RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

SER SOCIETY FOR ECOLOGICAL RESTORATION

ADVANCES IN MINING RESTORATION

PRACTICE AND TECHNICAL ARTICLE

Restoration seedbanks for mined land restoration

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Restoration seedbanks have become a key infrastructure resource in efforts to restore damaged and degraded environments across the globe. Large-scale ecological restoration typically utilizes large volumes of valuable, usually wild-collected seeds, but insufficient knowledge of seed biology (including storage requirements in some cases) and ecology for many species continues to hamper the utility of restoration seedbanks to meet this rising demand. Poor germination and establishment when seeds are deployed from seedbanks can stem from factors such as premature seed collection, low seed quality, poor processing, handling and storage, variable seed quality from year to year, and, critically, insufficient understanding of seed dormancy, seed germination traits, and the ecological requirements for germination stimulation. While these factors may impact the success of seed-based ecological restoration both synergistically and idiosyncratically, they can be universally addressed by adopting best practice principles in seedbank management and operation and through an improved understanding of the seed biology and ecology of stored species. Drawing upon an industry case study in seedbanking for post-mining ecological restoration, we outline how optimizing seed storage conditions and a focus on seed biology and ecology in the operation of a restoration seedbank can deliver broad and immediate benefit and cost-efficiency to native seed use. Such improvements are crucial in developing more effective approaches for returning biodiverse plant communities to highly modified landscapes and are foundational for meeting the aspirations for ecological restoration at global scales in the coming decade.

Key words: recalcitrant seed, restoration capacity building, restoration efficiency, seed dormancy, seed storage, seed technology

Implications for Practice

- Restoration seedbanks can play a vital role in enhancing ecological restoration capacity following mining through strengthening the seed supply chain.
- Restoration seedbanks need to be based on best practice approaches for the collection, processing, storage, dormancy alleviation, and delivery to site of seeds.
- Seeds from framework and keystone species, those that stimulate key ecological processes, species with limited dispersal, and species that do not naturally form a soil seedbank should be prioritized for collection, storage, and direct seeding of restoration sites.
- Understanding seed dormancy and seed ecology of native species is fundamental for improving germination-on-demand and maximizing in situ seedling recruitment.

Introduction

There has been a broad transitional shift by seed biologists and restoration practitioners since 2000 to move conservation-oriented seedbanking efforts alongside restoration-focused activities to address landscape scale environmental damage (Merritt & Dixon 2011). For example, over 21 community-based seedbanks of various sizes and sophistication are now active across Australia to support the rapidly developing restoration economy (Van Moort et al. 2021). This paradigm shift has seen restoration seedbanks become increasingly important for meeting both regional and global restoration targets that have taken seedbanks as originally conceived, well beyond their

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Author contributions: SRT, MJ, ATC conceived and developed the first draft; all authors made equal contributions to the material covered and the discussion of all topics in subsequent drafts.

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doi: 10.1111/rec.13667
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13667/suppinfo

traditional agricultural, horticultural, and conservation focus (Mortlock 2000; León-Lobos et al. 2012; Erickson et al. 2017).

Unlike conservation seedbanks, restoration seedbanks process and exit substantial quantities of seed to support multispecies restoration programs that require seed supply processes that are robust, reliable, scalable, and increasingly sustainable (Mortlock 2000; Koch 2007*b*; Erickson et al. 2017). The seed supply chain therefore needs a specific workflow around which the management of seedbanks specifically for restoration purposes can be structured, with many interrelated steps where targeted seed-centered improvements can be achieved incrementally to optimize on-ground restoration outcomes (Fig. 1).

Seeds stored in restoration seedbanks are generally sourced each year from a similar suite of framework species and from regions in which seasonal seeding activities are to be undertaken (Erickson et al. 2017). In Australia, large volumes of seeds are sourced principally from wild populations at substantial environmental and economic cost rather than obtained from dedicated seed production areas that offer greater reliability and critically are far more sustainable in the medium to long term (Nevill et al. 2018). Consequently, restoration seedbanks are an integral investment in terms of infrastructure, technical expertise, and seed stock, and are crucial in supporting the complex and interdisciplinary process of reestablishing native vegetation on lands that have been damaged, degraded, or modified by human disturbance (Mortlock 2000; Merritt & Dixon 2011; Erickson et al. 2017).

