



PRACTICAL ARTICLE

Dormancy and germination: making every seed count in restoration

Olga A. Kildisheva^{1,2} , Kingsley W. Dixon³, Fernando A. O. Silveira⁴, Ted Chapman⁵, Alice Di Sacco⁵, Andrea Mondoni⁶, Shane R. Turner^{3,7,8}, Adam T. Cross³ 

From 50 to 90% of wild plant species worldwide produce seeds that are dormant upon maturity, with specific dormancy traits driven by species' occurrence geography, growth form, and genetic factors. While dormancy is a beneficial adaptation for intact natural systems, it can limit plant recruitment in restoration scenarios because seeds may take several seasons to lose dormancy and consequently show low or erratic germination. During this time, seed predation, weed competition, soil erosion, and seed viability loss can lead to plant re-establishment failure. Understanding and considering seed dormancy and germination traits in restoration planning are thus critical to ensuring effective seed management and seed use efficiency. There are five known dormancy classes (physiological, physical, combinational, morphological, and morphophysiological), each requiring specific cues to alleviate dormancy and enable germination. The dormancy status of a seed can be determined through a series of simple steps that account for initial seed quality and assess germination across a range of environmental conditions. In this article, we outline the steps of the dormancy classification process and the various corresponding methodologies for ex situ dormancy alleviation. We also highlight the importance of record-keeping and reporting of seed accession information (e.g. geographic coordinates of the seed collection location, cleaning and quality information, storage conditions, and dormancy testing data) to ensure that these factors are adequately considered in restoration planning.

Key words: dormancy classification, dormancy cycling, seed fill, seed quality, seed testing

Implications for Practice

- Seed dormancy occurs in more than 50% of wild plant species. The lack of understanding and consideration of dormancy and germination traits in restoration planning often contributes to plant establishment failure.
- Seed quality, dormancy, and germination traits can be assessed following a series of standard seed testing steps.
- To improve outcomes, considerations outlined in this article should be a standard component of any seed-based restoration planning.

Introduction

Unlike crop plants that are subject to extensive breeding, the seeds of many wild plant species exhibit some degree of seed dormancy. Seed dormancy regulates germination through various physical and/or physiological means imposed by the seed coat, or within the embryo (Baskin & Baskin 2014). Dormancy can facilitate the persistence of seeds through unfavorable periods ensuring germination occurs when environmental conditions are most likely to lead to seedling establishment. Freshly collected, viable seeds are considered to be dormant if they do not germinate within 4 to 6 weeks under conditions that can be considered ideal (e.g. sufficient moisture and suitable

temperatures) to support the germination process (Baskin & Baskin 12004b; Baskin & Baskin 12004c).

The loss of dormancy is driven by the detection of environmental cues such as temporal changes in moisture and temperature, which seeds can “sense” through a number of mechanisms (Baskin & Baskin 2014). However, for some species with complex germination requirements, even after dormancy has been

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¹Verdant Consulting Group, LLC, Seattle, WA 98115, U.S.A.

²Address correspondence to O. Kildisheva, email olga.kildisheva@gmail.com

³Centre for Mine Site Restoration, School of Molecular and Life Sciences, Curtin University, Bentley, WA 6102, Australia

⁴Department of Genetics, Ecology and Evolution, Federal University of Minas Gerais, Belo Horizonte, Brazil

⁵Conservation Science, Royal Botanic Gardens Kew, Millennium Seed Bank, Wakehurst, Ardingly, West Sussex RH17 6TN, UK

⁶Department of Earth and Environmental Science, University of Pavia, Pavia, Italy

⁷Kings Park Science, Department of Biodiversity, Conservation and Attractions, Kings Park, WA 6005, Australia

⁸School of Biological Sciences, University of Western Australia, Crawley, WA 6009, Australia

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lost, germination will only ensue under specific environmental conditions such as light or dark (indicating the degree of openings or disturbance in vegetation) or in response to chemical cues such as smoke compounds, nitrates, or ethylene (indicating favorable germination conditions). The requirements for dormancy alleviation and germination stimulation vary between seed dormancy classes, and in some cases between different populations of the same species (Ellison 2001; Tieu et al. 12001*b*).

When seed dormancy and germination requirements of species are not adequately considered in restoration planning, they can lead to high levels (more than 90%) of plant establishment failure and seed wastage (James et al. 2011; Merritt & Dixon 2011; Commander et al. 2013; James et al. 2013). To improve restoration success and achieve project goals at a reasonable cost, every seed must have the best opportunity to germinate and establish (Turner et al. 2013).

