RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

PRACTICAL ARTICLE

Seed storage: maintaining seed viability and vigor for restoration use

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Effective seed storage after sourcing (harvesting or purchasing) is critical to restoration practitioners and native seed producers, as it is key to maintaining seed viability. Inadequate seed storage can lead to a waste of both natural and economic resources when seeds of poor quality are sown. When working with native species with unknown storage behavior, general assumptions can be made based on studies on related species, and standard practices may be applied with caution; however, an investigation should be conducted to understand if specific storage requirements are needed and for how long seeds can be stored before they lose significant viability. In this paper of the Special Issue *Standards for Native Seeds in Ecological Restoration*, we provide an overview of the key concepts in seed storage and the steps to take for effective storage of native seeds for restoration use.

Key words: ecological restoration, native seed, seed banking, seed longevity, seed moisture content, seed storage behavior

Implications for Practice

- Appropriate seed storage is critical to maintain seed viability and to increase success in restoration activities.
- When working with an unknown species, the seed storage behavior should be determined using a protocol, in order to know how to properly store its seeds.
- After seed collection and before seed storage, using research-based protocols, seed moisture content should be assessed and, according to the seed storage behavior, seeds should be dried to the appropriate level of moisture content and relative humidity and packaged for storage in an appropriate airtight container.
- For orthodox species, seeds can be usually stored at −18°C for more than 5 years.
- For recalcitrant species, seeds should be stored moist at ≥10°C for less than 1 year.

Introduction

Native seeds may not always be intended for use immediately following their collection, and often need to be stored for varying amounts of time before their delivery to the restoration site or use in propagation programs. However, seeds age during storage, resulting in decline in quality and ultimately loss of viability if storage conditions are not appropriate (Harrington 1972).

The deleterious effects of seed aging occur largely due to oxidative processes (Walters et al. 2010), which can lead to deterioration of the proteins (including enzymes; Goel et al. 2003), lipids (and hence cellular membranes: Harman & Mattick 1976), RNA (Fleming et al. 2019), and DNA (El-Maarouf-Bouteau et al. 2011). All of these adversely affect cellular and metabolic integrity of seeds and seedlings (Kranner 2013). Increasing seed age can reduce germination vigor as the seed metabolic system begins to break down, resulting in seeds being slow or even unable to germinate, and poor seedling development and lower establishment for aged seeds that do germinate. Thus, effective seed storage relies on slowing down seeds' normal metabolism as much as possible without incurring damage.

Moisture, temperature, and the proportion of oxygen are key environmental factors that affect seed deterioration and loss of viability. Reducing seed moisture content (MC) to certain thresholds increases longevity in a predictable manner for approximately 90% of species (Roberts 1973). These species are classified as being "orthodox" in their seed storage requirements, and generally retain viability and germinability even

Author contributions: MD, RF conceived and edited structure and content of the manuscript; all authors contributed with content and revisions.

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doi: 10.1111/rec.13174

Contributed article in Pedrini, S., Dixon K.W. and Cross, A.T. (Eds) (2020). Standards for Native Seeds in Ecological Restoration. Special Issue 28:S3 pp: S213–S303. The Special Issue is supported by the Australian Research Council Industrial Transformation Training Centre for Mine Site Restoration (ICI150100041).