Although seedbanks can have high capital costs in the establishment phase, with effective planning and management they can offer significant return on investment through improved restoration capacity (Merritt & Dixon 2011). This economic return is further improved by best practice management and economies of scale, as cost per unit can be lowered through scaling-up activities and technology-driven specialization of the storage environment as well as strategic investment in equipment and seed research and development (Madsen et al. 2016; De Vitis et al. 2020; Pedrini & Dixon 2020). Nevertheless, whereas conservation seedbanks commonly rely on intensive nursery-based propagation of scarce and hard-to-replace seeds to maximize the chances of reproductive success, restoration seedbanks in comparison principally deliver seed to site via direct sowing in most cases (Mortlock 2000; Guerrant Jr & Kaye 2007; Erickson et al. 2017). Therefore, to improve seed use efficiency restoration seedbanks are increasingly reliant on seed technologies to optimize each stage of the seedbank workflow with emphasis in more recent times on the development of seed enhancement and novel mechanized delivery systems to improve direct seeding outcomes (Fig. 1) (Pedrini et al. 2020; Masarei et al. 2021).

Indeed, over the last 5 years a number of state (RIAWA 2021), national (Commander 2021), and international (Pedrini & Dixon 2020) best practice guidelines centered around the use of wild seeds have been produced to support the rapidly growing global industry in the sourcing, supply, and sale of native seeds for sustainable use in ecological restoration (Gann et al. 2019; Pedrini & Dixon 2020). These guidelines and standards have been produced to inform and support practitioners, volunteers, and professionals alike working in different areas, including seed collection, seed storage, seed testing, nursery production, direct

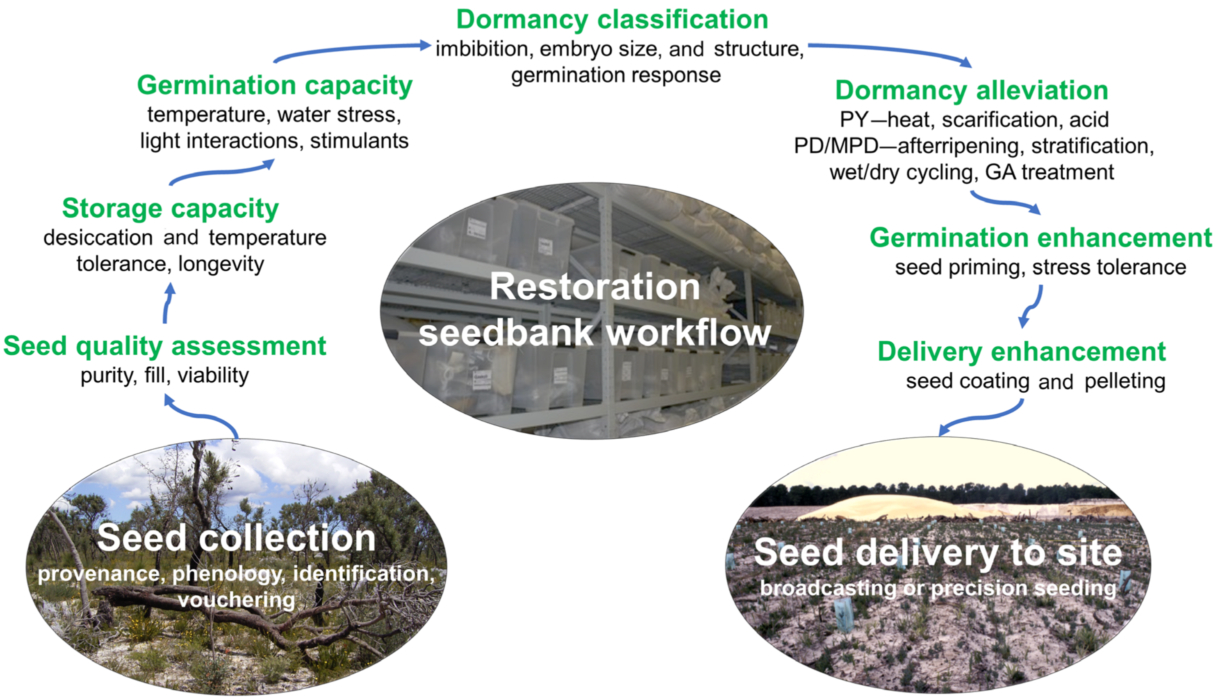

Figure 1. Core functions and workflow of restoration seedbanks interposed between the points of seed collection and seed delivery to in situ restoration site. Each step can, in different ways, significantly impact in situ recruitment success. GA, gibberellic acid; MPD, morphophysiologically dormant; PD, physiologically dormant; PY, physically dormant.

seeding, seed research and development, management, policy development, and policy implementation (Gann et al. 2019; Commander 2021; Martyn Yenson et al. 2021). These guidelines and standards are designed to address seed-related factors that are currently constraining and distorting the national and global native seed industry, including limited availability of seed, variable seed quality, inappropriate storage conditions, and low rates of in situ seedling establishment (McDonald et al. 2016; Gann et al. 2019). Standards provide seed buyers, end users, and funding bodies with a level of confidence and reliability in the sourcing of quality native seeds, and a pathway toward global best practice in sustainable native seed use (Pedrini & Dixon 2020).

