Florabank Guidelines

Module 12

Seed Enhancement Technologies

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Key points

Seed enhancement technologies (SETs) are post-harvest treatments applied to seeds to improve seed delivery, germination, plant performance, and tolerance to environmental stress.

Some SETs aim to *physically alter* the shape of seeds or their delivery unit, whilst others *manipulate the physiology* of the seeds to improve the germination and emergence capacity.

A range of *additives* can be incorporated in SETs that target specific barriers to restoration, such as soil surfactants that break down water repellent soils or germination regulators that either promote more rapid or delayed plant recruitment.

A range of SETs including seed coating, priming, extruded pelleting, acid digestion and flash flaming are being developed for native seeds.

Introduction

This guideline offers an introduction to the use of seed enhancement technologies (SETs), a group of seed pre-treatments being increasingly developed for improving the use of native seeds in restoration (Copeland et al. 2021; Madsen et al. 2016a). SETs are a natural extension to the application of treatments to manage seed dormancy, yet aim to further 'enhance' the recruitment capacity of seeds beyond what standard dormancy breaking treatments offer. SETs can be specifically designed to target certain barriers that prevent successful plant establishment (e.g. seed coatings that protect native seeds during herbicide spraying). In addition, SETs also offer opportunities to improve the precision of seed delivery for diverse native seeds, at large-scales, as many of the technologies target seed material that has limited flow through traditional agriculture seeding mechanisms. Overall, combined with optimised collection, cleaning, storage, and dormancy management, SETs aim to make every seed count in restoration.

Although in their infancy for seeds of wild plants, the development of SETs offers a suite of new tools and approaches to consider in large-scale seeding efforts. This guideline has been written to introduce this rapidly growing area of seed management, and to summarise how SETs are currently being developed and utilised in the native seed market, with the hope that these technologies will be more readily adopted in ecological restoration practices.

In the following sections we introduce:

- what SETs are;
- the origins of SETs and how they have largely been developed out of the agricultural industry;
- what each technology is designed to do;
- some examples of how these technologies have been applied to native seeds to date; and,
- what limitations still exist to scaling up the use of SETs and how these limitations are being addressed.

What are seed enhancement technologies?

Seed enhancement technologies can be defined as any post-harvest treatment, technique, or additive that may be applied to seeds to improve seed delivery, protection, germination, plant performance, and/or the tolerance of seeds or plants to environmental stress (Erickson et al. 2019; Madsen et al. 2018; Taylor et al. 1998). For ecological restoration, SETs are typically developed to:

- improve the physical characteristics of the seeds, such as size and shape, to aid in handling and flow through, and distribution by, machinery;
- alter the physiological status of the seeds to further improve germination and seedling establishment;
- deliver compounds or additives that provide additional benefits to seed protection or recruitment such as micronutrients, germination stimulants, microbiota, fungicides, growth regulators, and others (Halmer 2008) (Figure 1).

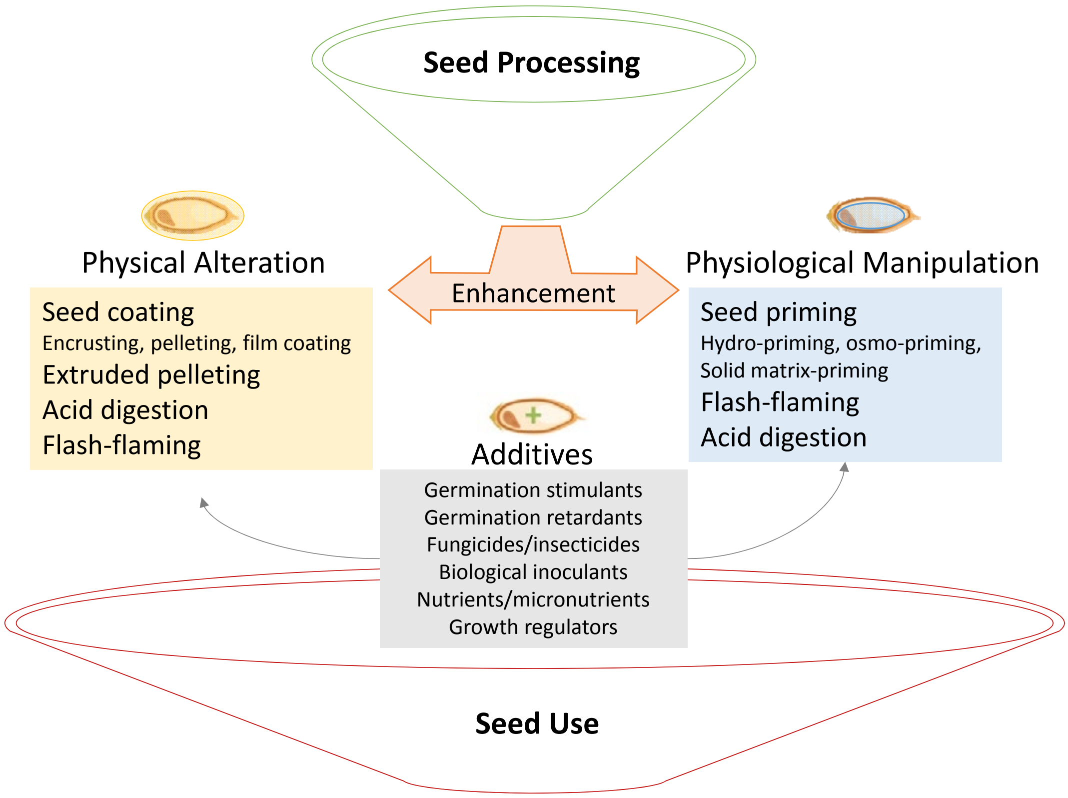

Figure 1. Seed enhancement technologies are developing rapidly for use with native seeds. Once seeds have been harvested, cleaned, and processed, seed enhancement technologies can further improve the use of these seeds in direct seeding or nursery propagation through manipulating both their physical characteristics and physiological status, and further tailored with the use of other additives (figure adapted from Halmer 2008).

The origins of seed enhancement technologies in agriculture and horticulture and how these are now being used for native seeds

The development of SETs largely stems from the agricultural, horticultural, and ornamental plant industries. Crop uniformity, reliable field establishment, plant yield and saleability are key components that come from these production systems (Halmer 2008). With this, many farmers and practitioners, over many decades, have sought new methods that can make sowing seeds much easier, quicker, and cheaper. This includes a focus on techniques to improve aerial delivery, broadcasting and direct seeding with equipment (Bennett 2016). In addition, increasing the speed, uniformity and vigour at which a seed batch germinates has been a central goal of SET development.

At a time when large-scale restoration is increasingly being attempted, practitioners have naturally applied this SET experience and expert knowledge and shifted this focus to native seeds (Beveridge et al. 2019; Erickson et al. 2019; Guzzomi et al. 2016; Madsen et al. 2016a; Madsen et al. 2018; Pedrini et al. 2018). New tools and technologies are now being applied to a wide range of native seeds that have considerable natural variation in size, shape, weight, and growth characteristics. Once proven feasible, the application of SETs should support and enable seeding efforts in natural systems to move forward more efficiently and at the scales required to meet ecological restoration needs.