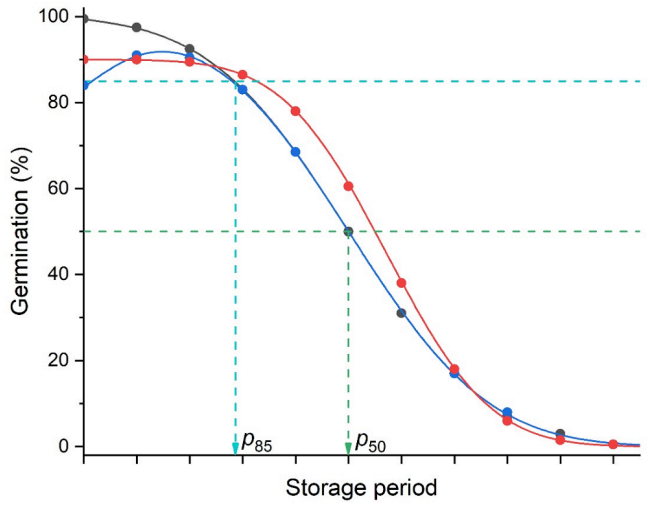

Figure 1. Seed survival curves showing the pattern of viability loss (decline in ability to germinate upon removal from storage) for orthodox seeds during storage at constant moisture content and temperature. The black symbols and line show the "typical" sigmoidal pattern. Also indicated are the time when ability to germinate falls to 85% (p_{85}), the viability standard used by most crop gene banks, and the time when ability to germinate falls to 50% (p_{50}), which is often used as a measure of seed longevity. The blue symbols and line show the survival curve for a seed lot that has some dormant seeds at the start of storage; the dormancy is broken during storage. Lastly, the red symbols and line show the survival curve for a seed lot that shows less than 100% germination at the start of storage but the viability is nonetheless maintained during the first period of storage, before declining.

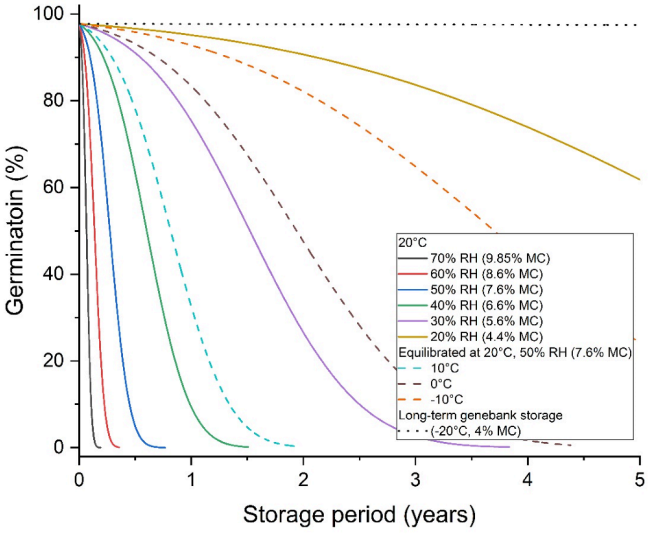

Figure 2. Predicted survival curves for seeds of foxglove (*Digitalis purpurea* L.) stored at 20°C and 20–70% RH. Also shown are the corresponding predicted seed moisture content (MC; % fresh weight) and survival curves for seeds equilibrated at 20°C and 50% RH, then sealed inside an air-tight container before storage at −10°C to +10°C. predictions are based on calculations made using the Seed viability constants menu of the Seed information database (Royal Botanic Gardens Kew 2020).

after storage for long periods under suitably dry, cool conditions (Figs. 1 & 2).

For orthodox seeds, the quantitative effects of both drying and cooling have been modeled in the improved viability equations of Ellis and Roberts (see Pritchard & Dickie 2003). In general, for each 1% decrease in seed moisture (when seed MC ranges between 5 and 14%) and for each 5°C decrease in storage temperature (between 0°C and 50°C) the life of the seed is doubled (Harrington 1972). Basic principles for orthodox seed storage are thus, low seed MC and low temperature. For their short-term storage (<18 months; Hong & Ellis 1996), a temperature between 0°C and 5°C is sufficient to maintain the viability of dry seeds. For longer periods of storage, seeds should be stored at −18°C to −20°C (Hong & Ellis 1996). Seeds should be dried to 3–7% MC (fresh weight basis; see below) and placed in airtight containers (Food and Agriculture Organization (FAO)/International Plant Genetic Resources Institution 1994).

At the other extreme, species that produce seeds that are damaged by and do not survive dehydration are classified as "recalcitrant" (Roberts 1973; Wyse & Dickie 2017). Recalcitrant storage behaviors are more prevalent in woody species from the moist tropics, and the possibilities for successful long-term seed banking of these plants at low temperature (<5°C) may be relatively limited (see Elliot et al. 2013; p 165–166). The viability of recalcitrant seeds can be maintained when the seeds are only allowed to dry slightly, if at all, with oxygen freely available, and at MCs just less than fully imbibed and above the value which results in chilling damage (the value at which the seeds are shed or in equilibrium with 98–99% relative humidity [RH]), at optimum storage temperatures which vary from about 7°C to 17°C among species of tropical origin, and between −3°C and 5°C among those adapted to temperate climates (Hong et al. 1996). The values of the lowest safe MC vary between 23 and 61.5% (fresh weight basis; Hong & Ellis 1996), and the seeds may require rewetting occasionally (Dumroese et al. 2009). Since nondormant recalcitrant seeds need oxygen to maintain their metabolism, the containers should allow gas exchange. For this purpose, 0.075–1.0 mm (3–4 mils) thickness polyethylene bags can be used, as they allow a good water vapor transmission rate for seeds (Bonner & Karrfalt 2008; see Box 1).