As with other topics in this special issue, disturbance by mineral extraction provides an example of high-intensity disturbance and a tractable context in which to research and highlight current issues in restoration seedbanking. The restoration of lands degraded by mining activities is often a regulatory requirement that aligns closely with mine closure (Stevens & Dixon 2017). As the importance of applying best practices in seed handling and investing in adequate seed storage facilities has become better understood, restoration seedbanks have become a mainstay for many resource extraction companies to support on-ground restoration activities (Cromer & Norman 2006; Koch 2007*b*; Erickson et al. 2017).

Here we aim to highlight the utility and functionality of an industry restoration seedbank (Hanson Construction Materials [Hanson]) in the southwest Australian biodiversity hotspot as an example of how biodiverse seedbanking is implemented in the mining industry. We show how this seedbank works within established standards and operational principles in relation to seed storage, seed biology, and seed ecology. We also highlight the current barriers and opportunities to enhance the potential of biodiverse seedbanks in supporting the growing complexity and scale of ecological restoration activities in the mining industry both locally and globally.

Hanson Construction Materials

Approximately 300 native plant species are found across Hanson's sandmining leases, though over 1,000 species have been recorded from associated *Banksia* woodland communities on the Swan Coastal Plain (Commonwealth of Australia 2016). Most diversity is associated with the lower sclerophyllous understory, which comprises a species-rich mix of larger woody shrubs (Proteaceae, Myrtaceae), smaller native woody perennials (Ericaceae, Fabaceae), rushes (Restionaceae), sedges (Cyperaceae) and herbaceous perennial (Stylidiaceae, Haemodoraceae) and annual species (Araliaceae, Asteraceae) (Commonwealth of Australia 2016). The overstory, by comparison, is dominated by a comparatively small number of *Banksia*, *Corymbia*, and *Eucalyptus* species (Rokich 2016).

General Restoration Approach

Following sand mining, the native vegetation requires significant restoration works involving both abiotic and biotic engineering (Rokich et al. 2000; Turner et al. 2006; Rokich 2016). The area requiring restoration ranges from 1 to 10 ha/year (usually around 3–4 ha). Respread topsoil is an important part of the restoration approach and can, depending on its quality, return over 70% of perennial (seeder) species including many that are difficult to germinate from seeds under ex situ conditions (Rokich et al. 2002). Nevertheless, the density of seedling emergence and plant recovery from respread topsoil can be lower than that observed from predisturbed reference sites, and often misses key functional groups such as serotinous species (Rokich & Dixon 2007). Consequently, to improve seedling density and species diversity particularly from key groups, seeds from a targeted range of native species are broadcast as part of scheduled restoration activities as one of the last phases of revegetation works (Rokich et al. 2002).

Direct Seeding Using Stored Seeds

Core native species used for direct seeding are taxa that usually do not form a persistent soil seedbank, have low return from topsoil, are important keystone and framework taxa, or shorter-lived colonizer species that provide soil stabilization, nitrogen, and nurse-species support (Table 1). Hanson regularly incorporates 19–24 species into their seeding mix from eight families which contains geosporous (∼48%) and serotinous species (52%) (Table 1). Most species (58%) regularly used for direct seeding possess nondormant seeds, while the remainder have some form of easily resolved seed dormancy (42%) (Table 2). Approximately one-third of the species utilized for direct seeding have physically dormant (PY) seeds (Table 1) and are briefly treated with hot water (HW) to overcome water impermeability (Merritt & Turner 2016). The seeding rate is dependent on the landscape being restored, the availability and quality of the topsoil seedbank, as well as other factors that require consideration as part of the restoration program. Generally, however, direct seeding at a rate of approximately 2 kg/ha (∼1.3 kg/ha if *Macrozamia fraseri* seeds are not included; Table 1; Box 1) is undertaken in late autumn/early winter (May–June) immediately prior to the onset of cooler wetter conditions when in situ germination typically occurs. Depending on the species, between 34 (for the large-seeded cycad, *M. fraseri*; Box 2) and approximately 277,000 (for minute-seeded species such as *Kunzea glabrescens*) seeds are sown per hectare (Table 1).

Seed Dormancy and Germination Capacity

To understand the potential impact of seed dormancy across the entire seedbank, each of the approximately 201 species currently in storage (Table S1) were assigned to one of five seed dormancy classes based on either what is currently known about the species (Merritt & Turner 2016) or which can be inferred from related taxa (Baskin & Baskin 2014) (Table S1). Through this filtering we found that 23% of all the species within the seedbank are considered to have nondormant seeds (Table 2; Table S1). In contrast, 77% of species are predicted to have some form of seed dormancy, which is broadly in line with estimates made for other ecosystems (Baskin & Baskin 2014; Erickson et al. 2016). Forty-four percent of species are predicted to

Table 1. Attributes of the core 24 native species regularly seeded by Hanson across restoration sites following sand mining in *Banksia* woodland located in southwest Western Australia ranked by their individual seed mass. Gray shading highlights species which have a thousand seed weight (TSW) less than 5 g and which may benefit from the application of seed coating technologies to enhance in situ sowing traits (Madsen et al. 2016; Pedrini et al. 2020). ND, non dormant; PY, physically dormant; HW, hotwater; PD, physiologically dormant; MD, morphologically dormant.