What SET options are currently available and commonly used with native seeds?

Coating

Arguably the most widely used SET that stems from the agricultural industry is seed coating, which applies layers of glues/polymers to bind layers of mineral powders to the outside of seeds to alter their physical appearance. Seed coating can be broadly subdivided into 'film coating', 'encrusting', or 'pelleting', with the main difference being the thickness of the coat (Pedrini et al. 2017). Most commonly, coating is applied via a rotary seed coater, pan coater, or fluidised bed (Figure 2). In the coating process, seeds move inside the machine driven by spinning mechanisms or by compressed air. When seeds are flowing inside the coating machine, successive layers of glues/polymers and powders are progressively added to the outside of the seeds until a desired artificial covering is achieved. The longer and more times this layering process is conducted, the thicker the coat becomes. The coating can vary in size, thickness, and composition, depending on the products used. For example, when a water-soluble polymer and calcium carbonate powder are added in increments of 20% to spinifex (*Triodia* spp.) grass florets, the coating thickness and weight increase almost linearly (Table 1).

Seed coating can be used to:

- create uniform seed sizes;
- increase the weight of small, light seeds, which can ease mechanised delivery; and
- add beneficial products such as microbiota (e.g. rhizobia in agricultural seeds), predation deterrents, germination stimulants, or fungicides, among others.

For example, small *Eucalyptus* seeds are often sown through direct seeding machines with a bulking agent such as vermiculite or rice hulls to ensure these small 'volume' batches are spread evenly over broad areas. As an alternative, these small seeds could be coated to bulk up the individual seeds to improve their handling and delivery (Hoose et al. 2019). The seed coating can also act as a carrier for beneficial ingredients such as a fungicide (Figure 2) to prevent fungal attack (Nuyttens et al. 2013), or anti-predation agents such as capsaicin to prevent granivory (Pearson et al. 2018; Taylor et al. 2020). In areas that need pre-emergent herbicide applications to remove the seedbanks of undesirable plants, native seeds may be coated with a herbicide-adsorbing material such as activated carbon to protect them from herbicide toxicity and allow for seedling establishment in the absence of competition (Madsen et al. 2014).

Figure 2. *Eucalyptus* seeds native to the Northern Tablelands of New South Wales (A) before coating are small and, at times, difficult to handle. After coating with mycorrhizae inoculants in a commercial-scale pan coater (B) seed handling was improved (C) and higher seedling establishment was promoted (Ruiz-Talonia et al. un-published).

Table 1. Coating recipe applied to 250 mL / 30 g of limestone spinifex (*Triodia wiseana*) florets in a rotary drum coater. The amount of material can be altered as long as the proportions between the polymer/ binder (Selvol™-205, Sekisui Specialty Chemicals America, Dallas, TX, U.S.A.) and calcium carbonate powder (Omyacarb©, Omya Australia Pty. Limited, Lindfield, NSW, AU) are kept relatively consistent. Table adopted from Guzzomi et al. (2016).

Coating Step	Coating Product	Product Mass (g)	Total Mass (g)	Directions
1	Selvol-205	1.76	22.00	During Step 1, the Selvol binder is applied slowly (5-6 seconds) in its entirety onto the central atomising disc of the coater, followed by the application of the Omyacarb powder in one quick burst over 2-4 seconds.
	Omyacarb	90.00	90.00	
2	Selvol-205	1.82	22.70	During the Step 2, the binder is continuously added to the atomising disc via an automated liquid pump. As the material gets 'wetter' the powder is added in successive bursts to prevent seed clumping. These steps continue until both products are applied completely. However, the coating is finished with a final portion of the polymer.
	Omyacarb	109.00	109.00	
Total		202.58	243.70	

Coating at scale

Seed coating is already carried out at large (e.g. multi-tonne) scales in the agricultural industry (Bennett 2016). Many agricultural seed suppliers utilise factory-scale coating units; therefore, scale is not an issue in the adoption of this technology for native seeds. However, to advance the use of coating at scale current research is focussed on (1) whether native seeds are sensitive to traditional coating practices, (2) what coating approaches are best suited for different native plant seeds and (3) what is the optimal physical, mechanical, and biological composition of the resulting coatings. Understanding the full potential and limitations of a particular SET can aid in the selection of the best SET for a particular species or site conditions. This can aid in decisions such as whether inoculating seeds with a germination stimulant through the coating material is more effective than delivering these beneficial additives through alternative technologies, such as priming.

There are many commercial seed coating options and services that exist to coat seeds and access should not be a hinderance to the technology uptake. Further, low-cost methods of coating native seeds, termed 'seed balls' (Gornish et al. 2020), are currently available and already being trialled by community groups (e.g. https://extension.arizona.edu/pubs/how-construct-bicycle-powered-seed-pelletizer-use-gardening-restoration).

Priming (hydro-, osmo-, matrix-priming)

Seed priming is another widely used technique for seed enhancement applications, developed to alter the physiological status of seeds to benefit performance. Priming promotes rapid and uniform germination and synchronised emergence in non-dormant seed batches (Farooq et al. 2019). Quicker and earlier establishment in cropping systems can provide significant advantages with respect to more vigorous early growth, more productive individual plants, a competitive advantage over emerging weeds and higher crop yields (Farooq et al. 2019; Harris et al. 2002; Paparella et al. 2015). When seedbed conditions are suboptimal or deteriorate, small differences in earlier and rapid establishment can be crucial (Farooq et al. 2019; Harris et al. 2002).

In nature, rapid, early germination can promote higher seedling survival due to:

- reduced opportunity to experience environmental stressors (i.e. limited/excess water, high winds) at early life stages and a narrower timeframe for predation or depletion (i.e. viability loss, desiccation) of seeds from the soil seedbank;
- greater competitive advantage allowing seedlings to exploit available resources ahead of competing species, and
- positive effects on plant survival, growth and fitness as earlier germination is associated with greater height and survival, probably due to earlier development traits to avoid (or mitigate) environmental stressors (Abe et al. 2008).

However, direct evidence of the advantages of early establishment in nature, though present (Kulpa and Leger 2012; Leger et al. 2019), is still scarce. For this reason, practitioners often choose to treat a proportion of a seed lot to hedge against the risk of seeding failure. Finding the balance between treating seeds to obtain a restoration-ready seed lot and maintaining the bet-hedging potential of seeds is a key consideration in the development of SETs in the future, and something that requires field testing (see 'Where to now with SETs' section below).

Priming is a pre-sowing treatment that involves the controlled-hydration of seeds in water (**hydro-priming**), osmotic solutions (**osmo-priming**) (Paparella et al. 2015), or in a solid carrier (**solid matrix priming**) (Farooq et al. 2019; Madsen et al. 2018), followed usually by their re-drying for ease of handling and sowing. A simple priming set-up can include a series of waterproof containers or columns where seeds can easily be placed and removed from the priming medium. For hydro- or osmo-priming, the addition of aeration helps to keep seeds moving and avoids anaerobic conditions. Priming units can be built to suit the user, scale of operation, and targeted applications (Figure 3). For instance, they can be built to fit current incubators that then provide an avenue to control temperature, air flow/volume, and treatment timings more accurately.