Between these two extremes represented by orthodox and recalcitrant seeds there is a continuum of storage behaviors, referred to as "intermediate" species (Ellis et al. 1990; Walters 2015), which exhibits characteristics of both groups and that usually tolerate drying only in part or under specific circumstances. These species may still maintain good levels (i.e. 70%) of seed viability after short- or long-term storage at 5°C (Chau et al. 2019). For restoration applications, short- and medium-term seed storage may be sufficient.

Conducting seed storage behavior experiments can help assigning a species to a particular category based on seed responses to desiccation and storage at different temperatures

Box 1 Facilities and Equipment for Seed Storage

Facilities required for seed storage depend on the amount of seeds to be stored and the expected length of storage. Most long- (10–-100 years or more) and medium-term (from 18 months to 5 or 6 years; Hong & Ellis 1996) seed storage will have cold storage facilities with a climate control (temperature and humidity) system, and temporary processing and holding facilities. Short-term seed storage (from 3 to 18 months; Hong & Ellis 1996) needs to consider moisture control, rodents, insects, fungi, and fire (Justice & Bass 1978), which also applies to longer-term seed banks. For storage at temperatures above 0°C, home refrigerators may be sufficient, provided the RH is maintained at the desired level and constantly monitored.

Freezer storage is usually maintained at −18°C to −20°C. Where possible, backup generators and safety alarms in case of power failure are beneficial risk-management tools. Depending on the size and the need of the operation, and on the resources available, solutions for cold storage can range from standard home to walk-in refrigerators and freezers.

Orthodox seeds should be dried and stored in sealed moisture-proof containers that prohibit absorption of moisture from the atmosphere. On the other hand, recalcitrant seeds need good air movement during their short-term storage. Glass and moisture-proof plastics are useful containers but note the breakage risk of glass.

Seeds can be dried using desiccants such as zeolites, silica gel, charcoal, or even rice. For example, silica gel under optimal conditions can absorb up to 33% of its dry weight.

Humidity can be monitored through the use of indicators such as humidity indicator cards, but also silica gel, if it contains indicators that turn color when a certain amount of water has been absorbed (typically when RH of the air is ≥25%). In case silica gel is used, it should not be placed in direct contact with the seeds to avoid their damage.

Setting up a well-equipped seed storage facility can be costly as it requires significant infrastructure investment, but it can also be inappropriate for small-scale restoration projects that do not require long-term seed storage and large amounts of seeds. Seed banking can be very versatile, and even low-budget equipment, if used properly, can reach international standards for seed storage protocols on a small scale. For example, the Blue Drum Kits projects provide low-tech drying equipment for seed collection, processing, and storage (Martens 2018).

when they are at full maturity, but before germination begins (Fig. 3).

Regardless of the seed storage behavior, standard practices must be followed starting from seed collection and during postharvest seed management, prior to storing seeds, in order to ensure that a seed lot of good quality (i.e. high seed viability) reaches the storage facilities. In this article, we provide a compendium of best practices, tools, and standards for the steps between postharvest seed handling and seed storage, for applications in restoration.

Postharvest Seed Management and Short-Term Storage

Seeds should be collected at maturity, at the point of natural dispersal (Hay & Smith 2003), as seeds collected too early