Worldwide, 50–90% of wild plants produce seeds that are dormant upon maturity, with the specific dormancy traits contingent on factors including environmental conditions, geographic distribution, growth form, and genetics (Baskin & Baskin 2014). Seed dormancy is an evolutionary adaptation that can benefit long-term survival under intact natural conditions (Willis et al. 2014), but in the context of restoration where rapid plant re-establishment is critical to prevent further degradation, dormancy can pose a significant challenge (Turner et al. 2013). Because seeds may take several seasons to lose dormancy, when sown onto a restoration site following disturbance, they become susceptible to seed predators and pathogens, viability loss, and weed competition—which can lead to plant re-establishment failure. This can significantly reduce restoration success, particularly when working with more challenging species and complex plant communities (Broadhurst et al. 2016). Additionally, specialized dormancy and germination requirements can also constrain efforts to increase the scale and diversity of *ex situ* native seed production, limiting the ability of practitioners to work with multiple species at larger scales (Miller et al. 2017; Ladouceur et al. 2018). Understanding and considering seed dormancy and germination traits in restoration planning can help ensure seeds are managed in a way that promotes germination during periods that are most conducive to plant recruitment. The ability to define the seed dormancy class is the first step in determining the most effective means of dormancy alleviation and should be considered foundational knowledge for all restoration practitioners working with native seeds.

Seed Dormancy Classes

Five main classes of seed dormancy are currently recognized (Table 1), although in some cases these are further divided into sub-levels (Baskin & Baskin 12004*b*; Baskin & Baskin 12004*c*; Gama-Arachchige et al. 2013). Physiological dormancy (PD) is the most common form of seed dormancy worldwide, occurring in gymnosperms and all major angiosperm clades (or groups of species posited to have evolved from a common ancestor) (Baskin & Baskin 12003*b*; Finch-Savage & Leubner-Metzger 2006; Willis et al. 2014). The embryo of seeds with PD is fully developed (Fig. 1, Table 1) but has a low growth

potential. Due to this low growth potential, the embryo cannot overcome the mechanical constraints of the surrounding tissues (e.g. endosperm, seed coat, or fruit coat) without receiving cues from the surrounding environment. These cues initiate internal chemical signaling (resulting from changes in the ratio and sensitivity of internal seed hormones), which promotes dormancy loss and germination (Baskin & Baskin 12004*b*). PD is often alleviated by periods of cold or warm stratification or warm dry after-ripening. Three levels of PD are recognized: deep, intermediate, and nondeep (Baskin & Baskin 2014).

The outer surface of the fruit or seed coats of physically dormant (PY) seeds is typically covered by at least one (usually $\leq 200 \mu\text{M}$) layer of palisade (or palisade-like) cells (Fig. 2). These impermeable palisade layers are made up of sclereid cells that have thick lignified secondary walls, which resist water penetration into the seed (Langkamp 1987; Baskin et al. 2000; Gama-Arachchige et al. 2013). PY is released when the water-impermeable layer is degraded or damaged to the point that water uptake (imbibition) can occur. In natural conditions, this degradation often occurs in a specialized area of the seed, called the “water gap” (Baskin & Baskin 2014).

Seeds with combinational dormancy (PY + PD) have both a water-impermeable seed or fruit coat and a physiologically dormant embryo (Baskin et al. 2000; Baskin & Baskin 12004*a*). This dormancy class is relatively uncommon (Baskin & Baskin 12003*b*). Dormancy alleviation of PY + PD is a two-step process. First, it requires the impermeable palisade cell layer to be compromised to allow imbibition of water into the seed. Second, seeds must receive an environmental signal to promote sufficient embryo growth to overcome the mechanical restraint of the surrounding tissues (Baskin & Baskin 2014).

Morphologically dormant (MD) seed embryos are not fully developed at maturity (underdeveloped and small relative to the size of the endosperm) and must grow/mature prior to germination (Baskin & Baskin 12004*c*; Baskin & Baskin 2014). Embryos can be either undifferentiated (no clear structure; Fig. 3) or underdeveloped but differentiated with some rudimentary structures visible (i.e. radicle and cotyledons; Fig. 4). In seeds with MD, germination can be particularly slow even given the optimum germination conditions due to the required period of embryo development/growth prior to radicle emergence (Baskin & Baskin 12004*b*; Baskin & Baskin 12004*c*; Erickson et al. 2016).

Seeds with morphophysiological dormancy (MPD) have underdeveloped (or undifferentiated) embryos that are also physiologically dormant, and require an environmental signal to stimulate embryo growth as a precursor to final development (Baskin & Baskin 12004*b*; da Silva et al. 2007). MPD is a complex dormancy class, further subdivided into nine levels on the basis of the environmental conditions required for embryo growth (Baskin & Baskin 2014). The additional physiological component to dormancy means that radicle emergence requires significantly more time than that of seeds with MD alone (Baskin & Baskin 12004*c*; Scholten et al. 2009; Baskin & Baskin 2014; Erickson et al. 2016; Dalziel et al. 2018).

