








REVIEW ARTICLE

Seed enhancement: getting seeds restoration-ready

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Seed enhancement technologies such as seed priming and seed coating, developed by the agricultural seed industry, are standard procedures for the majority of crop and horticultural seeds. However, such technologies are only just being evaluated for native plant seeds despite the potential benefits of such treatments for improving restoration effectiveness. Key approaches applicable to native seed include: (1) seed priming, where seeds are hydrated under controlled conditions, and (2) seed coating, in which external materials and compounds are applied onto seeds through a diversity of treatments. These technologies are commonly employed to accelerate and synchronize germination and to improve seed vigor, seedling emergence, establishment, and to facilitate mechanized seed delivery to site, through standardizing seed size and shape. Seed enhancement technologies have now been tested on native seeds to overcome logistical and ecological barriers in restoration. However, further research is needed to extend the application of seed enhancements to a broader array of species, ecosystems, and regions as well as to evaluate new and innovative approaches such as the incorporation of beneficial soil microorganisms and plant growth regulators in the coatings. As techniques in native seed enhancement develop, these approaches need to be capable of being scaled-up to provide the tonnages of seed required for global restoration.

Key words: agglomerates, coating, encrusting, germination, pelleting, priming, seed technology

Implications for Practice

- Seed priming can provide synchronized, rapid, and on-demand germination, establishment, and confer resilience to a variety of stresses, improving plant survival in harsh environments.
- Seed coating technology modifies the shape and size of field-ready seed units, improving delivery to site, especially for small-seeded species, or for seeds with confounding appendages or complex morphology.
- Seed coating and priming can be used to deliver compounds such as germination promoters, protectants, and predator deterrents that have the potential to greatly improve seed emergence and plant establishment.
- Seed coating and priming can be used to broaden potential seed germination response as a bet-hedging strategy to compensate for often extreme spatial and temporal variability in the seedbed microclimate of disturbed systems.

Introduction

Seeds are the most cost-effective option for ecological restoration compared with the planting of seedlings, particularly at larger scales or in highly biodiverse ecosystems (Pérez et al. 2019). However, fewer than 10% of seeds deployed to field-based successfully establish to produce a mature plant (James et al. 2011; Merritt et al. 2011; Ceccon et al. 2016). Given the challenges and cost of procurement and production of native

seeds (Merritt & Dixon 2011) and the potential negative impacts of increasing seed collection rates on wild populations (Nevill et al. 2018), such a high failure rate is unsustainable and severely limits the success of seed-based restoration at the scales that are now required (Menz et al. 2013). Thus, there is an emerging need and market demand for techniques and technologies that improve restoration outcomes associated with direct seeding.

The high failure rates in seed-based restoration have been attributed to physiological, logistical, and ecological-environmental factors. These include low seed viability,

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dormancy, limited emergence, challenges in handling and delivery of seed mixes due to variation in seed size and morphology, and variability in the environmental conditions across restoration sites. As such, seed enhancement technologies (in which seeds are artificially treated to promote “germination and establishment on-demand”) represent an area where research and development are urgently required to improve the quality, deliverability, and reliability of native seed batches and to confer resilience to environmental stresses, such as moisture or temperature extremes, and ecological challenges (e.g. predation, competition, and disease).

However, seed enhancement technologies have received limited attention in ecological restoration for a variety of reasons including: extensive research and development needed to customize existing crop seed technologies to complex and diverse native seed types, high initial cost of equipment, and hurdles in scaling the enhancement processes. Yet, such technologies are a standard feature in the crop and horticulture seed supply chains as the benefits they provide far outweigh the costs (Pedrini et al. 2017). In recent years, seed enhancement technologies have been developed for ecological restoration with identified potential benefits if the technologies can be optimized and effectively scaled (Madsen et al. 2016a; Erickson et al. 2017).

The aim of this review is to present a broad and practical overview of the currently available seed enhancement technologies developed in agriculture (seed priming and seed coating) and provide examples of how such technologies have been applied in the context of ecological restoration.

Seed Priming

Seed priming refers to the controlled hydration of seeds before sowing, where seeds begin the germination process but are re-dried before germination proceeds to the point of radicle/epicotyl extension (Heydecker & Coolbaer 1977; Bradford 1986). Priming can reduce the variability in seed germination rate within a population, ensuring more uniform and rapid germination and establishment (Taylor et al. 1998; Jisha et al. 2013; Paparella et al. 2015; Bhanuprakash & Yogeesh 2016). It can also confer greater resilience to thermal, moisture, and osmotic (salt) stresses (Bruggink 2005) and therefore may be beneficial for plant establishment in harsh environments (Kildisheva 2019).