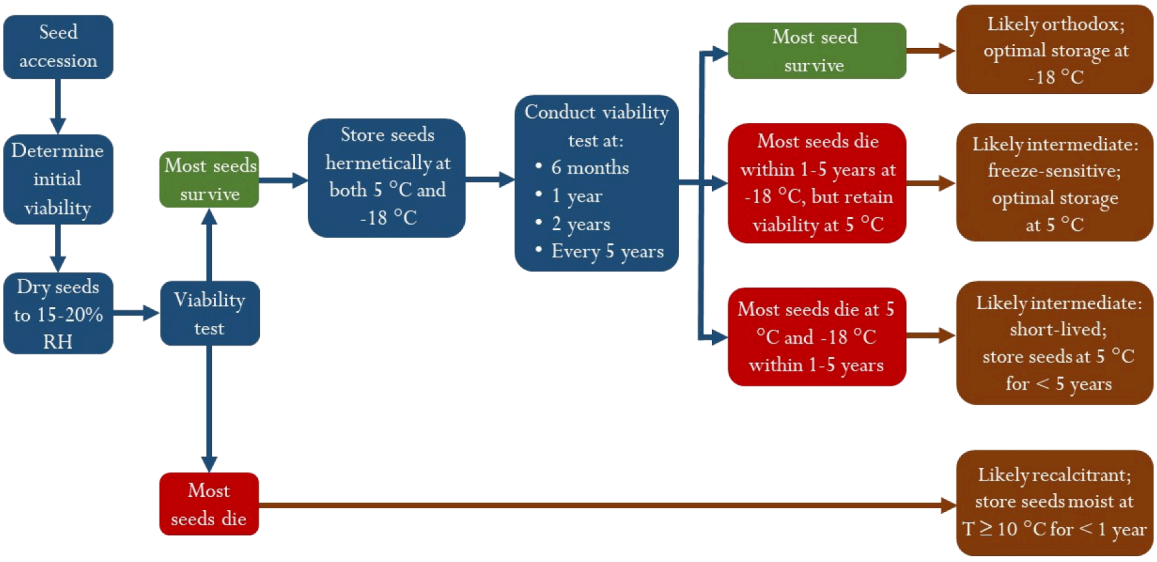

Figure 3. Protocol to determine seed storage behavior of an unknown species (adapted from Chau et al. 2019).

will be undeveloped and will lose viability when dried, or even fail to germinate altogether, whereas seeds collected too late may have reduced viability (see Pedrini et al. 2020).

The key to successful postharvest management and storage of orthodox seed collections is to understand and control the loss and absorption of moisture between seeds and the air surrounding them.

The use of a hygrometer provides a reliable, quick, and nondestructive method to measure equilibrium RH (eRH) of a seed sample, in the field or in the laboratory (Gold 2014). The seed eRH is the RH of air at equilibrium with seeds held in a sealed chamber (Gold & Manger 2014). If the hygrometer is used in the field, it should be kept in the shade, to avoid warming of the sample chamber and sensor, and seeds should be allowed at least 30 minutes in the sample chamber to reach equilibrium. Ideally, measurements should be taken under controlled conditions (e.g. 15% RH and 15°C) and with seeds at the same temperature than the sample chamber (Gold & Manger 2014). It is also possible to buy hygrometers which control temperature, although these are not suitable for field use.

After fruit/seed harvesting, depending on the maturity stage and the moisture status, the material should be handled in the most appropriate way to avoid any viability loss. For orthodox seeds from nonfleshy fruits, if seeds are collected when immature and wet (eRH of 85–100%) and still within the fruits, they should be held intact under shaded ambient conditions for 1–2 weeks for continued ripening, under either dry (daytime RH <50%) or humid (daytime RH >50%) ambient conditions; when seeds are collected at natural dispersal time (mature seeds) and the ambient conditions are dry (daytime RH <50%), if they are damp (eRH >50%), they should be left to dry in a thin layer, but if they are dry (eRH <50%), they can be held in loosely packed mesh or paper bags; in both cases (damp or dry seeds at dry ambient conditions), they should be kept drying in a well-ventilated, shaded location and stored in airtight containers overnight to minimize moisture uptake as the ambient humidity of the air can increase with cooler night-time temperatures; when either damp or dry mature seeds are collected under humid (daytime RH >50%) ambient conditions, they should be transferred to the seed bank as soon as possible or be dried with a desiccant (see Box 1) or placed in an air-conditioned room (Hay & Probert 2011).

If material is dried on carefully selected sizes of wire screen, seeds may fall through and be collected with greater ease.

Seeds that have been dried to equilibrium with ambient conditions of less than 70% RH are usually dry enough to store for short periods with minimal risk of losses due to fungal attack, but viability may drop within a year (Bradford et al. 2016). Seeds that have been dried to and kept at <50% RH will likely maintain viability for several years, while seeds maintained in a controlled dry environment at <25% RH often maintain viability for decades (Adams et al. 2016).

Fleshy fruits should be kept in aerated plastic bags until processing, with the bags opened regularly to avoid mold and fermentation; if flesh needs to be removed, this should be done using a sieve and cool running water; once cleaned and dry, these can be treated as dry seeds (Gold 2014).

Seed MC Calculation

A classic method to measure seed MC, although destructive, is to weigh the seeds both before and after drying them in the oven at 103°C for 17 hours (ISTA 2020). MC is usually calculated as a percentage of the total starting weight of the seed sample (i.e. fresh weight basis), but it may also be calculated as a proportion of the dry weight (dry weight basis). Here we provide both equations.

