Reconsidering how to dry orthodox seeds for improved ex situ conservation outcomes

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OPINION

Reconsidering how to dry orthodox seeds for improved ex situ conservation outcomes

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Societal Impact Statement

Ex situ seed conservation is an essential tool in our efforts to conserve wild and cultivated plant diversity, as mentioned in the Global Strategy for Plant Conservation and the Sustainable Development Goals. While there are established standards which seed banks follow, it is important that we continue to evaluate protocols and optimize processes. Here, we encourage seed banks to re-evaluate their seed drying protocols. There is increasing evidence that two-stage drying, an initial active drying phase followed by equilibrium drying to the target moisture content for storage, increases the subsequent longevity of seeds which will result in improved conservation outcomes.

Summary

Billions of seeds are stored around the world in seed banks—either conservation seed banks preserving species diversity or genebanks conserving primarily intra-species agrobiodiversity. As well as providing long-term conservation, many of these seed banks offer samples of seeds for use in restoration programs, breeding and other research activities. Most seed banks follow international standards to manage collections, with specific standards concerning each step in the conservation cycle. One of the standards describes the conditions under which seeds should be dried before packing and storage: Seeds should be dried to equilibrium in a controlled environment of 5°C–20°C and 10%–25% relative humidity. These conditions theoretically mean that seeds will be close to an optimum moisture content for the maintenance of viability during storage. However, considerable gains in subsequent longevity can potentially be achieved, particularly for seeds that are harvested before maturation drying is completed in planta, if a two-stage drying process is adopted. The first, brief active drying phase should be at 30°C–45°C and 20%–70% RH and should be followed by slower final drying towards equilibrium in a cool, dry environment (15°C ± 5°C with 15% ± 5% RH). We encourage seed banks to consider this two-stage drying approach, even before the genebank standards are revised. Conservation

research is important for improving current best practices to ensure the effective safeguarding of species and agricultural biodiversity.

KEYWORDS
ex situ plant conservation, genebank standards, orthodox seeds, seed conservation, seed drying, two-stage drying

1 | INTRODUCTION

The majority of plant species produce seeds that are described as "orthodox". These seeds not only tolerate considerable desiccation, but their storage longevity is increased in a predictable manner the cooler the temperature and the lower the moisture content (Roberts & Ellis, 1989; Ellis & Roberts, 1980). They have the remarkable potential to remain viable for long periods of time, perhaps hundreds or thousands of years (Sallon et al., 2024), under optimum storage conditions of low moisture content and low temperature. This natural survival strategy is applied when we store seeds in seed (gene) banks for the long-term conservation of crop and wild plant diversity. Collections of crop diversity are conserved in national, regional, and international genebanks. According to FAO (2025), there are more than "*850 national genebanks in 116 countries, as well as four regional and 13 international genebanks*". Collections of wild species, particularly native flora, are primarily conserved by botanic gardens. More than 400 botanic gardens globally maintain seed banks as part of their conservation work (BGCI, 2025). Furthermore, there are calls to increase seed conservation programs to ensure a supply of native seeds to meet habitat and species restoration goals (Goodale et al., 2023; National Academy of Sciences, Engineering, and Medicine, 2023).

While wild species seed banks focus on conserving multi-taxon diversity, genebanks generally focus on conserving agricultural diversity as a source of genes or traits for use in breeding and other research. Genebanks typically hold many thousands of accessions of one or a few crop species and their wild relatives. Given the importance of genebanks to food security, standards have been agreed setting out the principles and benchmarks of operations that genebanks should strive towards (FAO, 2014, 2022). These Genebank Standards are also largely followed, at least in relation to the storage conditions for orthodox seeds, by many seed banks conserving wild species (Commander, 2021; Royal Botanic Gardens Kew, 2022a). The Genebank Standards (FAO, 2014, 2022) should reflect best practice based on current scientific understanding and genebanks are encouraged (e.g., by funders) to adhere to them. It is therefore important that the standards continue to be appraised, and that further scientific evidence is generated to optimize operations and hence better conserve plant diversity (Whitehouse et al., 2020). The most critical operation is the actual seed storage. From the first (IPBGR, 1976) to the most recent (FAO, 2022) formal advice, genebanks have been recommended to maintain orthodox seeds dry (3%–7% moisture content) and cool (0°C–10°C for the medium-term, −18°C for long-term) for plant genetic resources conservation. Several decades of records from genebanks have shown this approach to be successful in limiting loss in seed viability (Baum et al., 2026; Ellis et al., 2018, 2019; Hay et al., 2013, 2021; Walters et al., 2005).