The Priming Process

The physiological processes that occur during seed priming (see Supplement S1) begins with water uptake. Water uptake (or imbibition) is modulated by seed coat permeability and the area of contact with, and hydraulic conductivity of, the growth substrate (Koller & Hadas 1982; Bradford 1995). Seed water uptake can be divided into three phases: (1) imbibition or the physical uptake of water, (2) “activation” of metabolic activity, and (3) embryo and radicle/epicotyl growth and commencement of mitosis (Fig. 1; Taylor et al. 1992; Bradford 1995).

For imbibition to occur, the seed coat must be permeable to water (Kildisheva et al. 2020). For seeds with a water-

impermeable seed coat, permeability must first be achieved by the opening of the water gap or through artificial means such as scarification or hot water treatment (Baskin & Baskin 2014). Once seeds are permeable, imbibition generally occurs within hours or days and water uptake subsides at the initiation of metabolic activity (Bradford 1995).

Seeds are tolerant to desiccation during the first two phases of water uptake, but become desiccation sensitive once embryo growth has been initiated (e.g. phase three; Taylor et al. 1992). Thus, effective priming treatments result in imbibition and activation of the germination process up to a point prior to embryo development so that seeds are poised to complete germination, but retain the ability to be dehydrated and stored prior to delivery to the restoration site, without major viability losses. The optimal priming duration can depend on several factors, including priming method, species biology, seed size, dormancy status, and germination speed (Powell et al. 1984; Karssen et al. 1989; Bradford 1995; Bruggink 2005). Similarly, the extent to which germination can visibly occur before seeds become desiccation-sensitive can also vary by species. For example, for most species if priming has induced visible radicle emergence, viability can be assumed to have been negatively impacted (Tarquis & Bradford 1992; McDonald 1998; Bruggink et al. 1999); however, seeds of some desert species can tolerate desiccation even after the radicle has fully emerged and commenced root extension (Gutterman 2002). Seed priming can be accomplished through a number of different means, including hydro-, chemo-, osmo-, and solid matrix priming (Taylor et al. 1992; Bruggink 2005; Paparella et al. 2015).

Hydro-Priming. Hydro-priming refers to the hydration of seeds in pure water, typically in aerated conditions (Fig. 2) and at temperatures considered favorable for germination (Ward & Powell 1983; Coolbear & McGill 1990; Gray et al. 1990; Harris et al. 1999). Because the extent of priming is controlled by treatment duration, hydro-priming is the least precise of the priming techniques and is applied in combination with other treatments (e.g. chemo- or hormone-priming) or immediately before sowing under nursery conditions (e.g. “soaking,” Luna et al. 2014).

Chemo- or Hormone-Priming. In chemo-priming or hormone-priming, germination promoters (e.g. cytokinins, jasmonates, gibberellins, and karrikins), inhibitors (e.g. ABA), or plant protective compounds (e.g. salicylic acid, fungicides) can be used to improve seed germination of dormant species, control germination timing to optimize recruitment, and protect seeds from biotic and abiotic stresses (Carrow & Duncan 2011; Górnik et al. 2014; Badrakh 2016; Erickson et al. 2017; Call 2018).

Osmo-Priming. Osmo-priming is a widespread priming approach that relies on the use of an osmoticum bathing solution at water potentials below 0 MPa that allows controlled hydration of seed. This is accomplished through the use of salts