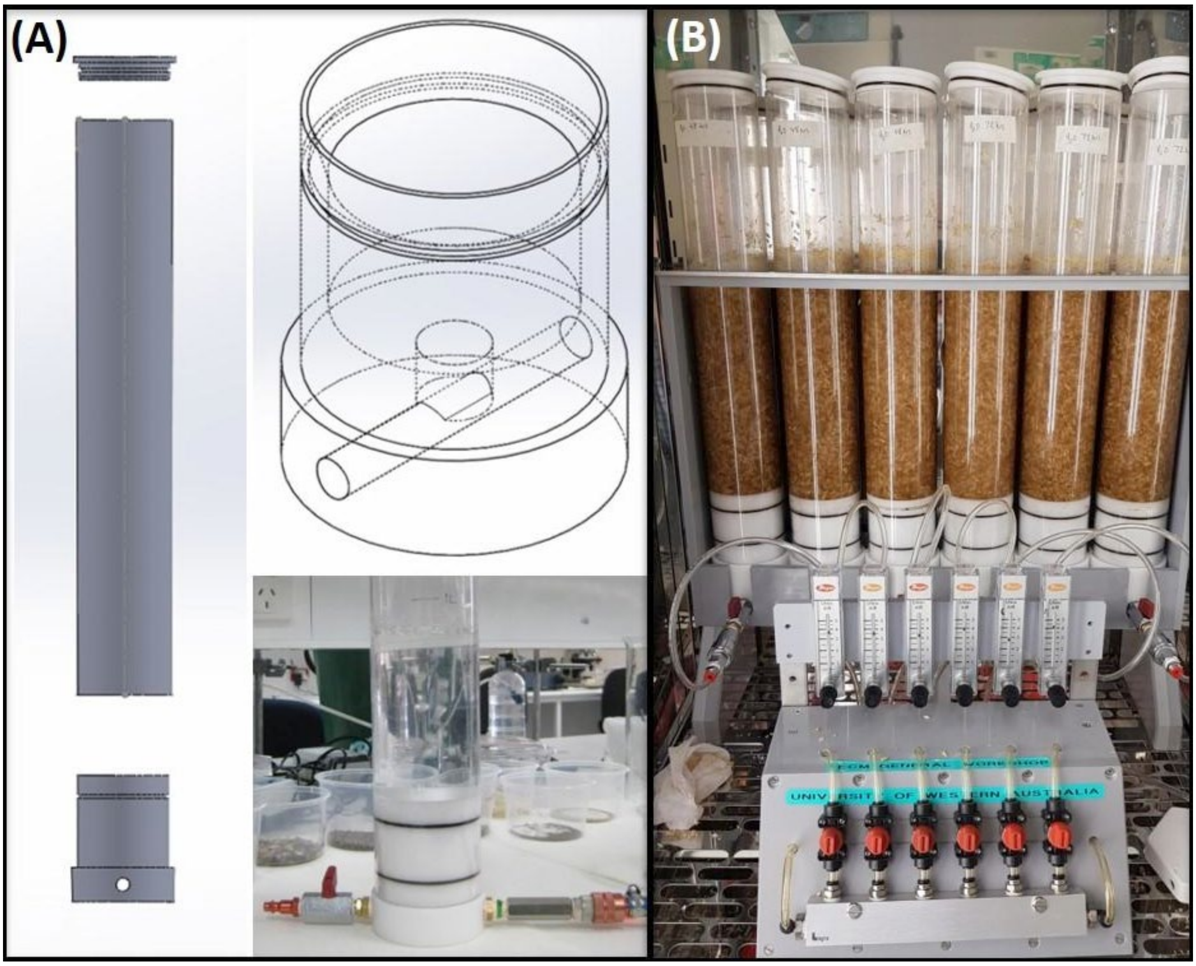

Figure 3. Design of the priming unit (left and middle) that possesses waterproof columns with built-in air cavities at the base of each unit, and the constructed unit during priming of soft spinifex (*Triodia pungens*) florets inside a temperature-controlled incubator (right). Air flow and rate is controlled in each column by flow meters and an aquarium pump (figure from Erickson et al. 2019).

For seeds that are hydro-primed, priming is managed by the time of submergence in the water, and the temperature during priming. To develop and optimise a hydro-priming treatment, seeds need to be tested over a range of priming times and removed progressively to test germination percent and speed. This trial-and-error testing is necessary because during priming the initial stages of seed germination commence (e.g. water uptake, increased metabolic activity, enzyme activation). But seeds must be removed from the priming conditions and dried before complete germination occurs (i.e. defined as emergence of the primary root / radicle). It is important to optimise the duration of hydro-priming – priming for too short a time period will limit the benefits, whilst priming for too long will result in premature germination and the loss of seeds. This need for trial-and-error to determine suitable protocols for priming and drying is one disadvantage of the technique, where optimal protocols can be specific to species and even to seed batches. However, once sown and exposed to appropriate conditions for germination, correctly primed seeds germinate faster, more uniformly, and have higher tolerance to environmental stress than untreated seeds (Farooq et al. 2019) (Figure 4).

Osmo-priming is priming in a solution of controlled water potential. The advantage of this technique is that germination during priming is prevented through lowering the water potential to a point that allows for pre-germinative metabolism, but insufficient to allow for radicle emergence. Osmo-priming is extensively used in horticultural industries and has the potential to be effective at improving seedling performance in broad-acre seeding efforts. Water potential of the priming solution is typically controlled using polyethylene glycol (which can be expensive when used at scale) or via the use of inorganic salts or organic molecules (Paparella et al. 2015). Osmo-priming can be used to promote seed germination across a broader temperature range and at reduced moisture availability (Figure 5). Osmo-priming has also promoted more rapid germination in many arid zone species tested for mine rehabilitation programs in Australia's arid north-west, where initial germination time for some species was reduced by half (Merritt and Erickson un-published). Additionally, osmo-priming allows for more precise control of the seed hydration process relative to hydro-priming, which is a concern for fast-germinating species, that can begin germination in a matter of hours.

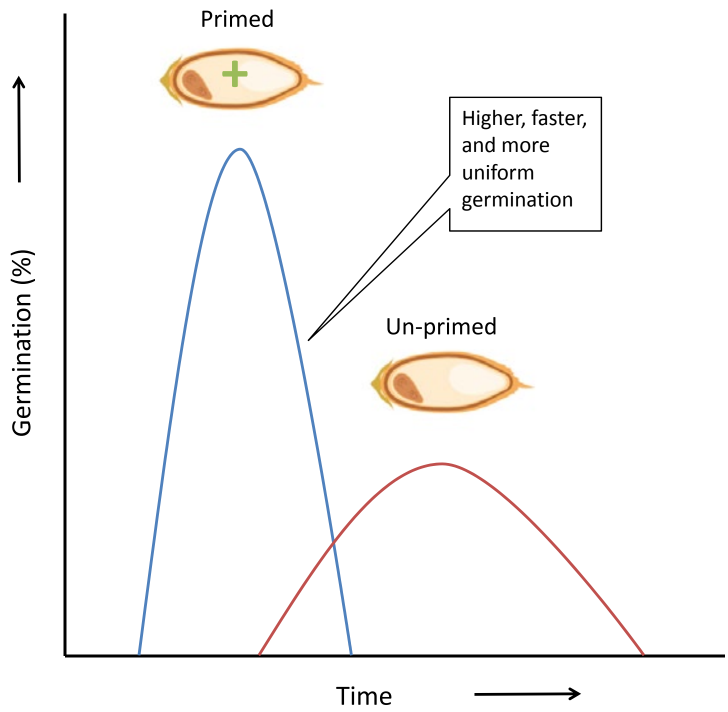

Figure 4. Effects of priming on the capacity and time required for seeds to germinate.