Fresh basis:

$$MC_{fb} = \frac{W_f - W_d}{W_f} \times 100$$

Dry basis:

$$MC_{db} = \frac{W_f - W_d}{W_d} \times 100$$

with MC_{fb} and MC_{db} being the MC calculated on fresh and dry basis, respectively; and W_f and W_d being the fresh and the dry weight of the same seed sample, respectively. In most seed studies, the basis of MC calculation is not stated and it is assumed to be on a fresh basis, according to the International Seed Testing Association (Bewley & Black 2012). Taking three or more samples as replicates for the MC determination would give a more accurate estimate of the MC of the harvested seed bulk. If the study species produces a large enough seed that could be weighed with accuracy, then the single seed could represent the replicate (and it would be better to sample five or more individual seeds). If the study species produces smaller seeds (<2 mg), and depending on the accuracy and precision of the scale used, it can be useful to first estimate the weight of 100 or 1,000 seeds and then take the measurement with a minimum of three or more replicate seed samples equivalent to 100 or 1,000 seeds, depending on seed availability.

Seed Longevity

Seed longevity is a measure of how long seeds can be stored and remain viable under a given set of conditions. Seed longevity in storage varies greatly among species (e.g. seed composition; Hong et al. 1996) and is also determined by the cumulative effect of environment during seed maturation and harvesting, the time of seed harvest (Hong & Ellis 1996), and the way seeds are handled immediately after harvest (e.g. duration and environment of drying and prestorage environment; Hay & Probert 2011). Several studies describe the relative longevity of seeds in medium- and long-term gene bank storage (Walters et al. 2005; Hay et al. 2013; Ellis et al. 2018). However, these studies relate to crop species with little information available for how long the seeds of native species can be stored without declines in viability and seedling vigor.

Under identical storage conditions, a seed collection of high initial viability would have greater longevity than a collection of the same species with a lower initial viability (e.g. Hay & Probert 1995). As a general rule, maximizing viability and, therefore, optimal potential longevity, is achieved by collecting seeds at or close to the timing of natural seed dispersal (Hay &

Box 2 Seed Storage Experiments

Seed storage experiments (SSEs) involve storing seeds under specific temperature and moisture conditions. They can provide valuable information to predict storability within short time frames. Conditions recommended to perform SSEs to assess relative seed longevity are 45°C and a seed MC that corresponds with 60% RH (Hay et al. 2019). SSEs will normally involve allowing seeds that have already dried to lower MC, to take up moisture, usually at a lower temperature (20°C), to avoid significant viability loss before the SSE starts. SSEs can be done either by placing seeds in aliquots which will be used for viability testing, over water and monitoring their change in weight (if seed MC is known), or by placing seeds over a 60% RH nonsaturated solution of LiCl (Hay et al. 2008) in a sealed container.

Samples are removed after different periods of time (typically up to 60–100 days) to assess viability and determine when viability falls to 50% during the SSE (p_{50}; Fig. 1). The equilibration period required may vary, but 1 week is usual for many orthodox seeds; seed equilibrium RH can be checked using a water activity instrument or seed MC determined using traditional methods (see section "Seed MC Calculation"), if there are sufficient seeds available for destructive testing.

Seeds to be used in the SSE must be transferred to moisture-proof containers or bags once they have equilibrated to the elevated moisture levels. These containers and bags are then exposed to the rapid aging temperature of 45°C. If bulk seeds are stored such that they are exposed to the air, then the aliquots of seeds for the SSE should be similarly stored in an open environment, over a 60% RH nonsaturated solution of LiCl (for valid comparisons across studies, for example, Probert et al. 2009; Merritt et al. 2014) in a sealed container that is placed at 45°C.

The individual aliquots of seeds are removed after 1, 2, 5, 9, 20, 30, 50, 75, 100, and 125 days (Newton et al. 2014) or 2, 10, 15, and 30 days if the seed lot is expected to have poor longevity and few seeds available (Davies et al. 2006) to test the ability of the seeds to germinate. This germination data is then analyzed, usually through probit analysis, to estimate the p_{50} and provide an estimate for relative seed longevity (Figs. 1 & 2). The rankings can then be used to make appropriate decisions regarding use and/or viability monitoring (if appropriate) during storage.