Table 1. Classes of seed dormancy, adapted from Baskin and Baskin (2014) and Finch-Savage and Leubner-Metzger (2006). A number of genera include species with unusual or unknown dormancy states that defy known approaches of dormancy release. This includes species in *Astroloma*, *Leucopogon*, *Cosmelia*, *Epacris* (Ericaceae) with drupaceous fruits; dryland nut seeded Cyperaceae; many Australian Restionaceae; *Boronia* and *Philotheca* (Rutaceae) (Merritt et al. 2007). The families listed in the table are not meant to be an exhaustive and comprehensive list, but examples of families containing some species with a particular dormancy type.

Seed Dormancy Class	Seed Characteristics	Examples of Plant Families Containing Species With a Known Seed Dormancy Class
Nondormancy (ND)	Seeds imbibe water and germinate readily (within 4 weeks) over the widest range of environmental conditions possible for the species	Amaranthaceae, Asteraceae, Begoniaceae, Brassicaceae, Bromeliaceae, Dipterocarpaceae, Fagaceae, Lauraceae, Pinaceae, Rubiaceae, Velloziaceae, Xyridaceae
Physiological dormancy (PD)	Seeds imbibe water and possess fully developed embryos with a low growth potential, sometimes in combination with a mechanical constraint from the seed/fruit covering layers	Aceraceae, Amaranthaceae, Asteraceae, Balsaminaceae, Brassicaceae, Byblidaceae, Caryophyllaceae, Commelinaceae, Cucurbitaceae, Cupressaceae, Dioncophyllaceae, Droseraceae, Drosophyllaceae, Ephedraceae, Ericaceae, Euphorbiaceae, Fagaceae, Iridaceae, Lamiaceae, Lauraceae, Lentibulariaceae, Melastomataceae, Myrtaceae, Nymphaeaceae, Oleaceae, Pinaceae, Plantaginaceae, Poaceae, Rosaceae, Rubiaceae, Rutaceae, Sapindaceae, Solanaceae, Ulmaceae, Urticaceae, Violaceae, Vitaceae
Physical dormancy (PY)	The seed or fruit coat is impermeable (preventing the uptake of water)	Anacardiaceae, Biebersteiniaceae, Bixaceae, Cannaceae, Cistaceae, Convolvulaceae, Cucurbitaceae, Dipterocarpaceae, Fabaceae, Geraniaceae, Lauraceae, Malvaceae, Nelumbonaceae, Rhamnaceae, Sapindaceae, Sarcocaulaceae, Sphaerosepalaceae, Surianaceae
Combinational dormancy (PY + PD)	The seed or fruit coat is impermeable (preventing the uptake of water) and seed embryos are physiologically dormant	Anacardiaceae, Fabaceae, Geraniaceae, Rhamnaceae, Sapindaceae
Morphological dormancy (MD)	Seeds readily imbibe water; however, embryos are underdeveloped but differentiated and require time to grow before germination	Annonaceae, Apiaceae, Arecaceae, Aristolochiaceae, Campanulaceae, Caprifoliaceae, Cycaceae, Gentianaceae, Iridaceae, Lentibulariaceae, Papaveraceae, Ranunculaceae, Rubiaceae, Sarraceniaceae, Vitaceae
Morphophysiological dormancy (MPD)	Seeds readily imbibe water but have embryos that are underdeveloped and/or undifferentiated and physiologically dormant	Allicaceae, Annonaceae, Apiaceae, Araliaceae, Ericaceae, Gentianaceae, Ginkgoaceae, Lentibulariaceae, Liliaceae, Magnoliaceae, Papaveraceae, Primulaceae, Ranunculaceae, Taxaceae, Zamiaceae



Figure 1. Internal seed morphology of *Ricinocarpos brevis* (Euphorbiaceae), a critically endangered species producing seeds with physiological seed dormancy and a fully developed linear embryo (Image: A. Fontaine).