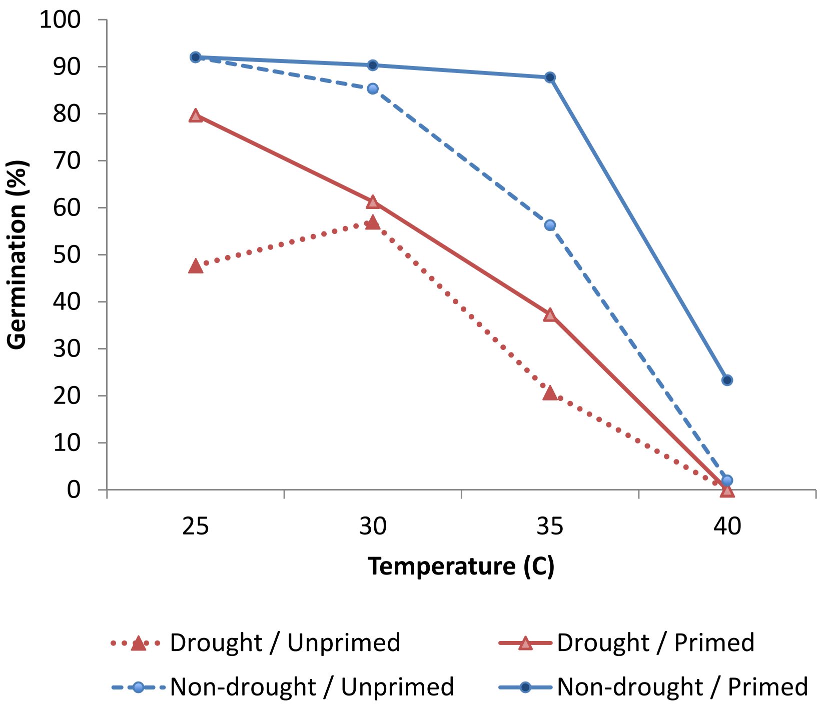

Figure 5. Osmo-priming (in –1.25 MPa solution for 7 days) enabled seeds of the perennial shrub *Acacia bivenosa* to continue germinating to a greater extent (solid lines) compared to un-primed seeds (dotted/dashed lines), even as temperatures increased from 25 to 40°C. Similarly, osmo-priming offset some of the negative effects of drought (-0.5 MPa; red triangles) which reduced germination across all treatments compared to conditions non-drought (0 MPa; blue circles).

Solid matrix priming (SMP) incorporates seeds in a solid substrate (matrix) that is moistened with water to achieve a desired water potential for priming (Farooq et al. 2019; Rogis et al. 2004; Taylor et al. 1988). The matrix can be composed of organic and inorganic materials, such as compost, vermiculite, charcoal, sawdust, granulated clay particles, and sodium polypropionate gel (Farooq et al. 2019; Paparella et al. 2015). Although air and temperature should be controlled throughout the process, SMP does not require the continuous aeration or the large volume of priming solution per quantity of seed that is necessary in hydro- or osmo-priming.

The main limitation with SMP is that after priming, the seeds must be separated from solid matrix material without harming the seeds. This step can add considerable time, and likely extra cost, for treating seeds using SMP. This can be overcome or addressed by incorporating the primed seeds and associated solid matrix material into extruded seed pellets (Madsen et al. 2018) (see 'Extruded pelleting' below). This approach negates the need to separate the seeds from the priming matrix material prior to planting, and may aid in improving growing conditions after planting (Madsen et al. 2018).

Priming at scale

The successful use of priming for restoration depends on the ability to easily and uniformly prime large quantities of seeds at one time. There are no known commercial services that offer this service for native seeds in Australia that we are aware of at this time. To help address this, operational-scale priming units (see laboratory-scale example in Figure 3) are required. In general, a priming unit needs:

- a container, bucket, or water-proof column that can be filled with a priming solution and seeds (free floating or encased in mesh bags for smaller seeds);
- an air-pump to aerate the priming solution to allow seeds to remain in an oxygen-rich environment (aeration is optimal, but not a critical element for short durations of priming); and
- an ability to adjust the air flow rates of the aeration unit (some seeds circulate within the priming solution less than others so increased air flow allows movement to be controlled).

Such a unit can be used for both hydro- and osmo-priming and is effective for treating a range of species and diversity of seed traits (like shape, size, and structure) and there is the potential to scale the units to accommodate larger numbers of seeds to support operational-scale restoration efforts. Priming solutions can also be amended with chemical stimulants to further enhance seed germination (see 'What other compounds can be added…' section below). Knowledge surrounding the scale-up of solid matrix priming for native seeds is currently being evaluated in combination with extruded pelleting technologies.

Following priming, seeds are typically re-dried prior to sowing. Seed drying is ideally undertaken in a controlled and slow manner, as the drying conditions can influence the efficacy of the priming treatment, and the longevity of the primed seeds. Rapid drying for instance can lead to cell damage or deterioration. Generally, seeds should be dried at a constant and moderate temperature, and low relative humidity, to (or near to) their original moisture content. Because priming can reduce seed longevity the storage period should be minimised (Farooq et al. 2019).

Extruded pelleting

Extruded pelleting is a process of encasing one or more seeds in a mixture of organic and inorganic materials (soil/mineral products, water-holding gels, and beneficial organic matter and chemical agents) (Table 2, Figure 6). These pellets facilitate sowing, provide a microsite (i.e. small area with favourable germination conditions for the seedling), and protect seeds from deleterious factors (such as pathogens, predators, herbicide toxicity) (Gornish et al. 2020; Madsen et al. 2016a). Extruded pelleting differs from the thin layers of material added during the seed coating process (introduced above) by the fact that the soil-seed material is mixed and extruded through a die(s) or moulded into a larger matrix. Extruded pelleting can be accomplished in several different ways.

An early and effective method suitable for large batch production (many kilograms per hour) is through the use of mechanical extruders traditionally employed in pasta manufacturing that are modified to produce extruded seed pellets (Madsen et al. 2016b). Extruded pellet dimensions can also be tailored via die selection for different seed sizes and sowing specifications (Baughman et al. 2021). Various names have been used to date that describe the different size, shape, design, and method of production of extruded pellets. Just to name a few, there are pods, pillows, coins, balls, biscuits, and cookies.

Table 2. Example of materials used in pellet formulations. Table adapted from Brown et al. (2019).