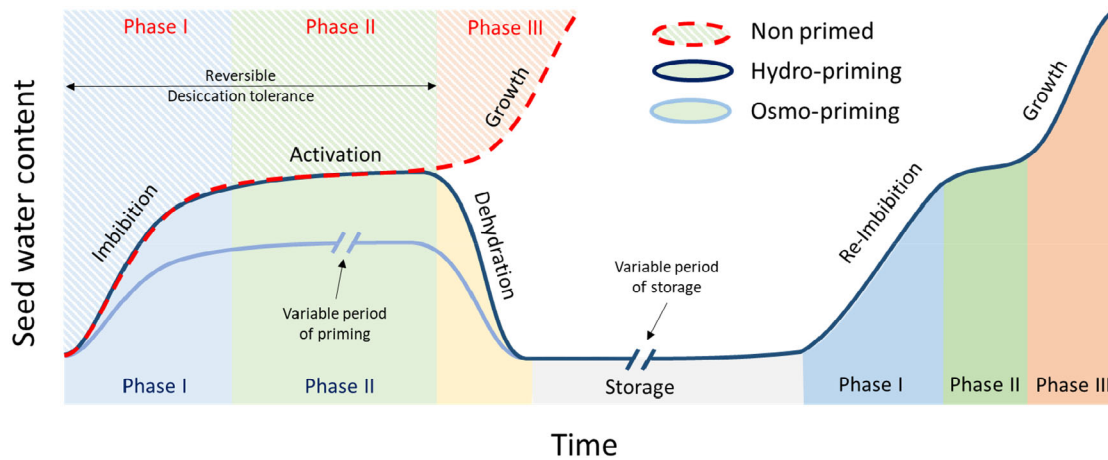


Figure 1. Seed water uptake can be divided into three phases: imbibition, the initiation of germination (activation), and embryo and radicle/epicotyl growth (growth). In seed priming, imbibition is interrupted at the beginning of the growth phase and seed are dried back to be stored.

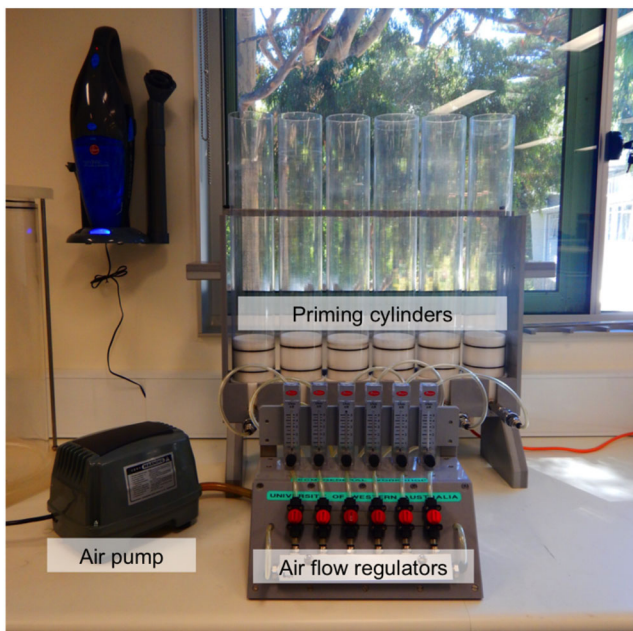


Figure 2. Custom-built seed priming unit used for hydro-, osmo-, and chemo-priming seeds was developed at the University of Western Australia and Kings Park Botanic Garden. This six-cylinder unit is able to treat 1–2 kg of pure seeds of numerous native species and differing morphologies (Erickson et al. 2019; Kildisheva 2019). Cylinders are filled with priming solution and connected to an air pump (Hailea Air Pump, IPX4, Guang Dong, China; flow rate ca. 3–4 L/min) to promote aeration during priming (image modified from Kildisheva 2019).

(e.g. KNO_3 , NaCl , CuSO_4), polyethylene glycol (PEG), or mannitol ($\text{C}_6\text{H}_{14}\text{O}_6$) (Yadav et al. 2011; Amirkhiz et al. 2012).

Matrix Priming. Solid matrix priming is another approach in which seeds are primed in a solid substrate (e.g. compost, clay, peat, sand, or vermiculite) moistened with water to achieve

desired water potentials for priming (Taylor et al. 1988). In some cases, matrix priming can be more effective than osmotic priming (Harman & Taylor 1988; Taylor et al. 1988), presumably because the process is thought to simulate natural seedbed conditions and because oxygen is freely available to seeds throughout the priming duration. Matrix priming has demonstrated positive results by improving germination and emergence of both horticultural and wild plant species (Bosma et al. 2002; Madsen et al. 2018) and has the potential to be combined with other seed technologies.

Seed Priming Materials and Equipment. In the seed industry, hydro-, osmo-, or chemo-priming is accomplished using a number of approaches, such as incubation trays moistened with polyethylene glycol (PEG) or other solutes; incubation inside aerated solution (e.g. PEG, inorganic salts, mannitol) typically inside large upright cylinders; or membrane priming, where PEG and seeds are separated by a semipermeable membrane to improve aeration needed to maintain seed viability (Bruggink 2005). Smaller-scale priming units have been developed for restoration use. For example, Erickson et al. (2019) describe a six-cylinder priming apparatus developed for seed priming for mine site restoration (Fig. 2). The unit can be used for hydro-, osmo-, and chemo-priming and is able to treat 1–2 kg of pure seeds. It has been tested across a range of osmotic potentials, aeration rates, and seed morphologies of different native species—and has proven effective at treatment delivery (Erickson et al. 2019; Kildisheva 2019).