Dormancy Cycling

The seeds of many species with PD or MPD can cycle between nondormant and dormant states (Baskin & Baskin 2014; Finch-Savage & Footitt 2017). This process occurs over weeks or months, usually in the soil seed bank. The seeds of many species are capable of cycling seasonally over many years before germination finally occurs. Dormancy cycling generally ensues in response to environmental cues (e.g. changes in light conditions or soil temperature and moisture), as these conditions become either more suitable (moving into the optimal growing season) or less suitable (moving away from the optimal growing season) to support germination (Baskin & Baskin 2004c; Duarte & Garcia 2015). Dormancy cycling has also been reported for seeds stored under constant temperature and moisture, suggesting the presence of an “endogenous rhythm” or a “biological clock” within seeds that is somewhat independent of changing environmental conditions (Froud-Williams et al. 1986; Jones



Figure 2. Internal seed morphology of *Adansonia gregorii* (Malvaceae), a species producing seeds with a folded embryo and physical seed dormancy. The water-imperious layer of cells (palisade) is located in the outer testa, which is clearly distinguishable in the insert as a lighter band just under the surface of the seed coat. The palisade layer in this species is just approximately 150 μM in thickness (Image: A. Fontaine).



Figure 3. Internal seed morphology of *Burchardia congesta* (Colchicaceae), a species producing seeds with a small undifferentiated embryo <1 mm in length compared to the rest of the seed which is >2 mm long. This species has MD (Image: A. Fontaine).

et al. 1998; Tieu et al. 12001a). Seeds that are partially through a dormancy cycle, either on their way to becoming fully dormant or on their way to becoming completely nondormant, may be conditionally dormant (Baskin & Baskin 12004b). These seeds may still be cued to germinate, but only under a much more limited set of conditions (i.e. a narrower range of temperatures) than seeds in which dormancy has been alleviated (Baskin & Baskin 2014).

Biogeographic Variation in Seed Dormancy

As seed dormancy is driven primarily by environmental factors, it is perhaps unsurprising that studies have shown regional

patterns in seed dormancy across all of the world's major terrestrial biomes (Baskin & Baskin 12003b; Baskin & Baskin 2014). Seed dormancy is most common in species from ecologically challenging, climatically unpredictable, or highly seasonal regions: the percentage of species with some form of seed dormancy ranges from ca. 50% in tropical rainforests, ca. 57% in tropical semi-evergreen forest, to over 90% in cold deserts (Baskin & Baskin 12003b; Baskin & Baskin 2014) and old climatically stable environments such as southwest Australia (Merritt et al. 2007; but see Dayrell et al. 2017). Species with PY are more common in ecosystems with marked wet and dry seasons (e.g. matorral and cold deserts; Rubio de Casas et al. 2017), while species with underdeveloped embryos are more common in mesic environments such as broadleaved evergreen forests (MD) or deciduous forests (MPD) (Baskin & Baskin 2014). PD is well represented in species from most biomes, but subtle differences in germination strategies can occur even between relatively similar ecosystems depending upon their environmental conditions. For example, species from alpine and subarctic habitats most commonly have PD that is alleviated by cold stratification over winter, with germination occurring in early summer when the risk from frost is lowest (Niederfringer Schlag & Erschbamer 2000; Schwienbacher et al. 2011; Marcante et al. 2012; Körner 2013; Bernareggi et al. 2015; Tudela-Isanta et al. 12018a; Tudela-Isanta et al. 12018b). However, for populations of the same species distributed across an environmental gradient, germination and dormancy patterns may differ. For example, subarctic populations may be less dormant, germinate more readily under optimal conditions, and may have a warmer suitable temperature range for germination compared to alpine populations (Mondoni et al. 2018). Similar patterns exist in many other bioregions (Baskin & Baskin 2014).

Intra- and Inter-specific Variation in Seed Dormancy

The depth of seed dormancy (or the extent to which germination is inhibited in the absence of appropriate dormancy alleviation conditions) can vary considerably between families, genera, species, and within individuals (Thomas et al. 1979; Langkamp 1987; Baskin & Baskin 2014; Barga et al. 2017; Cross et al. 2018; Seglias et al. 2018). Species within the same family often possess different seed dormancy classes. For example, the Rubiaceae contains species with seeds that are nondormant (*Ochreinauclea missionis*; Jose et al. 2002), PD (*Gardenia ovularis*; Osunkoya & Swanborough 2001), MD (*Coffea arabica*; da Silva et al. 2004), and MPD (*Amaioua corymbosa*; Sautu et al. 2007). Within a single species, seeds generally fall under the same dormancy class, but the proportion of seeds in which dormancy has been induced and the depth of that dormancy may vary on a population or individual plant level, as a result of biogeography, genetic factors, and the environmental conditions experienced during seed development and maturation (Andersson & Milberg 1998; Tieu et al. 12001b; Donohue 2009; Bernareggi et al. 2015; Liyanage & Ooi 2015; Liyanage & Ooi 2016). Finally, in some cases, the proportion of dormant seeds may also vary within the same inflorescence (Baskin & Baskin 2014). For example, in many



Figure 4. Internal morphology of a morphologically dormant (MD) seed of *Clematis linearifolia* (Ranunculaceae), a species producing seeds with a small, underdeveloped linear embryo (<1 mm in length; image on the left). The embryos can grow to >5 mm before radicle emergence occurs (image on the right). The embryo requires sufficient time to grow prior to germination, and, as a result, the sowing window must account for the period required for the embryo to reach maturity, which can only occur under specific soil moisture and temperature conditions (Image: A. Fontaine).

species of Asteraceae, the achenes produced by the central disc (tubular) flowers may be more or less dormant than those produced by the peripheral (ligulate) flowers (Marks & Akosim 1984; Brandel 2007).