Genus	*Family*	*Seed Syndrome*	*Seed Dormancy Type and Seed Pretreatment (If Applicable)*	*Life-form*	*Rationale for Inclusion*	*Rate (g/ha)*	*TSW (g)*	*Approximate Number of Seeds Sown Per Hectare*	*Approximate Amount (g) Used Annually (10 ha)*
Melaleuca seriata	Myrtaceae	Bradysporous	ND	Shrub, 0.25–1 m high	Framework keystone species	10	0.036	21,667	100
Kunzea glabrescens	Myrtaceae	Bradysporous	ND	Shrub, 1.5–4 m high	Framework keystone species	10	0.13	277,778	100
Beaufortia elegans	Myrtaceae	Bradysporous	ND	Erect shrub, 0.3–1(−2) m high	Framework keystone species	10	0.28	76,923	100
Eremaea pauciflora	Myrtaceae	Bradysporous	ND	Erect to spreading shrub, to 4 m high	Framework keystone species	30	0.54	36,101	300
Regelia inops	Myrtaceae	Bradysporous	ND	Erect, often spreading shrub, 0.75–2.5 m high	Framework keystone species	8	0.78	55,866	80
Gompholobium tomemtosum	Fabaceae	Geosporous	PY—HW for 30–120 seconds	Shrub, 0.3–1 m tall	Nitrogen fixation	30	1.4	10,191	300
Bossiaea eriocarpa	Fabaceae	Geosporous	PY—HW for 30–120 seconds	Erect or straggly and spreading shrub, 0.2–1 m high	Nitrogen fixation	40	1.9	20,994	400
Allocasuarina huegeliana	Casuarinaceae	Bradysporous	ND	Dioecious tree, 4–10 m high	Framework keystone species	75	2.2	21,053	750
Austrostipa spp.	Poaceae	Geosporous	PD—afterripening(?)	Tufted annual to perennial grass-like herbs, 0.15–0.7 m high	Rapid growth soil stabilization	65	3.0	34,722	650
Gastrolobium capitatum	Fabaceae	Geosporous	PY—HW for 30–120 seconds	Prostrate to low, bushy shrub, to 1 m high	Nitrogen fixation	50	4.4	11,371	500
Allocasuarina fraseriana	Casuarinaceae	Bradysporous	ND	Tree up to 15 m tall	Framework keystone species	15	4.4	3,401	150
Acacia pulchella	Fabaceae	Geosporous	PY—HW for 30–120 seconds	Shrub, 0.5–2 m tall	Nitrogen fixation	75	5.1	14,706	750
Jacksonia furcellata	Fabaceae	Geosporous	PY—HW for 30–120 seconds	Prostrate to decumbent or weeping erect shrub, 0.4–4(−6) m high	Nitrogen fixation	30	6.0	4,969	300

Table 1. Continued

Genus	*Family*	*Seed Syndrome*	*Seed Dormancy Type and Seed Pretreatment (If Applicable)*	*Life-form*	*Rationale for Inclusion*	*Rate (g/ha)*	*TSW (g)*	*Approximate Number of Seeds Sown Per Hectare*	*Approximate Amount (g) Used Annually (10 ha)*
Eucalyptus todtiana	Myrtaceae	Bradysporous	ND	Mallee or tree, 2–8(−15) m high.	Framework keystone species	20	6.8	2,941	200
Eucalyptus marginata	Myrtaceae	Bradysporous	ND	Tree, to 40 m high	Framework keystone species	40	7.8	51,28	400
Jacksonia floribunda	Fabaceae	Geosporous	PY—HW for 30–120 seconds	Prostrate, decumbent, erect, or ascending shrub (0.05–) 0.25–3 m high	Nitrogen fixation	25	8.7	2,877	250
Xanthorrhoea preissii	Xanthorrhoeaceae	Geosporous	ND	Perennial tree-like monocot, to 5 m high	Framework keystone species	60	15.6	3,849	600
Hovea pungens	Fabaceae	Geosporous	PY—HW for 30–120 seconds	Erect, pungent shrub, 0.2–1.8 m high	Nitrogen fixation	10	20.0	500	100
Hovea trisperma	Fabaceae	Geosporous	PY—HW for 30–120 seconds	Straggling, weak to ascending shrub, 0.1–0.7 m high	Nitrogen fixation	10	22.2	451	100
Nuytsia floribunda	Loranthaceae	Bradysporous	MD	Tree or shrub, to 10 m high, root parasite	Framework keystone species	100	65.0	1,538	1,000
Banksia menziesii	Proteaceae	Bradysporous	ND	Lignotuberous tree or shrub, 1.3–7 m high	Framework keystone species	250	81.9	3,053	2,500
Banksia attenuata	Proteaceae	Bradysporous	ND	Lignotuberous tree or shrub, 0.4–10 m high	Framework keystone species	250	98.0	2,551	2,500
Corymbia calophylla	Myrtaceae	Bradysporous	ND	Tree or mallee, (rarely), to 40(−60) m high	Framework keystone species	40	101.2	395	400
Macrozamia fraseri	Zamiaceae	Geosporous	MD/MPD(?)	Tree/cycad, trunk variable; dull strongly keeled leaves with narrow to medium leaflets; large, broad cones	Framework keystone species	650	19,000	34	6,500
							Total	613,059	19,020