Solid matrix priming can be used to treat large quantities of seed by storage in a matrix media (e.g. peat, vermiculite), typically inside a drum that rotates around a central axis to ensure even moisture distribution (Rowse 1996; Bruggink 2005). Another method, “drum priming,” involves mixing seeds with a specific quantity of water to raise the seed moisture content to the desired level, either in a static or rotating drum (Khan 1992; Bruggink 2005).

Seed Priming in Ecological Restoration

Although priming is used extensively in the agricultural industry, examples of its use in ecological restoration with native plant species remain limited, despite the potential for considerable benefits. Seed priming has been successfully used to stimulate the germination of pioneer tree species, which are commonly used in the tropical forests (Rodrigues et al. 2009). For example, hydro-priming (immersion in water for 16 hours) and osmo-priming (polyethylene glycol-PEG 8000, -0.8 MPa for 56 and 88 hours) improved seedling establishment of a pioneer tree species *Guazuma ulmifolia* (Brancalion & Tay 2010). Priming also induced rapid germination of several tree species (*Albizia saman*, *Cedrela odorata*, *Enterolobium cyclocarpum*, and *Swietenia macrophylla*) native to the tropical semideciduous forest of Veracruz, Mexico. Natural priming (manual seed burial, similar to matrix priming described above) was effective for *A. saman*, *C. odorata*, and *S. macrophylla* while hydro-priming enhanced the performance of *E. cyclocarpum* seeds (Peraza-Villarreal et al. 2018). Hardegee and Van Vactor (2000) reported that matrix priming enhanced total emergence of four North American bunchgrass species (*Elymus elymoides*, *Elymus lanceolatus*, *Poa sandbergii*, and *Pseudoroegneria spicata*) in the field, but the range of effects on germination were contingent upon seed lot, planting date, and soil type.

Priming has been used in combination with other pre-sowing techniques, for example Wagner et al. (2011) investigated the response of 10 difficult-to-establish species from European calcareous grasslands to: osmo-priming (PEG 6000, osmotic potential of -21.0 MPa), osmo-priming combined with gibberellic acid (GA_3), or cold stratification treatments. Germination was enhanced by osmo-priming (*Campanula glomerata*, *Filipendula vulgaris*, and *Helianthemum nummularium*) and osmo-priming + GA_3 (*Thymus pulegioides*). Interestingly, the addition of GA_3 to the osmo-priming solution promoted germination in suboptimal conditions (e.g. drought, light/dark) or substituted for the temperature fluctuation requirement of some species, thus expanding the germination “niche” of the tested species to a wider range of environmental conditions (Wagner et al. 2011; Lewandrowski et al. 2018; Kildisheva et al. 2019).

The ability to promote more rapid germination across a wider range of conditions may be particularly salient in regions where environmental conditions are highly stochastic, such as drylands (Pedrero-López et al. 2016; Erickson et al. 2017; Kildisheva 2019). Erickson et al. (2017) and Kildisheva et al. (2019) reported on the potential for the integration of seed priming into the restoration tool kit in the context of mine rehabilitation, either alone or in combination with other seed enhancement techniques. Priming with karrikinolide, a smoke-derived germination stimulant, was shown to improve germination and emergence of *Triodia pungens* L. (Erickson et al. 2017; Kildisheva 2019)—a keystone species in the Pilbara bioregion of Western Australia (Nicholas et al. 2009). Priming was particularly effective when combined with seed coating, possibly by acting to expand the capacity of plants to take advantage of available precipitation more effectively and facilitating greater root development to increase survival under increasingly arid conditions (Kildisheva 2019).

Madsen et al. (2018) demonstrated how solid matrix priming (-0.5 to -2.5 MPa for up to 12 days) can be effectively combined with seed coating technologies (e.g. seed “pods”) to improve emergence and establishment density of two grass species (*Poa fendleriana* and *P. spicata*) seeded on the Kaibab Plateau in Arizona. Results show that emergence from the primed-seed pods was 66–82% faster than for non-treated seeds. Additionally, the final density of *P. spicata* seedlings originating from primed-seed pods was 2.9- to 3.8-fold higher than non-treated seeds.

Thus, while the evidence of use in restoration remains to be broadly tested, seed priming has the potential to improve restoration outcomes, especially when combined with other seed enhancement technologies. However, effective adoption of priming into restoration practice requires an in-depth understanding of species-specific seed biology (Hardegee 1996), site-dependent recruitment limitations, and seed delivery methods to ensure cost-effective integration (Bujalski & Niemi 1991).