Material Type	Product Description	Producer
Activated carbon	Acticarb PS1000F	Activated Carbon Technologies Pty Ltd., Harrisdale, WA, AU.
Bentonite clay	Bentonite Milled E	Bentonite Products WA Pty Ltd., Watheroo, WA, AU.
Diatomaceous earth	Diatomite Fines (<0.6 mm)	Mount Sylvia Diatomite Pty Ltd., Gatton, Qld, AU.
Sand	Silica	Hanson Australia Pty Ltd.
Starch	Starch 1500, partially pre-gelatinised maize starch	Colorcon Inc., West Point, PA, U.S.A.
Water-holding crystals	Stockosorb 660 Powder	Evonik Industries AG, Essen, Germany

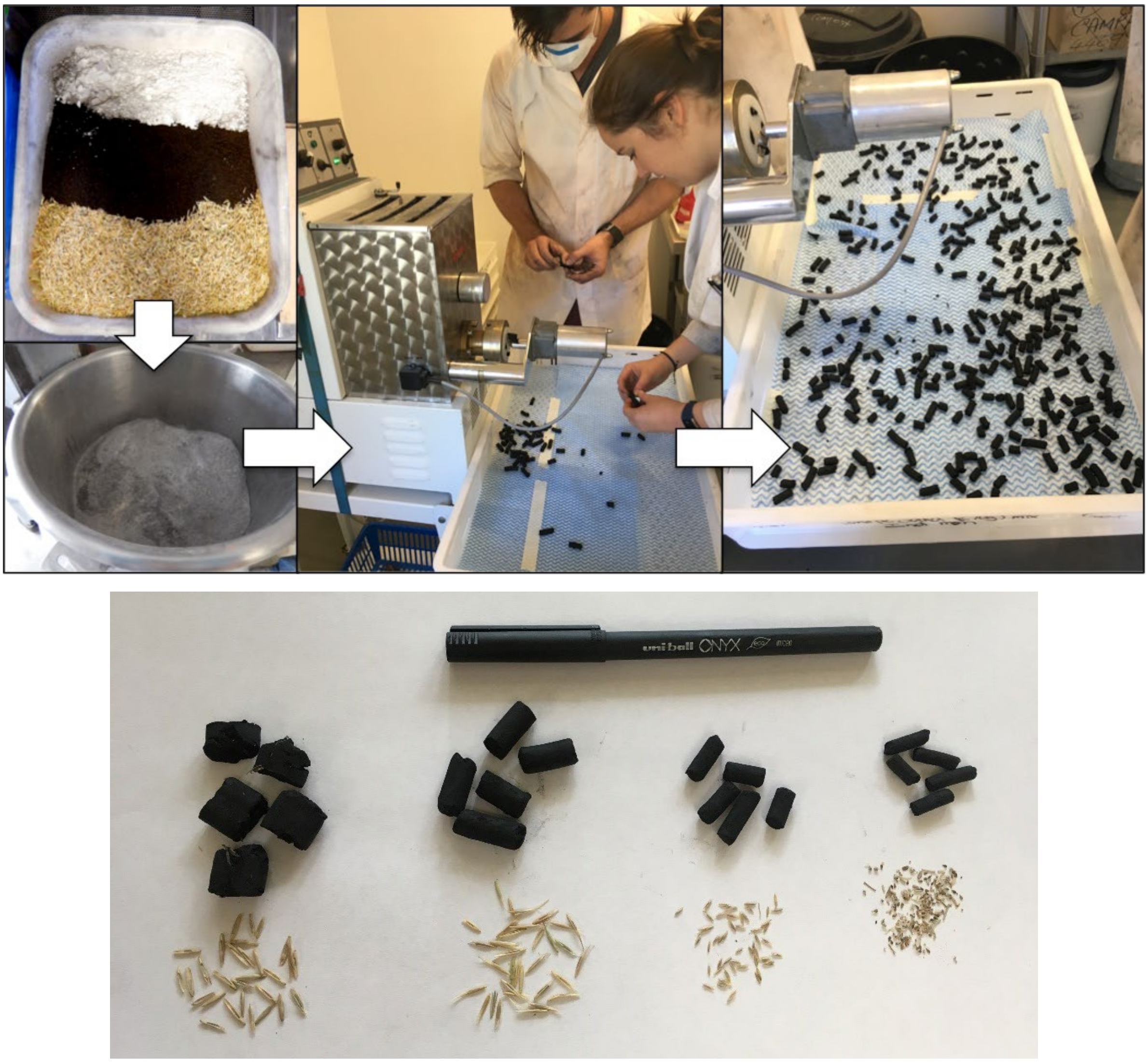

Figure 6. The extruded pelleting process begins with a mixture of organic, inorganic materials, seeds and water that make up the "dough" (top left images) which forms the extruded pellets. The dough is placed into the extruder unit (a wet-extrusion, pasta-style unit shown here; top middle), which produces extruded pellets that can be laid out on a flat drying tray and dried at constant conditions (e.g. ca. 25-40°C with a forced air drier; top right) prior to use or storage. The pellet dimensions and number of seeds per pellet are easily customisable to ensure optimised embedding of seed (see recent examples in Baughman et al. 2021; Ritchie et al. 2020; Stock et al. 2020). (Photos: V. Brown and O. Baughman)

Extruded pelleting at scale

The current extruded pelleting methods that utilise equipment such as modified pasta making machines are useful for proof-of-concept efforts but have limited scaleability. For instance, the high water content required for this wet-extrusion process translates into the need to handle heavy pellet material that must be dried quickly, which presents challenges to efficient large-scale production (e.g. hundreds of kilograms). Further, the pressure imposed on the dough during extrusion, and the time required to process whole batches can produce harder pellets with a lower water holding capacity and reduced emergence potential (Erickson et al. 2019).

Other extrusion pathways are currently being investigated, including using industrial pelleting mills traditionally used to create feed and fuel pellets (Figure 7). Initial work using native seeds in these kinds of mills has met some challenges associated with seed damage from internal mill processes. Research to identify recipe formulations and fine-tune the industrial pellet production processes that reduce seed damage and enable efficient drying and handling at-scale are the next critical steps to ensuring effective scale-up of this SET. The potential to produce large quantities of extruded pellets in industrial mills (up to many tonnes per hour) holds major promise but is still in its infancy in much of the native or agricultural seed industries. It will require investment of time and capital, along with close partnerships between seed practitioners and industry to optimise mill processes to be more suitable to handle live seeds without causing damage.

Figure 7. Example of a commonly used industrial pelleting mill and drying unit used for small-scale industrial applications, capable of producing ≥2 tonnes per hour. Larger sizes are also common. Use of such mills to produce SETs is in its infancy but the customisability and scalability offered is promising. (Photo: O. Baughman)

Flash flaming

The presence of hairs, bristles, awns and appendages on fruits or seeds of many Australian species, particularly on grass florets, interferes with seed coating, priming, and mechanised direct-seeding processes (e.g. glues/polymers and powders fail to adhere during the coating process, and these seed types block the hoppers in seed metering devices). Historically, practitioners often avoid these types of fruits and seeds due to the difficulty in seeding these species at scale (e.g. Poaceae, Amaranthaceae, and Asteraceae). This overlooks many species worthy of seeding when plant diversity is a key focus of the seeding program. On the other hand, some practitioners modify their direct seeding machines to suit certain fluffy fruit or seeds (Module 14 – Direct Seeding). While such modifications provide a solution to individual practitioners through trial and error, word of mouth advice, and customisation (Gibson-Roy and Delpratt 2015), they do not provide an optimal universal solution for operationally handling seeds and fruits with un-wanted appendages, especially at large scales.