Table 2. The assignment of seed dormancy classes for seeds of 201 native species (40 families) collected from *Banksia* woodland floristic communities used by Hanson for restoration following sand mining. Classification is based on a range of traits from the species themselves (Merritt & Turner 2016), or if not directly known inferred from closely related species or in several cases the families to which the species belong (Baskin & Baskin 2014). The attributes used for classification include water uptake capacity, embryo size relative to the rest of the seed, and germination capacity when seeds are fresh and untreated. The far-right shaded column outlines the proportion of species ($n = 89$) used for restoration from the hot semiarid (~300 mm) Pilbara region in Western Australia assigned to the same dormancy classes (adapted from Erickson et al. 2016). PD, physiologically dormant; PY, physically dormant.

Dormancy class	*Abbreviation*	*Number of Species in Seedbank*	*Number of Families Where this Class is Observed*	*Proportion (%) of Banked Species*	*Proportion (%) of Pilbara Species*
Nondormant	ND	47	5	23.4 (47 spp.)	27.0 (24 spp.)
Morphological	MD	3	2	1.5 (3 spp.)	1.1 (1 sp.)
Morphophysiological	MPD	31	11	15.4 (31 spp.)	3.4 (3 spp.)
Physical (PY and PY + PD)	PY	31	2	15.4 (31 spp.)	34.8 (31 spp.)
Physiological	PD	89	23	44.3 (89 spp.)	33.7 (30 spp.)
	Total	201	NA	100 (201 spp.)	100 (89 spp.)

Box 1 Hanson seedbank overview.

Hanson contracts the services of a modern seed storage facility for the storage of all their *Banksia* woodland seeds for ongoing use in restoration programs. Seeds in this facility are stored at low humidity (~20% relative humidity [RH]) and temperature (5°C) with the collection details of all accessions (i.e. collection date and location) electronically stored. On receipt of new seed batches some level of processing is undertaken to extract seeds from fruits through drying and/or threshing, with larger nonseed material removed using a range of different equipment and approaches. The seedbank contains multiple accessions (each collection year is kept separate) of approximately 200 species from approximately 40 families, representing a significant proportion of the floristic diversity found across Hanson's southwest mine operations (Table S1). While Hanson maintain a standing stock of approximately 700 kg of seeds, just 20 species account for over 90% of their holdings by mass, including *Macrozamia fraseri* which is by far the largest seed stored (thousand seed weight [TSW] = ~18,000 g). The remaining approximately 180 species within the seedbank make up just 10% (~70 kg) of the total seed holdings, though most of these taxa such as *Anigozanthos*, *Kunzea*, *Stylidium*, and *Trachymene* spp. have very small seeds (TSW ≤ 1 g). Indeed, when species are ranked according to the calculated number of seeds stored, Myrtaceae spp. are by far the most numerous in the seedbank, accounting for 17 out of the top 20 species in terms of the largest number of seeds held in the collection, with all of the top 20 species (in terms of total number of seeds held) having a TSW of <3.0 g. Consequently, the total number of seeds in the bank is still substantial for many species even when small amounts are maintained in storage (e.g. *Stylidium brunonianum*—8.9 g stored = ~445,000 seeds) and more than sufficient to support large-scale restoration efforts over several years, seeding at a rate of 5,000 to 20,000 seeds per hectare (Tables 1 & S1)

Box 2 *Macrozamia fraseri* (Zamiaceae).