Identification of Seed Dormancy

Restoration practitioners must be able to correctly assign seed dormancy classes because treatments to alleviate seed dormancy are specific to each class (Silveira 2013; Erickson et al. 2016; Kildisheva et al. 2018a; Kildisheva 2019). Applying the wrong treatment can at best result in failure to break dormancy and at worst kill the seeds. In addition, if seeds are broadcast to field sites, sufficient time is needed to ensure dormancy release is followed by favorable soil moisture and temperatures to enable germination to proceed.

By undertaking simple trials (i.e. seed quality, germination, embryo, and imbibition testing) using readily available materials, seeds of most species can be easily assigned to one of the five dormancy classes (Figs. 5 & 6). This information is generally sufficient to inform and facilitate better seed management and restoration planning. In some complex cases, however, subsequent classification of seed dormancy to sub-levels may be needed and can be more involved, requiring a series of experimental studies (Baskin & Baskin 2004c; Hilhorst et al. 2010; Hilhorst 2011).

Seed Quality Determination

Seed fill and viability should be assessed prior to beginning a seed dormancy investigation (Dayrell et al. 2017) and should ideally be conducted on representative samples both at the beginning and the conclusion of germination testing. The methods to achieve this include cut testing, x-ray (fill only), and tetrazolium evaluation (Bonner & Karrfalt 2008; Luna

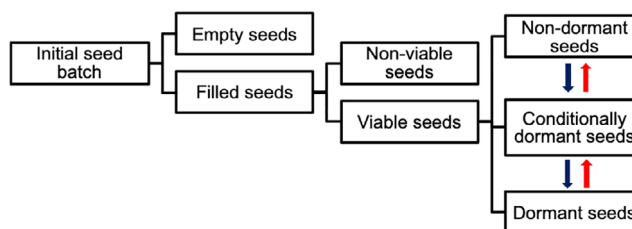


Figure 5. A framework that outlines key factors that should be considered prior to commencing seed dormancy classification. Confounding factors such as empty (embryo-less) seeds and nonviable seeds are discarded (unlike the International Rules for Seed Testing standards [ISTA 2020]) to accurately determine the percentage of dormant seeds. The red arrows indicate the path of dormancy loss whereas the blue arrows indicate the path of secondary dormancy acquisition (modified from Baskin & Baskin 2014).

et al. 2009). The percentage of unfilled, damaged, embryo-less or nonviable seeds must be reported in order for accurate estimates of percentage of dormant seeds (Fig. 5; see Frischie et al. 2020) for more details.

Germination Testing

The next step in classifying seed dormancy is to establish whether freshly collected seeds (within 2 weeks of seed collection; Baskin & Baskin 2004a; Baskin & Baskin 2004c; Baskin et al. 2006) germinate readily over a broad range of environmental conditions (Finch-Savage & Leubner-Metzger 2006). Seeds should be incubated on a neutral medium (e.g. moist filter paper or water agar), under a wide range of experimental temperatures that simulate conditions of the natural environment where the species occurs, for at least 4 weeks. The number of germinated seeds should be counted periodically, with germination determined by the protrusion of the radicle from the seed coat, to a length of at least 2 mm. If a large proportion (>75%)

