensure an efficient harvest, while conditions in native settings are less frequently altered and species experience periodic establishment. In spite of these environmental differences, goals in cropping and native plant establishment have similarities. For example, both systems suffer from pressure by undesirable species and use herbicides for control of those species. However, negative impacts of herbicides have been reported for both desired crop and native species (e.g. Rokich et al. 2009; Ding et al. 2011; Peterson et al. 2020).

physiological requirements of each species used in a seed enhancement technology must be taken into account and an iterative process of seed enhancement technology testing and field validation are needed (Table 1, step 4; Fig. 1). When applying seed enhancement technologies, especially when multiple technologies are applied simultaneously, the combination ratio and order of seed enhancement technologies are critical to achieve optimal results (Berto et al. 2021). For example, seeds with hairs or awns may need to be flamed to improve seed morphology before the seed can be coated or primed efficiently (Berto et al. 2021). This process may take multiple iterations for native species compared with agricultural species as variability in seed physiology and climatic conditions can alter the efficacy of a particular seed enhancement (e.g. Davies et al. 2018; Box 1).

Seed Enhancement Technologies Incorporating Activated Carbon: A Case Study for the Great Basin and Banksia Woodlands

In both the Great Basin and Banksia Woodlands (Fig. 2A) seed-based restoration techniques are used as a response to large-scale ecosystem degradation. The Great Basin is a cold desert, characterized by low annual precipitation that has historically occurred as winter snow fall (Fig. 2B; Svejcar et al. 2017). Banksia Woodlands are a Mediterranean Climate Ecosystem with cool wet winters and hot dry summers (Fig. 2C; Ritchie et al. 2021). Though structurally and functionally different, these two ecosystems suffer from similar persistent threats of degradation leading to a high risk of species extinction and local extirpation (Davies 2011; Ritchie et al. 2021). For both ecosystems, hot, dry summers pose a major threat to seedling desiccation and mortality, making early emergence and seedling growth prior to hostile summer conditions imperative, especially in degraded sites where conditions may be harsher than reference states, such as reduced microsite protection or altered soil conditions (Benigno et al. 2014; Svejcar et al. 2017). In the Great Basin, seed-based restoration often involves drill or aerial seeding in autumn due to optimal conditions for equipment, but seeds are then subject to mortality due to winter freezes (Fig. 2B; Svejcar et al. 2017). In Banksia Woodlands, seed-based restoration is conducted in late autumn before the onset of winter rains; however, soil hydrophobicity may not be broken in time for seeds to be exposed to the necessary moisture levels they need for germination (Fig. 2C; Ritchie et al. 2021). On top of these thresholds, further limitations to native seedling establishment are presented due to competition from exotic species (Svejcar et al. 2017; Ritchie et al. 2021).

Step 1: Characterizing Current Degree of Degradation

The need for novel approaches to seed-based ecological restoration in the Great Basin and Banksia Woodlands emerged as a result of seeding failures that use a direct transfer of agricultural technologies without considering barriers to seedling establishment (Masarei et al. 2021). These two ecosystems have high rates of exotic plant invasion that alter fire cycles and create positive feedback loops leading to alternative stable states of exotic plant dominance (D'Antonio & Vitousek 1992; Ritchie et al. 2021). Conversion to exotic plant dominance creates an increased risk of native plant extinction within the ecosystem (Davies et al. 2021; Ritchie et al. 2021). In the Great Basin, exotic annual grasses (*Bromus tectorum* L. and *Taeniatherum caput-medusae* L. (Nevski)) shorten fire intervals and increase the size of fires due to continuous fine fuel loads (Balch et al. 2013). Native perennial vegetation is generally not tolerant of frequent fires and thus declines (D'Antonio & Vitousek 1992). Exotic annual grasses are also highly competitive with native perennial vegetation, in particular, bunchgrass seedlings (Rafferty & Young 2002). Subsequently, exotic annual grass invasion exponentially decreases biodiversity (Davies 2011). This has led to exotic annual grasses dominating millions of hectares of rangelands in the Great Basin and creating major challenges to restoration of native species (Davies et al. 2021). Resources for restoration are limited, thus more effective restoration practices are needed.