For Hanson, one of the more interesting species of restoration importance is the Zamia palm (*Macrozamia fraseri*) which is a species of cycad (gymnosperm). *Macrozamia fraseri* has been regularly used for direct seeding of Hanson restoration sites (Table 1) with consistently poor outcomes. To understand more about the underlying impediments preliminary studies were implemented on stored *M. fraseri* seeds of different ages (4 months to 6 years old) to understand more about the basic seed biology of this species. Results have been enlightening, as while seeds were shown to be germinable under some conditions (albeit very slowly—3–6 months), significant barriers to conventional storage conditions (~5°C and 20%) were identified. *Macrozamia fraseri* seeds were found to rapidly lose viability when stored under standard seedbanking conditions (5°C and 20% RH) with no viable seed found in accessions older than 3 years (Fig. 2). As well, fresh (<6 months old) viable seeds (Fig. 2A) were found to have a very high moisture content (45.8 ± 5.4%—fresh weight basis) which dropped significantly to <36% for accessions older than 3 years that were determined to be nonviable (Fig. 2B). When the fresh seed moisture content of *M. fraseri* is compared against data from a range of desiccation-sensitive rainforest species (Sommerville et al. 2021—fig. 7A) the *M. fraseri* values neatly fall within the interquartile range (~43–58%) of the desiccation-sensitive species. All data so far collected strongly suggest that seeds of *M. fraseri* are desiccation sensitive, which is unusual in a Mediterranean environment (Wyse & Dickie 2017) and imposes novel storage approaches and restoration requirements (Norman & Mullins 2005). Based on these new insights different methods are currently in development to facilitate the return of *M. fraseri* to restoration sites that accommodate their unusual seed biology. These are centered around developing better short-term seed storage techniques and greenstock production systems rather than relying solely on direct in situ seeding of conventionally stored seeds.

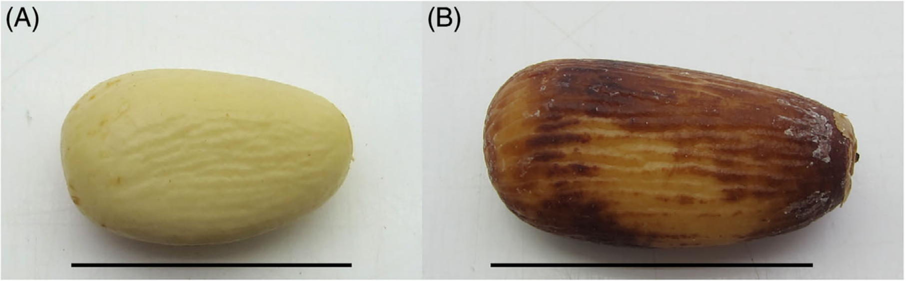

Figure 2. Intact endosperms of *Macrozamia fraseri* after the removal of the outer sarcotesta (red fleshy layer), sclerotesta (hard bony layer) and endotesta (inner membranous layer). (A) Viable endosperm derived from a seed stored for approximately 4 months (2020 collection) at 5°C and 20% RH. (B) Nonviable endosperm from a seed stored for approximately 3 years (2017–2020) under similar storage conditions. Scale bar = 35 mm.

Table 3. Assignment of the approximately 201 species currently held within the Hanson seedbank to one of four germination classes. Classes 1 and 2 consist of species where seed dormancy is either not present or is well understood (and consequently can be reliably broken). Class 3 consists of species that may or may not have significant germination or dormancy blocks. Class 4 consists of well-identified highly problematic species with complex and problematic seed dormancy.

Class	*Description*	*Percentage of Species*
1	Nondormant—capacity to germinate on demand	23.4% (47 spp.)
2	Well-understood dormancy—capacity to germinate on demand	31.3% (63 spp.)
3	Potential dormancy/germination issues—limited information available	28.4% (57 spp.)
4	Significant germination problems (deeply dormant)	16.9% (34 spp.)

have physiological seed dormancy and depending on the species these may be easy to resolve (i.e. Asteraceae) or in some cases are likely to be exceptionally difficult to germinate (i.e. drupaceous Ericaceae; Table 2) (Merritt & Turner 2016). Physical seed dormancy is likely to occur in approximately 15% of species (Table S1).

Defining Germination Capacity by Germination Class

To assess the utility of the Hanson seedbank to obtain germination-on-demand, the species inventory was divided into four broad germination classes ranging from easy to exceptionally difficult to germinate (Tables 3 & S1). When combined, class 1 (nondormant species) and class 2 (species with well-understood and resolvable seed dormancy) account for approximately 54.7% of all the species held in the seedbank. This is the species fraction where germination-on-demand can be achieved based on current experience and information (Rokich et al. 2002; Merritt & Turner 2016; Rokich 2016). Most of these species are either nondormant, so germinate readily when provided with the right environmental conditions or possess a form of seed dormancy that is well understood and easy to overcome such as physical seed dormancy, nondeep physiological seed dormancy, or morphological seed dormancy (Kildisheva et al. 2020).