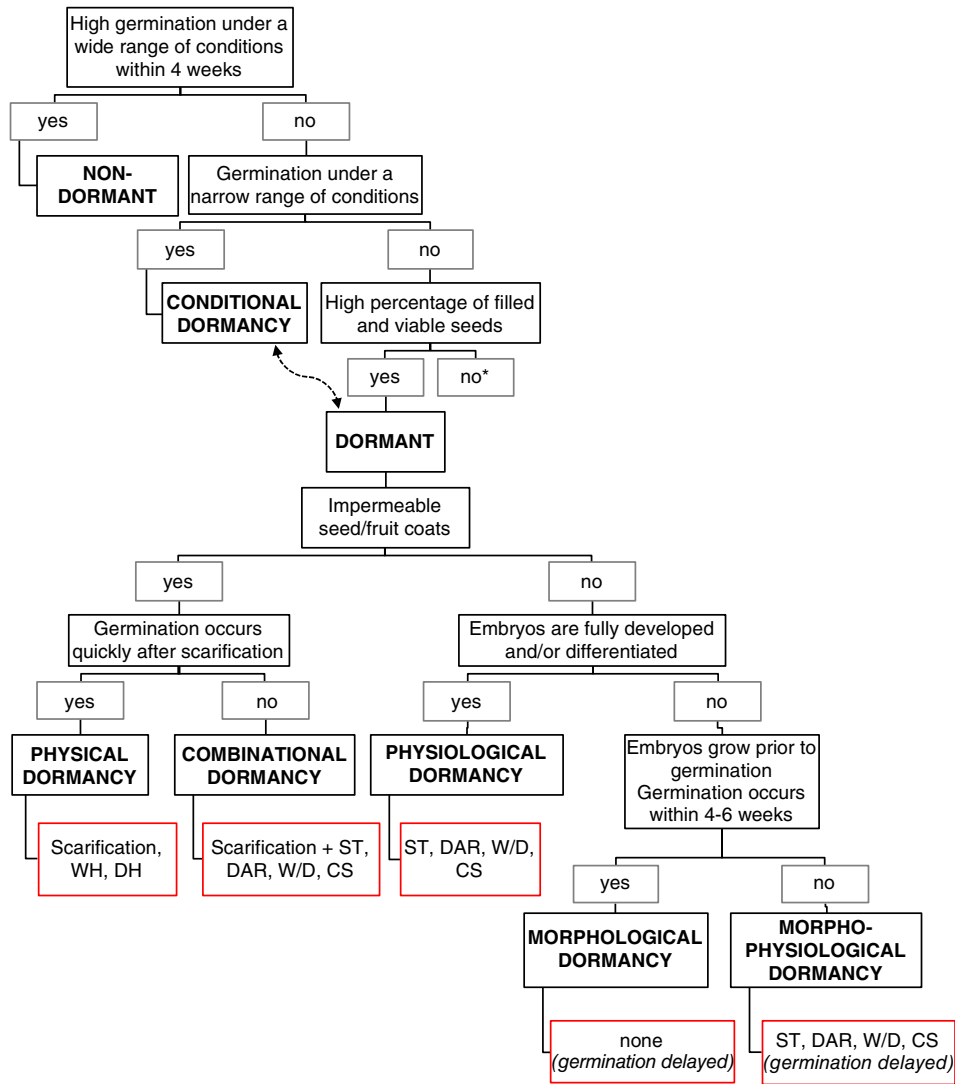


Figure 6. A decision tree for determination of seed dormancy classes following the classification system of (Baskin & Baskin 12004c). The first step is to determine whether seeds are nondormant, conditionally dormant, or dormant. Germination assessment should be based on a 4-week period after collection. The asterisk indicates problems with seed quality that preclude accurate dormancy classification. Subsequently, it may be necessary to determine the classes of primary seed dormancy to understand the appropriate action needed for dormancy alleviation (shown in the red boxes), where CS—chemical stimulants (e.g. ethylene, gibberellic acid, karrikinolide), DAR—dry after ripening, DH—dry heat (placement in >90–100°C environment), ST—warm/cold stratification, W/D—wet/dry cycling, WH—wet heat (submergence in 70–90°C water). The dashed line indicates the potential for dormancy cycling; however, this only relates to seeds with a physiological dormancy component (physiological, combinational, and morphophysiological dormancy).

of viable seeds germinate in less than 4 weeks over a wide range of temperatures, they are considered to be nondormant (Erickson et al. 2016). Conversely, if germination is low or does not occur across the tested range of conditions seeds may be dormant.

Imbibition Testing and Scarification

If dormancy is suspected, imbibition testing should be undertaken to determine whether seed/fruit coats are water-permeable (Silveira et al. 2012). Water-impermeable seeds are physically dormant and will require scarification and subsequent germination testing to determine if physiological dormancy is also

present. If seeds are able to absorb water but have poor germination, such seeds will require a detailed inspection of embryo development. In such cases, fully developed and/or differentiated embryos indicate physiological dormancy (Fig. 6).

In the case of water-impermeable seed/fruit coats, monitoring germination following scarification is needed to classify seeds as having physical dormancy or combinational dormancy (Fig. 6). Physically dormant seeds will germinate rapidly and to a high extent after scarification. If germination is low even after scarification, this implies poor growth potential of the embryo induced by physiological dormancy; such seeds have combinational (physical + physiological) dormancy (Baskin & Baskin 2014; Kildisheva et al. 2018a).