Seed Coating

Seeds of native species vary widely in shape and size, posing challenges for handling and mechanical sowing, such as lack of flowability and bridging (where seed cross-link and block the seed delivery system). By applying external material to the seed, seed batches can become more homogeneous and easier to manipulate in the deployment to the restoration site (Hoose et al. 2019). Moreover, an artificial coating can be loaded with active ingredients that, once released to the seed or in the surrounding soil, protect the seed from pathogens and improve germination, survival, and growth (Taylor et al. 1998; Halmer 2008).

Seed coating has been widely employed by the agricultural industry for decades, but so far, its application to native seeds remains limited to experimental trials. A significant impediment to the implementation of seed coating for ecological restoration using native plant species is the limited access to the expertise and seed coating techniques that are mostly confidentially confined to the agrochemical industry that specializes in seed coating of agricultural and horticultural species (Pedrini et al. 2017).

Seed Coating Types, Materials, and Equipment

Three major seed coatings have been developed for agricultural, forestry, and horticultural species that have relevance to restoration (Fig. 3). These include *film coating*, where a thin layer of material is applied to the seed (less than 5–10% of the weight of the seed); *encrusting*, in which materials that increase the weight and volume of the seed are added but the shape of the original seed is still recognizable; and *pelleting*, in which materials are added to the seed to create an oval-spherical shape where the initial seed shape is indiscernible (Taylor et al. 1998; Halmer 2008). Further variations of seed coating have been developed and adapted in recent years for native plant seeds, such as *agglomerates* or *conglomerates* (Madsen et al.

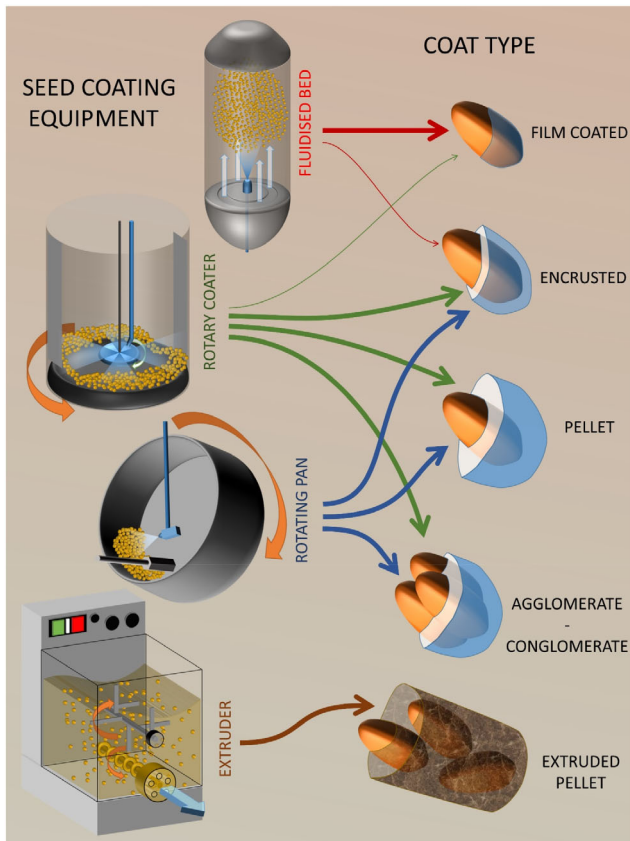


Figure 3. Examples of seed coating equipment and seed coating type. Images adapted from Pedrini et al. 2017.

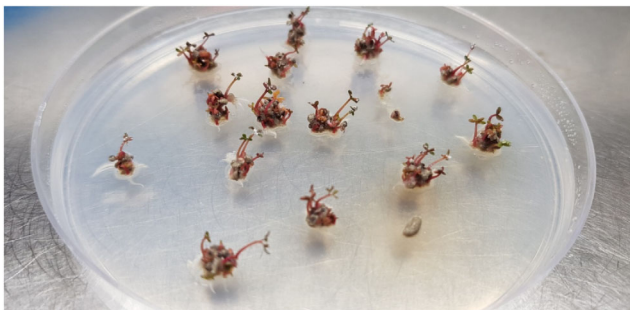


Figure 4. Agglomerates of *Eucalyptus loxophleba* made with diatomaceous earth and polyvinyl alcohol (approx. 5 seeds per pellet).