Flash flaming is a newly developed SET (Guzzomi et al. 2016), which employs a strategically placed flame inside an open-topped drum with a spinning base (Figure 8) to remove undesired appendages, primarily to improve flow rates through seeding mechanisms – removing the need to modify equipment (Berto et al. 2020; Erickson et al. 2019; Ling et al. 2019). The spinning base projects the seeds up on to the wall of the drum and keeps seeds in motion – creating a continuous ‘stream’ of seeds. With the correct placement of the torch, the flame can precisely remove un-wanted appendages. This process is typically gentler than most mechanical cleaning processes, occurring gradually as the stream of material repeatedly passes the flame.

Flash flaming at scale

Flash flaming drums capable of accommodating large-scale seeding operations (e.g. hundreds of kilograms of spinifex / *Triodia* spp. florets) have recently been developed (Figure 8). These one-cubic-metre drums can be used to substantially reduce batch volume and weight, as well as to increase the seed bulk density (i.e. more seeds per volume) and 'flowability' through direct seeding machinery (Berto et al. 2020; Erickson et al. 2019; Ling et al. 2019). Species that possess un-wanted 'combustible' appendages will likely benefit from this technology. On-going research efforts are being led out of The University of Western Australia which are investigating commercial scale-up and industry adoption of this technology.

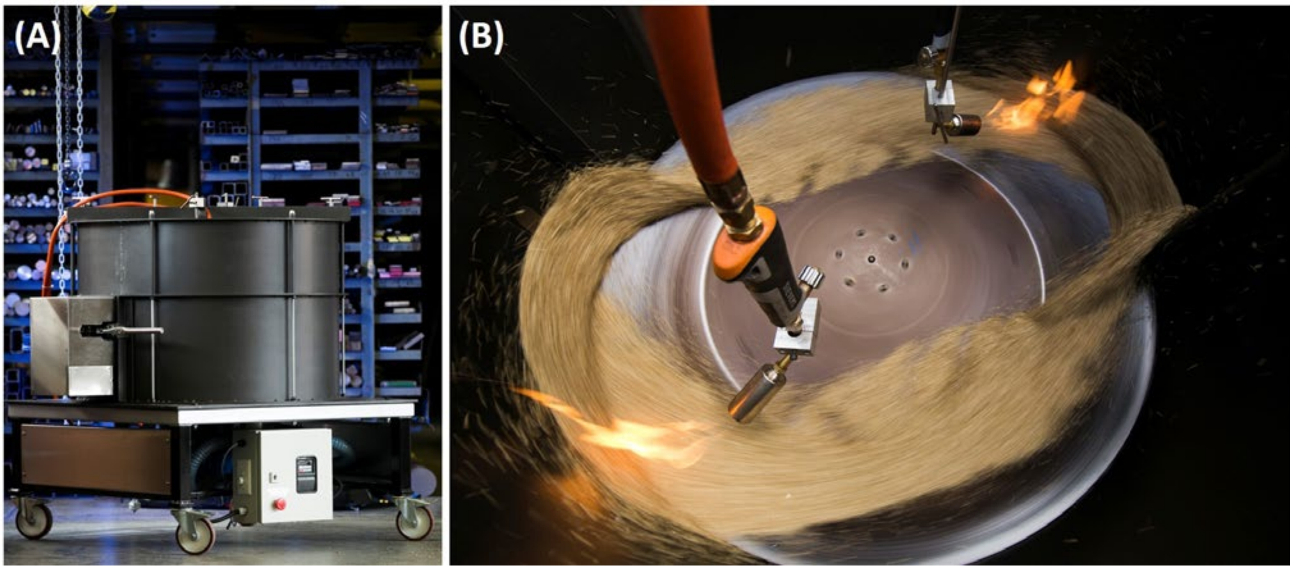

Figure 8. The newly constructed flash flaming apparatus contains (A) a dual-flame set-up and (B) features that allow operators to control the air flow, rotation speed of the base plate, and removal of flamed material through the hopper shoot after flaming is complete (figure from Erickson et al. 2019).

Acid digestion

Similar to flash flaming, acid digestion aims to remove un-wanted appendages through immersion in concentrated sulphuric acid and controlling the 'digestion' time (Stevens et al. 2015). Recent evidence suggests this approach can offer similar benefits to what has been observed using flash flaming. Acid digestion approaches have also been combined with ribbed rubber mat cleaning to remove the acid-cleaned covering floret/fruit structures from seeds post-digestion (Pedrini et al. 2018). However, both approaches have not been scaled to date and concerns surrounding the handling and disposal of large quantities of acid need to be considered.

What other compounds can be added to benefit SET applications and their effectiveness?

An additional benefit of SETs such as priming, coating and extruded pelleting is that substances such as germination stimulants/retardants, fertilisers, or beneficial microbiota can be added to the recipes to further enhance the application of the technology. The addition of fertilisers and micro-nutrients in coatings is one of the most utilised techniques in agriculture (Bennett 2016). As SETs become more sophisticated, and practitioners identify which barriers are the biggest contributing factors to seeding failure, additives are being used in unison with the previously discussed technologies to further 'enhance' the SET being applied. Below are a range of additives for which there is some evidence of successful application to native seeds.

Germination stimulants

The benefits of germination promoting compounds such as smoke-derived products, gibberellic acid, and nitrates have long been recognised and used for Australian species (see also Module 11 – Seed Germination and Dormancy). For instance, aerosol smoke and smoke-water solutions have been used to improve the germination capacity of seeds of a very diverse range of Australian species (Dixon et al. 1995; Read et al. 2000; Turner et al. 2013). Smoke water can be easily applied by soaking seeds in a diluted solution overnight, or for up to 24-48 hours (Commander et al. 2009).

Priming seeds in solutions containing germination stimulants such as karrikinolide (Kulkarni et al. 2011), a smoke chemical shown to stimulate germination of many species in Australia (Erickson et al. 2016; Merritt et al. 2007; Nelson et al. 2012), can also aid practical applications such as mine rehabilitation (Erickson et al. 2019; Erickson et al. 2017; Kildisheva 2019). This additive can improve germination and seedling emergence even in the face of drought – an important benefit to establishment in degraded ecosystems (Figure 9) and is now being applied to kilograms of native seeds for use in broad-acre seeding programs (Erickson et al. 2019). The technique of priming with a chemical or hormone additive is at times called 'chemo-priming' or 'hormone-priming' (Farooq et al. 2019; Pedrini et al. 2020), but, this is an unnecessary naming convention given it is effectively hydro-priming with an additive. Other stimulants that can be used as an additive to priming, such as gibberellic acid, potassium nitrate, salicylic acid, and ethylene warrant further research for application to native seeds (Beveridge et al. 2019; Farooq et al. 2019).