Advice as to how genebanks should dry seeds to such low moisture contents before long-term storage has, however, been less consistent (Table 1). A range of environments has been recommended for use in genebanks to dry seeds, with temperature recommendations varying from 5°C to 60°C. Two-stage drying methods have sometimes been recommended, but in contrasting order: either a cool, dry environment followed by heated-air drying or vice versa. Cool and very dry seed drying treatments have been used successfully to dry seeds from a wide range of initial seed moisture contents and different stages of development in a wide range of species, for example, from cereal spikes (Pieta Filho & Ellis, 1991) to fleshy fruits (Demir & Ellis, 1992). Nonetheless, there is growing evidence that a two-stage approach to drying after harvest may provide superior subsequent seed longevity to the use of a single cool, dry environment throughout.

For a number of years, we have evaluated the impact of different drying protocols on the subsequent longevity of seeds of several species. Based on the results of our investigations to date, we propose here that a two-stage drying process, with initial, brief drying at a warm temperature (e.g., 30°C–40°C) followed by slower drying to equilibrium at 15°C ± 5°C with 15% ± 5% relative humidity (RH), may—perhaps often—result in greater longevity during subsequent long-term storage than the current recommended conditions for drying fresh seed accessions at harvest.

2 | CURRENT DRYING STANDARDS

Reducing the moisture content of seeds and then ensuring that it remains low during storage are crucial to the success of ex situ seed conservation. The first text on how to design a seed genebank facility, including advice on seed drying, was the report of a working group established by the International Board for Plant Genetic Resources (IBPGR, 1976). That report recognized that seeds for long-term genebank storage require further drying below the normal moisture contents typical of commercial seed practices, to very dry values of circa 5% (fresh weight basis). There was also an implicit expectation that the seeds being processed for storage would have already been dried to commercial levels before receipt at the genebank. The advice deliberately avoided drying seeds at very high temperatures initially. While heated air seed drying is rapid, maximum "safe" drying temperatures vary greatly among species and depend on the initial seed moisture

TABLE 1 Summary of recommended conditions to dry genebank seed accessions to low moisture contents (MC) for long-term storage.

No. of stages	Predrying	Final equilibration	Alternate advice	Notes	Source
2	40°C to 11% MC	60°C to 5% MC	Use of desiccants, particularly at second stage	Potential damage to longevity with high temperatures; high humidity in tropics a problem for heated air driers	IBPGR (1976)
1 or 2		Drying room: 15°C with 15% RH	Dry to 5% MC at 15% RH and 15°C or use heated air as stage 2 from 12% to 5% mc		IBPGR (1982)
1 or 2		Drying room: 15°C and 10%–15% RH with good air recirculation	Drying room: 17°C and 40%–45% RH, then 30°C with 10%–15% RH with air recirculation	Two-stage procedure suggested to reduce the drying times for larger seeds. If drying is delayed use a pre-drying holding environment of <17°C with <70% RH to limit insect damage.	Cromarty et al. (1982)
1				Use: Forced ventilation; appropriate humidity levels to avoid damage; low temperature avoiding solar radiation	Cromarty (1982)
1		Drying room: 15°C with 10%–%15% RH	Forced ventilation warm air drying	Alternate advised only in certain circumstances for particular crops in certain geographical locations	IBPGR (1985)
1		Drying room: 10°C–25°C with 10%–15% RH	Desiccant: Silica gel	Silica gel needs to be regularly regenerated.	FAO/IPGRI (1994)
2	Outside in shade or dry glass- or shadehouse in dry climate; or drying room or drying cabinet	Outside in shade or dry glass- or shadehouse; or drying room; or with silica gel; or with fan-assisted drying		First stage drying to a moisture content low enough for threshing but not too dry to avoid damage to seed.	Sackville-Hamilton and Chorlton (1997)
1 or 2	Outside in shade on open mesh shelves, if the climate is suitable; passive drying in a room with good ventilation and air circulation; or active drying under forced ventilation.	According to FAO/IPGRI (1994)	Options given for drying: Dehumidified drying (drying cabinets or walk-in drying rooms); desiccants (silica gel, calcium chloride); saturated salt solutions (calcium chloride, lithium chloride); self-defrosting refrigerator; shade-drying.	Two-stage drying recommended if moisture content is high (>15%).	Rao et al. (2006)
1		5°C–20°C with 10%–25% RH		Precise temperature and RH vary with species.	FAO (2014)
1		5°C–20°C with 10%–25% RH		Monitor drying using a digital moisture monitor, indicator silica gel or low-cost hygrometers, if available.	FAO (2022)

content and the design of the drier; furthermore, the warm humid environments of the tropics limit the use of these methods (Cromarty et al., 1982). In other words, cool drying temperatures were considered to be benign for most species, whereas high temperatures might damage some. This assumed that seeds were mature and greater loss in viability was inevitable if seeds were exposed to high temperatures, especially when their moisture content was still high – as quantified by the seed viability equation (Ellis & Roberts, 1980). For these reasons, cool and dry environments were recommended then (IPBGR, 1976) and indeed now (FAO, 2014, 2022).