Nevertheless, 45% of species which comprise both germination classes 3 and 4 remain either poorly studied, display erratic germination, or have intractable seed dormancy that is yet to be reliably resolved (Table 3) (Merritt et al. 2007). For example, 57 species were assigned to germination class 3 which accounts for 28% of all the species within the Hanson seedbank. These 57 species belong to 18 families with most species belonging to the Myrtaceae (17 species), Proteaceae (9 species), and Poaceae (6 species) (Table S1). Considerable information is already known for several of these families so aspects of the general seed biology can be obtained from literature on related species (Baskin & Baskin 2014). Yet there are several families assigned to this class for which little information is known about the seed biology of Australian taxa including the Commelinaceae, Haloragaceae, and Phyllanthaceae (Baskin & Baskin 2014).

Germination class 4 contains taxa well recognized as being difficult to germinate on demand such as *Persoonia saccata*, and drupaceous Ericaceae (i.e. *Styphelia* spp.) (Merritt & Turner 2016) (Table S1). A number of these species possess seeds that are dispersed in either dry indehiscent fruits (i.e. *Stirlingia latifolia*), or stony endocarps (*P. saccata*) and in most cases are known to form a persistent soil seedbank that is stimulated to germinate by either fire (i.e. smoke and/or heat) or physical soil disturbance which cannot be reliably replicated under either laboratory or nursery conditions at present (Rokich et al. 2000; Koch 2007*b*).

Discussion

Restoration seedbanks and their supporting workflow are much more than simply a makeshift repository for seeds prior to their deployment for ecological restoration. There are many places in the seed supply chain where targeted interventions and improvements can be applied to enhance germination and establishment capacity. Mining companies such as Hanson and their seed-based restoration programs are in many ways at the forefront of these efforts as they have been reinstating biodiverse native plant communities for decades using well-established iterative processes. Nevertheless, it is clear that significant knowledge gaps still remain particularly around seed dormancy and the provision of "germination ready" seeds as outlined in this paper.

These knowledge gaps should guide future research priorities as a way to broaden the suite of species available for direct seeding activities (Kildisheva et al. 2020; Pedrini & Dixon 2020).

Hanson direct seed up to 24 species across their restoration sites each year as a result of many years of field emergence studies and modeling. The species seeded and quantities sown depend on the outcomes to be delivered and are adjusted accordingly, and are also amended where topsoil is unavailable or deemed poor quality (i.e. post pine—Stanbury et al. 2018). Hanson sow seeds at a rate of 1–2 kg/ha which is at the lower end of seeding rates reported elsewhere, that is, Strehlow et al. (2017) (1.5–8.0 kg/ha), Elzenga et al. (2019) (4 kg/ha), and Merritt and Dixon (2011) (2–7 kg/ha).

Provenance-appropriate native seeds are seasonally collected through an established supplier network of external contractors. This workforce has intimate knowledge of the local floristic communities as seeds used for restoration are all wild collected from sites near to where seeds will be used for future restoration. Good floristic knowledge from site surveys of the predisturbed *Banksia* woodland guides and informs the seed procurement program (Rokich 2016; Erickson & Halford 2020). Seeds are harvested according to the rules and regulations associated with commercial seed collection licenses issued by the regulatory agency, the Department of Biodiversity Conservation and Attractions in Western Australia, with strict compliance enforced at all stages (Department of Biodiversity Conservation and Attractions 2018).

During storage, seeds are maintained at cool temperatures (~5°C) and low relative humidity (20%) which is broadly in line with current seedbanking standards for orthodox seeds (De Vitis et al. 2020; Pedrini & Dixon 2020). Nevertheless, there are occasional exceptions, with storage conditions and restoration approaches needing modification to better align with the seed biology of some native species to improve germinability and restoration success. For example, the seeds of the cycad *Macrozamia fraseri* have been found to be desiccation sensitive and appear to rapidly lose viability when stored for longer than 12 months and thus may be better suited for the production of greenstock for field planting (Turner unpublished results). As well, the seeds of species belonging to the Asteraceae (e.g. *Hyalosperma* and *Podotheca* spp.) and Poaceae (e.g. *Amphipogon* and *Austrostipa* spp.) may benefit from temporary warm dry storage (i.e. after-ripening) to overcome nondeep physiological dormancy (Baskin & Baskin 2014).

Seeds are stored within the seedbank from a few months to more than 5 years, thus potentially providing several years' worth of seed accessions for species central to restoration activities. Many of the species in storage are likely to be relatively longer lived such as Casuarinaceae, Fabaceae, Myrtaceae, and Proteaceae though there is a considerable number of species (>20 species) from families recognized as containing potentially shorter-lived taxa as well, such as the Asteraceae, Poaceae, and Stylidaceae (Merritt et al. 2021). Nevertheless, given the relatively rapid turnover of seed stock and the cool, dry storage conditions this is unlikely to cause significant problems such as declines in seed quality or viability though additional work is needed to confirm this (Merritt et al. 2021).