2012; Hoose et al. 2019), in which multiple seeds are clustered together into a single delivery unit (Fig. 4) and *extruded pellets* (Madsen et al. 2016b, 2018, Brown et al. 2019), when seeds are mixed with a relatively large amount of material and then passed through an extruder that forms and cuts the extruded material into desired shapes (usually cylindrical). To avoid confusion, it is important for restoration researchers and practitioners to consistently define the seed coating type according to the currently agreed agricultural definitions and allow for constructive

collaborations in the development of this technology with crop and horticulture seed companies and scientists.

In the seed industry, there are three main types of equipment in use (Fig. 3): *fluidized bed*, used for film coating; *rotary coater*, commonly employed on native seeds; and *pan coater*, used on very small seeds (Gregg & Billups 2010; Bennett & Lloyd 2015). Seed agglomerates can be made with either a rotary coater or pan coater. Extruded pellets instead require a specific machine, the *extruder*, that is similar to the ones used by the food industry to make pasta (Watkins 2014; Madsen et al. 2016b).

Seed coating is not always feasible on pure seed units for many native species without prior reduction or removal of external structures (Guzzomi et al. 2016; Pedrini et al. 2019), and extensive seed processing is sometimes required (Frischie et al. 2020).

Materials and compounds used to provide for the physical, thermal, and mechanical properties of the seed coating can be broadly divided into two groups: *binders*, usually polymers such as celluloses and gums that adhere to the seed and allow for the retention of other materials, and *fillers*, powdery materials used to increase the volume and weight of the original seed (e.g. clay, lime). A wider range of active ingredients, either biological or chemical, can be incorporated into coatings to improve seed survival (e.g. by protecting from pathogens and predators), aiding in germination (e.g. nutrients, hormones, plant growth promoters, symbionts), and improving stress resistance (e.g. salicylic acid, beneficial microbes) (Taylor et al. 1998; Rocha et al. 2019).

Seed Coating in Ecological Restoration

Seed coating technologies, particularly when combined with beneficial biological and chemical active ingredients or protectants, can play a role in the success of seed-based restoration programs (Table 1) by targeting specific challenges that limit plant recruitment on a site, such as variable soil moisture, low soil nutrients, pests, and diseases (Gornish et al. 2019). For example, the inclusion of a soil surfactant agent in the coating of *Pseudoroegneria spicata* (bluebunch wheatgrass), for post-fire restoration in the northwestern United States, improved seedling emergence and plant survival in water repellent soil (Madsen et al. 2013). Similarly, the inoculation of microorganisms in the coating improved seedling emergence and survival of two species on degraded rangeland in the Qinghai–Tibetan Plateau (Liu et al. 2010), while seeds coated in salicylic acid improved plant survival and growth for native grasses in Australia (Pedrini 2019). Seed predator repellents incorporated in seed coatings reduced seed consumption rates from rodents (Taylor et al. 2020) and improved plant establishment (Pearson et al. 2019).

Seed coating has also been tested as a means of controlling germination timing, for example, Richardson et al. (2019) delayed germination in *P. spicata* by applying abscisic acid (ABA) and delaying germination from late autumn, to spring, when conditions for seedling emergence and plant establishment would be more favorable.

Table 1. Studies on the application of seed coating to native species published in peer-reviewed journals from 2006 to 2020.