Caution must be used in extrapolating predictions from the models to survival under chilled or sub-zero storage (Pritchard & Dickie 2003; FAO 2013); however, with the presumed shorter storage periods required for most restoration applications, interpretation of results can be less conservative, making SSEs a particularly useful tool in these cases (see http://data.kew.org/sid/viability/index.html).

Smith 2003). For more information and guidance on native seed collection, see Pedrini et al. (2020).

For orthodox seeds, which can be dried without damage to low MC, and over a wide range of environments, the longevity increases with decrease in seed storage MC and temperature in a quantifiable and predictable way (Roberts 1973). Under optimal conditions of low MC and low temperature, viable seeds can show very long life spans (e.g. up to 100 years). The longevity of recalcitrant seeds, on the other hand, is short, and can range from a few weeks to a few months, for species adapted to tropical environments, or longer periods, for example, a few years, for species adapted to temperate environments (Hong et al. 1996 and literature therein).

It is hence reasonable to think that orthodox seeds, collected at the right time of maturity and handled and stored properly, could be used for postdisturbance restoration after many years from collection, while recalcitrant seeds would need to be collected shortly before their use.

Working With Unknown Species

The largest available dataset on seed desiccation sensitivity is the Seed Information Database (SID; Royal Botanic Gardens Kew 2020). Of the 18,174 taxa included in this database, 96% are desiccant tolerant; however, this dataset is strongly biased toward species that can be stored using conventional seed banking practices (Wyse & Dickie 2017). Wyse and Dickie (2017), using two different models (habitat- and taxonomy-based), estimated that approximately 8% of world's seed-plant species produce desiccation-sensitive seeds.

When working with a species for which seed storage behavior is not known, the best way to proceed would be to investigate specific requirements and behavior; however, when this is not possible, it could be helpful to refer to the storage behavior of closely related taxa. Adapting the original guidelines by Hong and Ellis (1996), Chau et al. (2019) developed a protocol to determine freeze-sensitive seed storage behavior (Fig. 3). This protocol involves the following steps: (1) determine initial seed viability of the study species after collection; (2) dry the seeds to 15–20% RH at ambient temperature (20°C); (3) perform a second viability test: if most of the seeds die the species is likely recalcitrant; if most of the seeds are viable then proceed storing them hermetically at both 5°C and −18°C; (4) conduct viability tests after 6 months, 1 year, 2 years, and every 5 years: if most of the seeds die at 5°C and −18°C within 1–5 years, the species is likely intermediate with short-lived seed storage behavior and seeds should be stored at 5°C for less than 5 years; if most of the seeds die within 1–5 years at −18°C but retain viability at 5°C, the species is likely intermediate with freeze-sensitive seed storage behavior and seeds should be stored at 5°C; if most of the seeds survive, the species is likely orthodox with optimal storage at −18°C (Fig. 3). If a species appears to be recalcitrant or short-lived, further testing at different desiccation levels could help identify more specific requirements.

To predict a species' seed storability, performing seed storage experiments is also useful (see Box 2).

Conclusions

The standards for seed storage here described, based on the available knowledge developed through decades of research work, represent the current best practice for native seeds for restoration use. They are meant to support and guide seed laboratory staff and restoration practitioners in the proper management of seed supplies after their harvest. When sourcing seeds for restoration, it is fundamental that every single decision and step regarding the activities prior to storage (i.e. seed harvest and postharvest management) is taken considering best practices to ensure that seeds of the highest possible quality enter the storage facilities. Then, proper protocols are critical to assess seed longevity and maintain high levels of seed viability under storage, and ultimately to supply native seeds of high quality for seed-based restoration projects. Seeds that are handled and stored improperly will have a shorter lifespan and die, and the restoration will fail. As new technologies are developed and knowledge on native seeds is advanced, these standards will likely be refined and improved.

Acknowledgments

The authors would like to acknowledge the role of the International Network for Seed-based Restoration board members for the support and help provided during the planning and preparation of the manuscript; A. Cross for the help provided with the editing of the early draft of the manuscript; and two anonymous reviewers who provided comments that helped to substantially and critically improve the quality of the manuscript. The first author is grateful to his institution, the Chicago Botanic Garden, and in particular to Drs. K. Havens and A. Kramer, for supporting his work on this manuscript. The Royal Botanic Gardens Kew is supported by a grant in aid from the UK Department of Environment Food and Rural Affairs'.

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Coordinating Editor: Stephen Murphy

Received: 16 December, 2019; First decision: 26 January, 2020; Revised: 6 April, 2020; Accepted: 7 April, 2020