The Hanson seedbank is diverse in species and families, representing considerable floristic variation across Hanson's mining leases. When compared to other restoration seedbanks such as those operated by Alcoa Australia (100–200 species) (Cromer & Norman 2006; Koch 2007*a*, 2007*b*) or an iron ore mine in the mid-west of Western Australia (~50 species) (A. Cross, personal communication, 2021) the diversity of species held is high, which has implications in terms of seed processing, seed quality, viability, storage requirements, longevity, germination, and seed dormancy (De Vitis et al. 2020; Frischie et al. 2020; Pedrini & Dixon 2020). Nevertheless, just 20 species in the seedbank account for over 90% of the seed holdings by mass, with approximately 12 of these species contributing to the bulk of the seed mixes used across Hanson's restoration sites each year as part of their direct seeding program.

Consequently, there is an increasing need to understand both the germination requirements and dormancy mechanisms of all the species in the Hanson seedbank (i.e. germination classes 3 and 4), not just those taxa which are currently utilized for direct seeding which are drawn from germination classes 1 and 2. It is germination class 3, which accounts for approximately 28% of all species currently in storage where we feel most short-term research effort should be placed to establish a solid understanding of their overall seed biology as a way to enhance future restoration activities. It is possible, even likely, that many of the species assigned to germination class 3 may prove to be germination compliant once their seed biology is better understood and key aspects of their attributes (i.e. seed quality, water permeability, germination responses to indicative conditions, and germination stimulants) are taken into account when developing effective and reliable techniques for germination-on-demand (Kildisheva et al. 2020).

On the other hand, species assigned to germination class 4, which account for 17% of species in the Hanson restoration seedbank, are more problematic to germinate-on-demand, with no cheap and reliable propagation protocols available at present (Merritt et al. 2007; Merritt & Turner 2016). Nevertheless, from a restoration perspective these are still important to include as part of the seedbanking program to build future restoration capacity in terms of boosting species diversity in anticipation that solutions to their current intractability are discovered (Merritt et al. 2007). Many of these species possess seeds that are known to form a persistent soil seedbank that is stimulated to germinate by either fire or physical disturbance of the soil potentially many years after dispersal (Rokich et al. 2000; Merritt et al. 2007). Consequently, species assigned to germination class 4 may require intensive multiyear research to develop reliable seed-based propagation approaches with seed burial and retrieval trials, a critical component of the experimental framework (Baskin & Baskin 2014). Such experiments will help establish when germination events occur naturally, the specific conditions that support in situ germination, the rate of seed viability decline while in the soil, and whether stimulants such as smoke are needed to promote germination (Rokich & Dixon 2007).

In summary, restoration seedbanks are critical in supporting integrated approaches for the restoration of post-mining environments (Cromer & Norman 2006; Koch 2007*b*; Erickson et al. 2017). Yet, as demonstrated here, there is still work to be done in unlocking their full potential to supply the growing needs of the global restoration movement especially in mine land restoration programs (Koch 2007*b*; Merritt & Turner 2016). A better understanding of the seed biology and seed ecology of banked species will inform both the storage approaches that need to be adopted, as well any pretreatments and dormancy alleviation required to maximize seed germination and establishment when deployed to restoration sites (Kildisheva et al. 2020; Pedrini & Dixon 2020). Although this case study focused on the unique *Banksia* woodlands of the southwest of Western Australia, the approach used is a useful template to identifying and resolving knowledge gaps as a means for improving the capacity of restoration seed banks to provide reliable and cost-effective seed-based restoration solutions.

Acknowledgments

The authors acknowledge the Wadjuk people of the Noongar nation, traditional owners of the land on which this work was undertaken, and pay their respects to Elders past, present, and emerging. This research was funded under the Australian Research Council Industrial Transformation Training Centre for Mine Site Restoration (ICI150100041). Hanson was a partner organization with the CMSR, with Hanson employee V.N. a contributing partner investigator within the center. Jason Stevens and David Willyams are thanked for providing usful comments on early drafts of the manuscript. The authors offer their gratitude to the five anonymous reviews that provided insightful and constructive comments. Open access publishing facilitated by Curtin University, as part of the Wiley - Curtin University agreement via the Council of Australian University Librarians. [Correction added on 18 May 2022, after first online publication: CAUL funding statement has been added.]

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Supporting Information

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

Table S1. Summary of various seed attributes of the species currently held in the Hanson Restoration Seedbank.

Coordinating Editor: Peter Török

Received: 9 November, 2021; First decision: 4 December, 2021; Revised: 2 March, 2022; Accepted: 4 March, 2022