In the northern distribution of Banksia Woodlands, 28,000 ha were cleared for forestry production (*Pinus pinaster* Aiton. pine plantations) in the 1940s (Stanbury et al. 2018). The pines are currently being felled to decrease pressure on local water

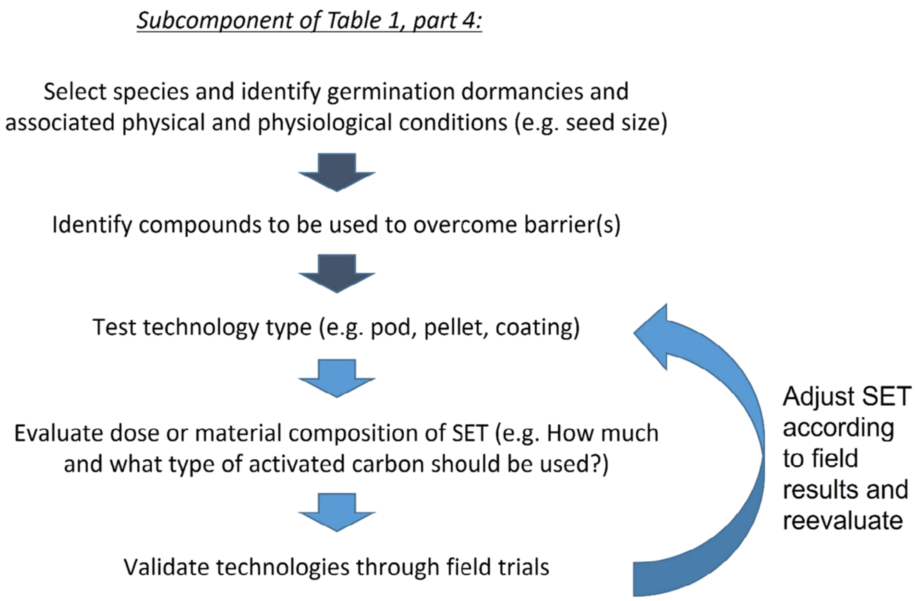

Figure 1. An iterative process for seed enhancement technologies (SETs) is needed in order to improve their use in ecosystem restoration.

resources and with their removal, invasive exotic plants have entered (Stanbury et al. 2018). *Ehrharta calycina* sm. (a perennial grass native to South Africa) is the most prevalent exotic plant species, which quickly dominates disturbed ecosystems when active exotic plant control is not implemented and alters fire cycles and patterns (Ritchie et al. 2021). Despite restoration solutions for Banksia Woodlands being identified for small-scale impacts (<10 ha) within post-sand extraction mining (Stevens et al. 2016), barriers to restoration of large-scale tracts (>10,000 ha) such as within the felled pine areas, remain unresolved (Stanbury et al. 2018). Similar to the Great Basin, exotic plant species in Banksia Woodlands alter fire cycles in the system (Ritchie et al. 2021) and outcompete native species seedlings (Stanbury et al. 2018). Large-scale restoration requirements, coupled with limited native seed resources, high densities of exotic plants and low native plant species establishment rates increases the need for plant establishment success from seeds. For example, key Banksia Woodlands species can cost between 0.75 and 1.00 AUD per seed (Ritchie et al. 2021) and with low establishment rates of these species (5–7%) the overall cost of restoration wherein the goal is to attain reference state conditions becomes expensive (Turner et al. 2006). As such, investment in seed enhancement technologies could be more beneficial for limited seed stock (Ritchie et al. 2020) and a more cost-effective approach if proven successful (Brown et al. 2021) for both these ecosystems.

Step 2: Targeting Exotic Plant Barriers to Native Seedling Establishment

Eliminating exotic plants and reestablishing native plant species is a major challenge. Competition from exotic plants as well as their ability to change soil nutrient status (Fisher et al. 2006), significantly reduces the likelihood of native or desirable plant establishment (Rafferty & Young 2002; Fisher et al. 2006; Stanbury et al. 2018). To control exotic plants, herbicides are often applied in both the Great Basin and Banksia Woodlands. However, native plant species are not resistant to herbicides (Terry et al. 2021*a*). In the Great Basin, seeding of desirable species is often conducted a year or two after preemergent herbicide application to an area with high exotic plant invasion, but by the time native plants can be seeded, exotic plants may also return (Madsen et al. 2013). For example, Morris et al. (2009) found that exotic annuals returned to pretreatment levels within 2 years of preemergent herbicide application (imazapic) in a Great Basin study. They also found that herbicide activity was influenced by annual precipitation, and that seeded species are vulnerable to herbicide. Similarly, in Banksia Woodlands commonly used postemergent herbicides (Fluazifop-p-butyl and glyphosate) have been found to significantly impede native species during germination, seedling emergence and establishment phases, reducing overall seedling health and development (Rokich et al. 2009; Munro 2019). The inefficiency of required time-lags with pre-emergent herbicides and the contradictions of the purported labeled postemergent herbicides creates vulnerabilities to native seeds. Thus, a way of protecting these seeds from herbicides is needed.