Publication	Ecosystem—Species	Coating Type, Machine, and Material	Active Ingredients	Experiment Results Compared to Uncoated Control
Taylor et al. (2020)	<i>Pseudoroegneria spicata</i>	Encrusting on rotary coater with bentonite clay and polyvinyl alcohol	Nine predator repellents such as peppers and oils.	Lab germination: similar to control. Feeding trial: reduced consumption by rodents in some treatments.
Pearson et al. (2019)	Twelve dominant species in intermountain grasslands of Western Montana (U.S.A.)	Encrusting on rotary coater with bentonite clay and polyvinyl alcohol	Predator repellent chili-pepper (<i>Capsicum chinense</i>)	Lab feeding trial: reduced consumption for treated seed in all species. Field plant establishment: variable in the first 3 years, but improved for treated seeds in fourth year.
Hoose et al. (2019)	<i>Artemisia tridentata</i> ssp. <i>wyomingensis</i>	Conglomeration on rotary coater with mineral soil (azomite), compost, and commercial binder	None	Seed flowability and broadcast delivery improved for treated seeds. Higher seed germination in lab trials but similar seedling emergence in the field.
Richardson et al. (2019)	<i>P. spicata</i>	Encrusting on rotary coater with calcium carbonate and commercial binder	Absciscic acid (ABA)	Seed treated with ABA showed a delay in germination tested in the lab.
Madsen et al. (2018)	<i>Poa fendleriana</i> , <i>P. spicata</i>	Extruded pellets with various clay filler materials, absorbents, bio-stimulants, plant protectants, water	Matrix priming prior extrusion	Seedling emergence improved in one soil type and seedling density improved.
Erickson et al. (2017)	<i>Tridia pungens</i>	Encrusting on rotary coater with calcium carbonate and polyvinyl alcohol	Hydro-priming with KAR ₁	Improved seedling emergence in rain manipulated shelter.
Madsen et al. (2016b)	<i>A. tridentata</i> ssp. <i>wyomingensis</i>	Extruded pellets with various clay filler materials, absorbents, water	Bio-stimulants, plant protectants	In soil, improved seed emergence at different sowing depth and increased growth.
Williams et al. (2016)	Four plant species native to arid and semiarid regions in western United States	Encrusting on rotary coater with biochar and polyvinyl alcohol	Biochar used as a promoter	Lab germination: neutral or negative impact on all species. Field trial: no difference in plant cover and biomass.
Madsen et al. (2014)	<i>P. spicata</i>	Encrusting on rotary coater and extruded pellets with activated carbon, diatomaceous earth, polyvinyl alcohol, and water.	Activated carbon used as herbicide safeners	Encrusted seeds and extruded pellets were protected from pre-emergence herbicide and resulted in higher seedling density, height, and biomass. Best results were given by extrusion.
Rushing et al. (2013)	<i>Panicum virgatum</i>	Non-specified coating type in pan coater with commercial coating powder and binder	Commercial herbicide safeners	Field trials: coating with safeners generally did not protect plants from herbicidal injury. Controlled hydration was more effective in delivering protection.
Madsen et al. (2012)	<i>P. spicata</i>	Agglomeration on rotary coater with diatomaceous earth and polyvinyl alcohol	None	Improved seedling emergence in clay and sandy soil. Increased aboveground biomass.
Liu et al. (2010)	<i>Lolium multiflorum</i> , <i>Astragalus sinicus</i>	Manual mixing of seeds and material with algal powder gums and wheat flour	Biologicals (<i>Aspergillus</i> sp. and <i>Streptomyces</i> sp.)	Indoor experiment: seedling emergence improved. Outdoor pot trial: growth improved.
Mangold and Sheley (2007)	<i>Agropyron cristatum</i>	Nondisclosed	Mycorrhizal, algae, beneficial <i>Bacillus</i> inoculums, vitamins, and growth hormone	In pot trial: seedling emergence reduced while seedling survivorship and biomass were not affected by either seed treatment.
Turner et al. (2006)	Eleven banksia woodland species in South Western Australia	Outsourced, nondisclosed	Outsourced, nondisclosed	Ex situ trial: in 10 species similar seedling emergence, in one reduced emergence. In situ trial: emergence improved in two species, similar for the others.

When agglomeration of multiple seeds per pellet was tested with *P. spicata*, the treatment improved seedling emergence and plant growth in crusting soils (Madsen et al. 2012). This approach also improved the handling and sowing efficiency of a small-seeded species, *Artemisia tridentata*, while increasing germination in laboratory conditions, but the improvement was not detected in field emergence (Hoose et al. 2019). However, Anderson (2020) found in a more extensive field trial across the Great Basin, United States, that the agglomeration technique improved *A. tridentata* seedling emergence and plant establishment in comparison to untreated seed.

Extruded pellets have been tested in dryland systems. For example, extruded pellets made with activated carbon, protected seeds of native grasses (*Elymus elymoides*, *P. spicata*, *Poa secunda*) and a shrub (*A. tridentata*) from pre-emergent herbicide and in some cases promoted higher seedling density, height, and biomass compared to the untreated control (Madsen et al. 2014; Clenet et al. 2019).

Other compounds have also been incorporated to address other specific establishment limitations. When seeds of a keystone shrub, *A. tridentata*, were incorporated into extruded pellets with super-absorbent polymers, seedling emergence was also improved, particularly in crusting soils, presumably resulting from the swelling action of the pellet that elevated the seeds in the soil and created a moisture-rich micro-environment (Madsen et al. 2016b).

However, the effectiveness of these techniques can vary between sites, years, species, coating formulations, application approaches, and the plant demographic stage being evaluated (Williams et al. 2016; Davies et al. 2018; Kildisheva et al. 2019).