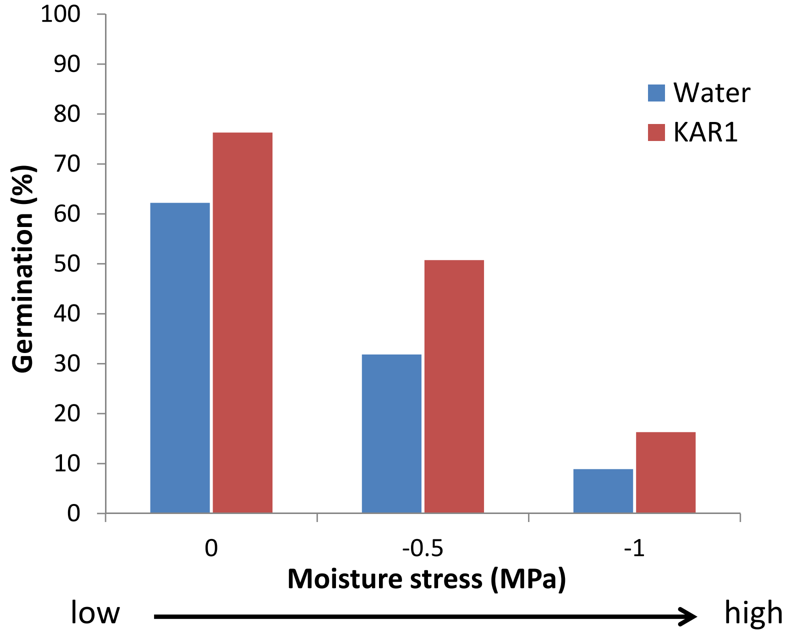

Figure 9. Seeds of soft spinifex (*Triodia pungens*) were hydro-primed in pure water or water with karrikinolide (KAR_1) for 9 hours. KAR_1 priming improved germination even under high levels of moisture stress (developed by Kildisheva 2019).

Germination retardants

In some instances, some seeds germinate too readily and may 'over commit' in certain restoration settings. This may be the case for seeds that have been treated to alleviate dormancy, or for seeds that are naturally non-dormant. To counteract this, and to create a 'practitioner-regulated' bet-hedging mechanism within a seed batch, some recent seed coating technologies have investigated the use of abscisic acid (ABA) – a dormancy inducing and regulating hormone – to delay germination (Richardson et al. 2019). This approach has been used in the northern hemisphere for broadacre seeding in the autumn prior to the onset of winter rains, snow, and frozen soil, but where germination is desired later in the winter or spring. In effect, adding ABA to seed coatings prevents undesirable premature germination in the early rain period. Although in its infancy, this coating application could benefit some direct seeding programs whereby seeding needs to occur when soils are dry and accessible (i.e. in autumn) to allow seeds to overwinter in the soil and be in place when conditions are favourable for plant growth in early spring.

Soil microbiota

The process of identifying and isolating beneficial soil microbiota that are known to assist in the recruitment and establishment of native species is rapidly growing (Chua et al. 2020; Muñoz-Rojas et al. 2018). Many plant species form co-evolutionary dependencies on microbiota (Hassani et al. 2019). This microbiota inhabit native soils, and in some cases provide an advantage to plants that are locally adapted. For instance, some plants have developed adaptations that specialise in the cultivation or uptake of local soil microbiota through their root systems (Urbina et al. 2018), and in some cases, an advantage is gained when plants are grown in local soils due to the microbiota present. There is also emerging evidence to indicate that microbiota can help convey physiological tolerance to environmental stressors to plant populations. For example, soil microbiota sourced from within a more arid part of the native range of a plant species can help induce greater drought tolerance to plant populations sourced from more mesic environments (de Vries et al. 2020; Remke et al. 2020). Harnessing these co-dependencies of plant genotypes and local microbiota will create new dimensions for SETs. One recent example is the use of locally sourced cyanobacteria as an additive in hydro-priming (Muñoz-Rojas et al. 2018). Initial findings of this work suggest that early-stage germination and vigour may be increased by the cyanobacteria. Further, researchers have recently shown locally sourced cyanobacteria can survive and be successfully deployed using extruded pellets (Román et al. 2020). Currently, the use of soil microbiota in SETs are being tested to explore how these microbes can be added to extruded pellets or coatings and whether the suggested advantages are realised for key restoration species.

Anti-predation compounds

Seeds planted on restored areas are often consumed by vertebrates such as birds and rodents (Pearson et al. 2018; Taylor et al. 2020), or removed from the planted site by invertebrates such as ants (De Falco et al. 2012; Dominguez-Haydar and Armbrecht 2011), leading to reduced plant establishment within the site. Coating seeds may decrease the granivores ability to detect the seed. Additionally, coating seeds with aversive products may further alter an animal's ability to consume the seed. For example, a recent study showed seeds coated in ghost pepper, neem oil, and activated carbon reduced rodent consumption by 47–50% (Taylor et al. 2020). Using anti-predation additives for seed coatings is a relatively new approach for native plant restoration programs that warrants investigation across many systems where granivores may contribute to seed losses post-sowing. Adverse effects of these coatings on non-target animals needs to be considered also.

Prevention of pathogen attack

Fungi, root rot, and 'water moulds' can contribute to restoration failures by causing seed decay and seedling disease (Fawke et al. 2015; Gilbert 2002). These pathogens can attack seeds and seedlings through soil-borne and seed-borne pathways. The severity of pathogen-related mortality has been shown to depend on the soil environment and the duration the seed is present in the soil prior to germination (Allen et al. 2018). High fungal activity is common under wet, cool soil conditions and the longer the seeds remain in the soil un-germinated the greater their exposure to attack. Fungal pathogenesis can also be exacerbated by soil stressors such as freeze-thaw cycles or drought conditions (Allen et al. 2018; Connolly and Orrock 2015).

Fungicide seed treatments commonly used in agriculture may offer a solution for overcoming pathogens limiting restoration seeding efforts. Due to the targeted nature of seed coatings, relatively small amounts of fungicide can produce a treatment effect, which reduces the potential of exposure of active substances to non-target organisms and increases the economic efficiency of the treatment (Nuyttens et al. 2013). In recent native seed coating assessments, Hoose (2020) applied a fungicide formula of mefenoxam, azoxystrobin, difenoconazole, and fludioxonil to control a suite of common seed-borne and soil-borne pathogens (Gornish et al. 2015). Repeatedly this fungicide coating has improved seedling emergence 83% of the time, producing, on average, a 59% increase in plant density. Future considerations for fungicide use, however, need to consider and evaluate the influence this targeted fungicide approach has on the target species and the beneficial soil organisms in the surrounding soil profile.