Step 3: Identify Potential Solutions to Exotic Plant Barriers

Activated carbon has been used widely in agriculture to improve herbicide selectivity, thereby reducing competition of unwanted species in cropped systems (Burr et al. 1972). Activated carbon is produced from carbon source materials and has the capacity to adsorb and immobilize herbicides (Bansal & Goyal 2005). In cropping systems, activated carbon is often applied in strip

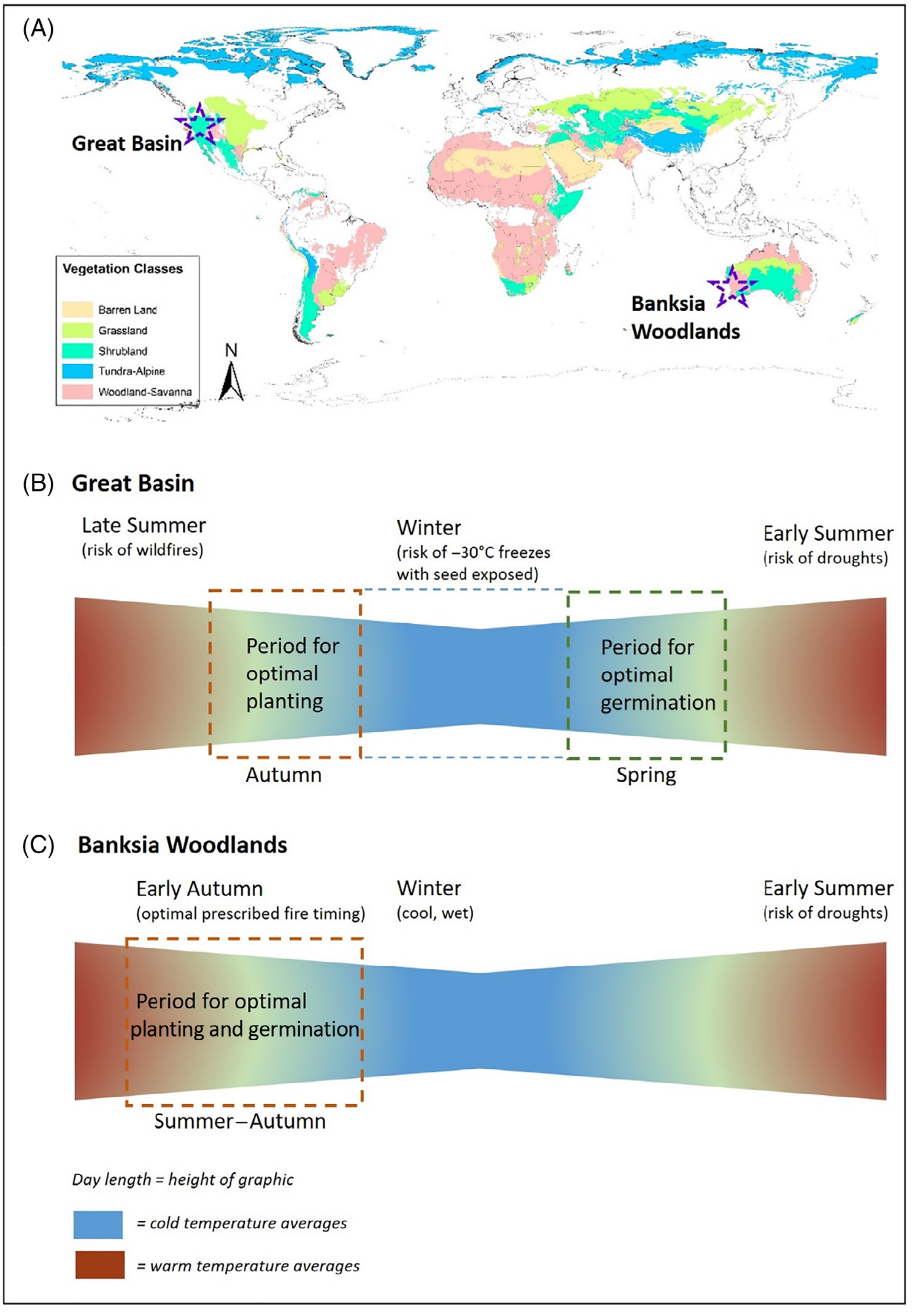

Figure 2. The Great Basin and Banksia Woodlands are distinct ecosystems occurring in the northern and southern hemispheres, respectively (A). In the Great Basin (B), conditions in autumn, when soil is hard, but not yet frozen are ideal for planting. However, many seeds germinate over winter and may be at high risk of mortality due to freezes. Similarly, planting conditions in spring are not ideal till later in the season and seeds germinating too close to summer may be at high risk of mortality due to summer drought. In Banksia Woodlands (C), autumn planting following prescribed burning and before the onset of winter rains is optimal as seedlings have multiple months to establish deep roots so that they may survive the summer drought.