Embryo Measurements

The extent of embryo development in mature seeds can further help identify the dormancy class. Dissecting seeds under a stereomicroscope and measuring embryo:seed length ratio (Forbis 2010; Erickson et al. 2016), is typically sufficient to determine the status of embryo development. If embryos are underdeveloped (length of the embryo increases prior to the point of radicle emergence) and/or undifferentiated (not differentiated into organs; Fig. 6), then monitoring embryo growth inside the seed periodically (e.g. every few days) is required (Baskin & Baskin 2014). If embryo growth leads to germination, seeds are morphologically dormant. Alternatively, when embryo growth is detected but germination remains low within 4 to 6 weeks, this may indicate that seeds have morphophysiological dormancy (Baskin & Baskin 2014; Erickson et al. 2016).

Seed Dormancy Alleviation

Determining the Approach

In the context of restoration, assuming that dormancy loss will occur naturally within the desired timeframe often results in seed losses and establishment failures (Broadhurst et al. 2016; Erickson et al. 2016; Erickson et al. 2017; Kildisheva 2019). Thus, relieving dormancy to promote greater and more predictable germination is generally beneficial, assuming that sowing occurs at an appropriate time to support seedling emergence and survival.

The process of determining the optimal methods for dormancy release should be based on the dormancy class and consider the phenology of the species as well as the environmental conditions experienced by seeds during maturation, dispersal, and germination. Where the environmental conditions for a particular plant population are not known, climate databases like WorldClim (Fick & Hijmans 2017) can be a useful tool.

Existing germination data for the same or related species can also provide valuable clues about potential dormancy behavior and alleviation requirements. For example, species with PY are known in a relatively restricted number (ca. 18) of families (Table 1) and scarification of the water-impermeable seed coat will often enable germination in species that belong to one of these families. Physiological dormancy, however, occurs far more widely across taxa and dormancy alleviation requirements for these species are closely linked to the climatic conditions (Willis et al. 2014; Seglias et al. 2018). Species-specific information, though limited, is available in the published literature (Baskin & Baskin 2014) and on RBG Kew's Seed Information Database (RBG Kew 2018). Related species are a useful, but not infallible, reference, as dormancy alleviation and germination requirements can vary within families, genera, as well as within and between populations and individuals of the same species (Baskin & Baskin 2014).

When little germination information exists for a particular taxon, or when the sequence of conditions needed to relieve dormancy in water-permeable seeds is unclear, the 'move-along' approach may be useful (Baskin & Baskin 12003a). This double germination phenology study is simple to carry out, requires a

small number of seeds, and can provide key germination information quickly.

In the 'move-along' experiment, freshly collected seeds are placed on agar plates, moist filter paper, or sand and cycled through a series of temperature regimes designed to replicate natural conditions. For temperate species, these conditions would represent the typical length of spring, summer, autumn, and winter seasons. Samples are split into groups, some begin the cycle with the summer and others with winter temperatures, while control samples remain at each temperature throughout the experiment (Baskin & Baskin 12003a). The point within the temperature cycle at which dormant seeds germinate indicates whether cold stratification, warm stratification, or a sequence of both is required to break dormancy. The conditions used in the move-along experiment can be modified to fit any bioregion, for example to include periods of dry after-ripening, drying and re-wetting, or be continued through multiple cycles over more than 1 year (Chia et al. 2016; Kildisheva 2019).

Existing Dormancy Alleviation Techniques

Many dormancy alleviation techniques have been developed, with the choice of technique reflecting the class of dormancy and environmental conditions that seed would naturally experience (Table 2). More information is available in the Kew's Technical Information Sheets (Davies et al. 12015a; Davies et al. 12015b). Whilst these techniques are well established in laboratory or nursery settings, their application and effectiveness in field scenarios and at restoration scales is less understood (Broadhurst et al. 2016). Some treatments can be scaled up (and mechanized)—scarification with sandpaper or a pneumatic scarifier, wet and dry heat, percussion, or acid scarification can be applied to large quantities of seed to break PY (Khadduri & Harrington 2002; Kimura & Islam 2012; Mondoni 2013; Hall et al. 2017; Kildisheva et al. 12018b), whilst flash flaming, dry after-ripening, smoke compounds, gibberellic acid, and other chemical stimulants can be applied to physiologically dormant seeds (Erickson et al. 2016; Guzzomi et al. 2016; Erickson et al. 2017; Hall et al. 2017; Lewandrowski et al. 2017). Understanding the scalability of a treatment technique is important to prevent embryo damage and ensure effectiveness. Additionally, the influence of a dormancy alleviation on germination timing must be adequately considered to increase the likelihood of survival following germination.