Soil surfactants

Water repellent soils are widespread in many natural environments globally, such as the dry regions of southern Australia (New South Wales, South Australia, and Western Australia) as well as regions in the western United States (Ruthrof et al. 2019) and can prevent the establishment of native plant species in restoration. Soil water repellence leads to decreased water infiltration and moisture retention in the seed zone, with resulting poor germination and seedling survival. Surfactant seed coatings, or inoculation of extruded pellets with soil surfactants (wetting agents), which are specifically designed to overcome water repellent soils, can increase plant establishment (Madsen et al. 2012). The benefits of adding soil surfactants to extruded pellets to improve recruitment micro-sites of repellent sands are currently showing promise in Proteaceous species of south-west Western Australia (Ritchie et al. 2020).

Where to now with SETs?

One of the key questions to resolve during the development of SETs for native seeds in restoration settings, relates to understanding if and when we have manipulated and altered the recruitment potential of seeds to such as degree that we have reduced the bet-hedging capacity of the seed batch. For instance, there are many SET treatments that aid in dormancy alleviation, alter germination speed, and/or provide other beneficial stimulants targeting specific site limitations and promote rapid and uniform germination. The ability of a seed batch to distribute germination over a range of conditions or through time may improve long-term plant recruitment and survival on restoration sites that have experienced a high level of disturbance, have limited regeneration opportunities (i.e. drylands), or have a high risk of post-germination mortality. When sowing SET-treated seeds into these conditions, are we reducing the natural "bet-hedging" strategies of the seeds? For the greatest success it is likely that we need to balance the need to sow seeds ready to germinate in the first-year post-seeding, given the right conditions, and the need for some seeds to form a persistent seedbank that can establish in subsequent years (Commander et al. 2019).

Each of the SETs described, when applied alone, seeks to maximise germination and successful emergence in a specific time and place. But where there are highly variable and unpredictable site conditions after sowing, this may spell disaster. Combining multiple SETs to modify germination properties (Figure 10) may improve the odds of success (Hardegree et al. 2020), with each technology being a "bet" on a different potential set of conditions.

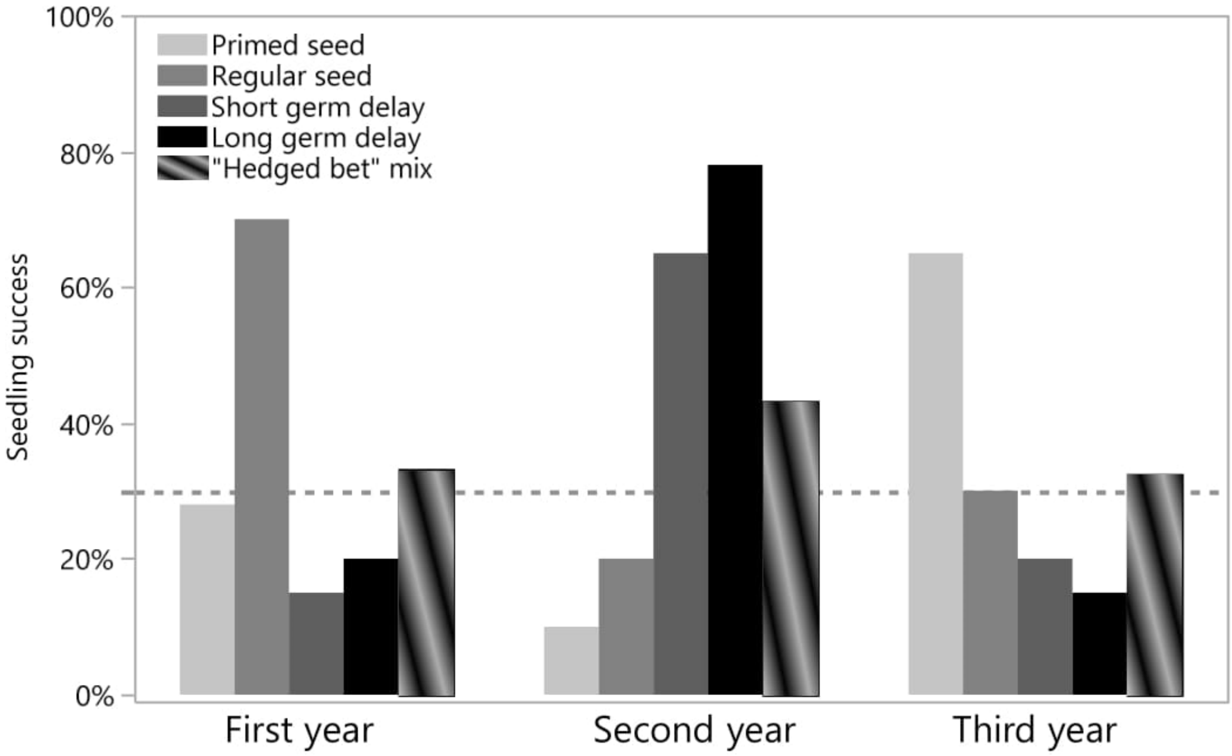

Figure 10. Simulated example of how multiple SETs that induce different germination timing (light through dark solid bars), deployed alone, could vary in success through time at a single site, but how a "hedged bet" equal mixture (25% of each) of those same technologies (striped bars) under the same conditions could provide more consistent success through time. In this hypothetical example, an acceptable level of success is considered to be 30% seedling establishment (dashed horizontal line).

With further development, such "bet-hedging" with multiple SETs could involve a single deployment of seed that results in multiple pulses of germination every few weeks, any one of which has enough seeds to generate a reasonable level of success if the given conditions favour it (Davies et al. 2018; Erickson et al. 2017). Furthermore, ensuring that the effect of the SET is only temporary (not affecting future generations) can help facilitate the initial recruitment of adult plants that would subsequently allow the seeded species to continue utilising their inherent, locally-adapted strategies to thrive on the site over the long-term. This is but one example of an evolutionarily grounded, SET-facilitated strategy to affect restoration success, and others are likely possible.

The challenge is to apply such a complex SET approach to native seeds, which are inherently variable in dormancy-loss and germination requirements, both within and between species. Seed enhancement technologies are sure to continue to be developed as practitioners and researchers further their knowledge of the barriers to success of specific restoration challenges (Copeland et al. 2021) and/or the species used. This is likely to include completely new technologies and ideas, as well as refinements, specialisations, and combinations of existing concepts.

The past has shown that additional developments will be most successful if they meet one or more of these general guiding principles:

- Specific and actionable barriers to restoration success should be identified first, then technologies developed to overcome those specific barriers.
- SETs should avoid impairing desirable seed properties (e.g. the application of a coating that improves geometry but impedes germination).

- The scale that the new SET will be applied should be considered early in the development process.
- SETs will not be the silver-bullet that solves all seed-based restoration issues. Species-specific SETs need to be considered as an extra 'tool in the shed' to be used in unison with well-established seed management practices and appropriate sowing machinery.
- When possible, SETs should seek to utilise the same traits and strategies already employed by plants in their evolution to their past and current environments. This requires such traits and strategies to be identified and understood.
- Potential consequences of SET applications also need to be considered (e.g. creating batches of seeds that commit to low rainfall events that are insufficient for plant survival).
- In what is a newly developing space, we encourage practitioners to learn through experimentation. Not all SETs will work in every ecosystem and on every species. Trial-and-error will be the key to determining the overall benefit of SET applications.

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