seeding where seed is sown in furrows and then activated carbon is distributed on top of the seed in a band (Lee 1973). However, banded distributions of activated carbon protect every seed in the furrow, which in a native ecosystem would include invading exotic plant species that have seed distributed throughout the soil surface. Activated carbon has a potentially beneficial application in desired plant restoration but the mode of application this far has been tailored such that activated carbon is applied directly around native seeds using coating or extruded pelleting to avoid the issue of protecting exotic plant seed that is present in the seed bed (Davies et al. 2017, 2018; Brown et al. 2019; Clenet et al. 2019; Terry et al. 2021*b*). For example, bluebunch wheatgrass (*Pseudoroegneria spicata*(Pursh) Á.Löve) seeds incorporated in extruded pellets containing activated carbon, were able to establish in the presence of a preemergent herbicide indaziflam (Clenet et al. 2019). These seedlings had greater density (59 plants per container) and biomass (0.56 g per container) than bare seed controls (i.e. not within extruded pellets) in which seedlings failed to establish or survive (0.07 plants per container and 0.0004 g per container) (Clenet et al. 2019). In a 2-year field trial testing imazapic applications with activated carbon extruded pellets and bare seed from one native shrub and six bunch grasses, Clenet et al. (2020) found overall greater densities of seedlings for all species except squirrel tail (*Elymus elymoides* (Raf.) Swezey) from extruded pellets. In particular, the positive effect of the extruded pellets was particularly pronounced for sagebrush (*Artemisia tridentata* Nutt.) and bluebunch (7× and 4× greater, respectively) (Clenet et al. 2020). Similarly, activated carbon coatings for bluebunch wheatgrass showed a benefit for plant biomass in a 2-year field trial with imazapic applications wherein coated seed produced approximately 5 g/m^2 and bare seed produced <1 g/m^2 (Terry et al. 2021*b*).

Step 4: Refining Seed Enhancement Technologies

By using seed enhancement technologies with activated carbon we can reduce exotic plant pressure through herbicide application, protect native seedlings and provide additional benefits such as improved plant growth (Clenet et al. 2019). However, limitations currently exist for seed enhancements, such as coating and extruded pelleting incorporating activated carbon, including pellet hardness which can potentially limit seed imbibition and inhibit radicle protrusion leading to reduced germination and emergence (Erickson et al. 2019), delayed or reduced germination and emergence based on pellet dimensions (Clenet et al. 2019; Baughman et al. 2021) and limited herbicide protection depending on activated carbon coating thickness (Madsen et al. 2014). For example, Terry et al. (2021*b*) did not find major differences in plant densities after 2 years for activated carbon coated and uncoated seed, which may be the result of too thin a layer of activated carbon around the seed. Currently, there is no recommended coating thickness based on seed size, seed shape, abiotic conditions or herbicide type, and development in this area would be required to enable effective herbicide adsorption in conjunction with minimizing potential adverse effects such as delayed germination and emergence. To refine these seed enhancement technologies, and overcome a number of these limitations, we suggest focusing future research efforts on alternative extrusion or coating methods such as conglomeration (Hoose et al. 2019) or using molds (Jawahar & Umarani 2020), alternatives to activated carbon such as biochar (Clay et al. 2016), and pinpointing exact quantities of activated carbon required for species-specific herbicide protection (Brown et al. 2019), dependent on herbicide type and concentration. We can also take into consideration environmental impacts by utilizing carbon-source materials derived from locally sourced plants such as *Eucalyptus* spp. and *Acacia* spp. wood chips (Ngernyen et al. 2006) and *Miscanthus* spp. and *Panicum virgatum* L.biomass (Doczekalska et al. 2020).

Conclusion

Recently, there has been a move beyond the use of traditional agricultural methods in restoration through emerging disciplines such as “restoration engineering” which takes an interdisciplinary approach to improving restoration outcomes (Masarei et al. 2021). Modifying agricultural technologies to fit within a native system restoration framework shows promise, especially the use of activated carbon technologies to overcome barriers presented by exotic plants (Davies et al. 2018; Brown et al. 2019; Clenet et al. 2019, 2020; Baughman et al. 2021; Terry et al. 2021*b*). However, more work is required to refine the use of activated carbon-based seed enhancement technologies, such as type of carbon source being used, amount of carbon applied relative to the type and amount of herbicide being applied and the specific needs of varying seed sizes and physiologies. Exotic plants are a major issue in restoration efforts globally (Shackelford et al. 2021), but other barriers to seedling establishment exist, such as hydrophobic surface soils, and the guide we present in this paper may be used to develop technologies for those barriers. Even a marginal increase in native species establishment with seed enhancement technologies could help to improve restoration efforts.

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Supporting Information

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

Table S1. Differences and similarities in biotic and abiotic conditions of seeded crop versus native systems.

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