Reintroduction may be planned to take advantage of natural opportunities for dormancy release, for example by sowing spring germinating species in autumn (Wagner et al. 2011), but this may not be sufficient in all cases (Kildisheva 2019). Creating multiple germination niches at different phases of the restoration process may be an effective approach especially in cases where site conditions are limiting or unpredictable (Davies et al. 2018). By relieving dormancy in only a portion of a seed batch sown onto a site, managers can incorporate additional bet-hedging and ensure that some recruitment occurs within the first growing season, while maintaining the rest of the seeds in a dormant state for potential later recruitment (Kildisheva 2019).

Table 2. Summary of the most commonly used dormancy alleviation techniques based on dormancy class.

Dormancy Class	Treatment	Description
PY	Scarification	Chip (with scalpel or secateurs), file, sand, abrade, or remove a portion of the seed coat to enable water uptake (imbibition), away from the root axis to avoid damaging the embryo.
	Dry heat	Place seed in an oven (90–100°C for up to 30 minutes, time and temperature vary by species, see Erickson et al. 2016).
	Wet heat	Immerse seed in hot water (70–90°C from 30 seconds to several minutes, time and temperature vary by species, see Erickson et al. 2016).
	Acid scarification	Immerse seed in concentrated sulfuric acid for up to 120 minutes.
	Percussion scarification	Place seeds inside a metal container (adjust the container size based on distance you want the seeds to travel within container). Placed on an industrial paint shaker and run for 3–20 minutes (see Khadduri & Harrington 2002 and Mondoni et al. 2013).
	Pneumatic scarification	Place seeds inside the scarification chamber lined with sandpaper or other abrasive material (e.g. using a Mater Pneumatic Scarifier, PSS2000, OEM, Inc. attached to an air compressor). Adjust the air pressure and scarify seeds for at least 20 seconds, depending on the thickness of the seed coat (see Kildisheva et al. 2018b).
PD	Cold stratification	Expose imbibed seed to cold temperatures (<10°C), mimicking winter conditions.
	Warm stratification	Expose imbibed seed to warm temperatures (>20°C), mimicking summer conditions.
	Dry after-ripening	Place dry seed in warm, moderately humid conditions (e.g. 50–60% relative humidity) for several weeks or months, mimicking a natural dry season.
	Mechanical nicking	Remove a portion of the seed coat close to the root tip with a scalpel.
	Flash flaming	Place seeds in a rotating drum with a direct flame for several seconds (see Guzzomi et al. 2016); distance from the flame and the processing duration vary by species.
	Chemical growth stimulants	Use chemicals such as potassium nitrate (KNO ₃), gibberellic acid (GA ₃), or smoke solutions (e.g. KAR ₁ or smoke water) to stimulate germination (see Baskin & Baskin 2014; Erickson et al. 2016).
PY + PD	Combination of the above treatments	Apply multiple treatments to release physical then physiological dormancy.
MD	Provide conditions for embryo development	Place imbibed seeds at a suitable temperature for 4 weeks, using environmental conditions at the time and place of natural dispersal as a guide.
MPD	Combination of PD and MD treatments	Use environmental conditions as a guide to determine the temperature cycles required for both embryo development and physiological dormancy release.

Labeling and Reporting of Seed Dormancy Status and Dormancy Alleviation Treatments

To ensure restoration outcomes meet their objectives and quality standards, it is important to maintain accurate records of the seed dormancy status and germination requirements across seed batches using standardized methods and criteria (Silveira 2013; Frischie et al. 2020). As a minimum, the following information should be reported for each seed batch:

- *Collection site description*, including geographic coordinates, soil type, and vegetation community
- *Collection information*, including the date of seed collection, the number of fruits sampled per individual, the number of individuals sampled, an estimate of population size, and sampling strategy
- *Seed cleaning and quality information*, including any techniques used to clean seeds, the percentages of seed fill, and the number of viable seeds
- *Seed storage information*, including the length and conditions under which seeds were stored
- *Dormancy testing data*, including the results of imbibition testing, the specific environmental conditions, the duration of seed germination experiments, the details of presowing treatments, and the germination results

Conclusions

The success of seed-based restoration efforts relies on the ability of practitioners to accurately predict germination requirements and ensure these are met through natural conditions at the restoration site or appropriate artificial presowing treatments. A thorough understanding of the quality, dormancy status, and germination requirements of the seeds sown is therefore essential. This information can be readily obtained for each seed accession through seed quality assessment and dormancy classification, following a series of standard seed testing steps. Accurate records that include seed collection, quality, cleaning, storage, and dormancy information for each seed batch (maintained from seed collection to seed use) are equally critical to ensuring restoration success. The seed dormancy and germination guidelines outlined in this article should be a standard component of any seed-based restoration planning process and should be considered in conjunction with the 'International principles and standards for native seeds in restoration' (Pedrini & Dixon 2020).

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