Furthermore, the scope of existing studies and the probable under-reporting of failed seeding experiments in restoration make it difficult to evaluate the true effectiveness of these technologies. Based on the agricultural seed literature, which includes reports of the negative effects of coating on seed germination and emergence (Pedrini et al. 2017), developing effective techniques may require time and substantial investment. For development efforts to be successful, scientists and practitioners alike need to share failures and challenges associated with seed coating native plant seeds, to help identify the potential limitations and improve the general understanding of the factors underpinning successful coating formulations in relation to specific ecological or logistical constraints.

In a few instances, seed coating was outsourced to private companies and coating specifications not disclosed (Turner et al. 2006; Mangold & Sheley 2007), making it difficult to replicate. Whenever feasible, seed scientists and users should collaborate with organizations and companies that are willing to share material and methods or try to develop seed coating recipes and protocols independently. For example, a recently published open-access tool for developing seed coating protocols (encrusting and pelleting) provides a practical step-by-step guide to develop species-specific seed coating treatments (Pedrini et al. 2018). This tool can be used for the testing of coating methods, materials, and active ingredients, using readily available seed coating equipment and chemical agents.

Economies of Seed Enhancement Technologies for Ecological Restoration

In spite of some evidence of successful application of seed priming and coating to treat seeds of native species, most of this work has been conducted in controlled experimental settings, and the costs and benefits related to the employment and scalability of these technologies have rarely been investigated. A baseline approach to estimate economies of seed coating should compare the cost for each successfully established plant from treated and untreated seeds (Pearson et al. 2019). Additionally, many external variables should be considered beyond the cost of seed coating material and personnel time. For example, if coating improves a seed's ballistic properties, allowing for a wider seed broadcast area, it will reduce seeding time and equipment use (e.g. fewer mechanized passes). Such benefits should be accounted for in the cost/benefit evaluations of seed coating in ecological restoration (Hoose et al. 2019) and to facilitate the adoption of seed enhancement technologies at scale.

Is Fast and Synchronized Germination Always Better? Bet-Hedging Strategies With Seed Enhancement Technologies

Soil seed beds (awaiting restoration seeding) can exhibit relatively high spatial variability in soil water availability and temperature (Hardegree et al. 2020) and often have logistical constraints that require seeding well in advance of germination and emergence (Rajagopalan & Lall 1998; Eiswerth & Scott Shonkwiler 2006; Boyd & Lemos 2015; Hardegree et al. 2018). Additionally, many restoration sites present challenging edaphic and environmental complexities that in cases of significant degradation can substantially differ from the natural reference site conditions (Seastedt et al. 2008; Coates et al. 2016). These include human-induced management disturbances, such as mining or grazing, as well as competition from invasive species.

Regardless of the source of the disturbance, natural environmental variability can also impose severe constraints on the timing and location of suitable microsites for establishment in any given year (Hardegree et al. 2016, 2018). Various seed enhancement techniques and technologies can be designed to shift the germination behavior of a given seed population to compensate for environmental changes that have diminished the probability of successful establishment (Angevine & Chabot 1979). However, it may be beneficial to broaden (rather than merely shift) the germination behavior of a desirable species (Madsen et al. 2016a; Erickson et al. 2017; Davies et al. 2018; Hardegree et al. 2020). This approach can provide a bet-hedging capability to compensate for both environmental and edaphic variability resulting from ecological disturbance and degradation factors (Davies et al. 2018; Lewandrowski et al. 2018; Kildisheva 2019). Seed priming and coating can be used to accelerate or delay a germination response, narrow or broaden the variability in seed germination rate within a population, or compensate for undesirable site conditions (Hardegree 2002; Madsen et al. 2016a; Kildisheva 2019).

Conclusion

The success of large-scale restoration using direct seeding will continue to depend on efficient and effective seed use. Seed enhancement technologies, though in their infancy in ecological restoration, are likely to provide major improvements in field establishment akin to that achieved for crop species. We have described how individual seed treatments can accelerate, delay, or stagger germination and emergence in the field but any or all of these effects need to be tailored to the site and local climatic conditions. These treatments should not be used indiscriminately for the sake of novelty or innovation but need to have proven benefit with deployment able to target specific ecological or logistical limitations and give every seed the optimum chance for germination, emergence, and successful establishment. Thus, the effectiveness of the development and use of seed enhancement technologies is contingent on dedicated research and implementation programs that work to understand and address the species- and site-specific challenges that limit plant recruitment from seed. As such, seed enhancement technologies must become part of a broader restoration strategy that integrates relevant issues of site conditions, species availability, and species performance.

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Supporting Information

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

Supplement S1. The physiology of seed priming

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