The "simplest solution" for drying seeds was proposed to be "*to provide a drying room maintained at about 15°C and 10%–15% RH with good air recirculation*", using refrigeration dehumidifiers (IBPGR, 1990). Such a drying system had already been adopted by some genebanks at that time. A refrigeration dehumidification system was also found to work well for high-moisture content seeds in research at the seed laboratory at the University of Reading (Demir & Ellis, 1992; Pieta Filho & Ellis, 1991), perhaps even allowing seeds with high moisture content caused by harvesting too early to continue maturing due to the slow drying rate. Slow drying at a higher humidity has also been recommended for conservation seed lots of wild species which have been harvested prematurely (Hay & Probert, 2011). In the first edition of the Genebank Standards (FAO/IPGRI, 1994), the recommendation was to dry seeds immediately upon receipt at 10°C–25°C and 10%–15% RH, using either a desiccant (e.g. silica gel) or drying chamber. These ranges, already broader than those in 1976, were broadened further in the current edition of the Genebank Standards: 5°C–20°C and 10%–25% RH (FAO, 2014). Nonetheless, many of the genebanks which were established in the 1960s onwards dry seeds in drying rooms at approximately 15°C and 15% RH (Hay et al., 2021).

In fact, the standards formulated in this way (FAO, 2014) suggest that it would be possible to dry seeds at the extreme combinations of 5°C and 10% RH, 20°C and 10% RH, 5°C and 25% RH, or 20°C and 25% RH and still comply with the recommendations (Figure 1). Based on seed moisture relations, that is, the relationship between seed moisture content and the RH at which they are equilibrated for drying, the two most interesting extremes are 20°C, 10% RH and 5°C, 25% RH. We can estimate the moisture content of seeds equilibrated under these conditions using Cromarty's equation (SER/INSR/RBG Kew, 2023). The estimated moisture contents will vary depending on the species, particularly seed oil content, but for *Digitalis purpurea* L. seeds, for example, the moisture content is predicted to reach 3.1% moisture content when equilibrated at 20°C and 10% RH or 5.7% moisture content when equilibrated at 5°C and 25% RH (Figure 2a). For more starchy seeds, the range is even greater; for example, for rice (*Oryza sativa* L.), the moisture content is predicted to reach 4.8% moisture content when equilibrated at 20°C and 10% RH or 8.7% moisture content when equilibrated at 5°C and 25% RH. These ranges are considerable and, since seed longevity is determined by moisture content (Ellis, 2022; Ellis & Roberts, 1980), depending on the drying conditions chosen, could lead to quite different longevities in genebank storage (Figure 2b,c). There will also be consequences for the storage potential of the seeds when they finally reach the genebank storage rooms due to ageing during the "drying" process or in cases when seeds are left in the drying room for long periods before packing (Figure 2a).

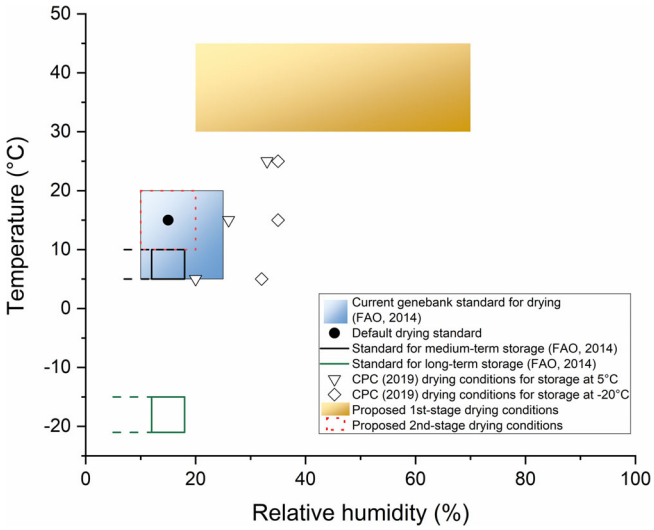

FIGURE 1 Recommended conditions (relative humidity (RH), temperature) for drying orthodox seeds according to FAO (2014); the darker the shading, the higher the equilibrium moisture content of the seeds. After drying, seeds are packed for medium-term storage at 5°C–10°C or for long-term storage at −18°C ± 3°C, with 15% ± 3% RH. The dashed lines extending from the black and green boxes indicate that although the storage temperature and RH are specified in the standards, if seeds are dried and then packed hermetically, we do not actually know what the equilibrium RH of the storage environment would be for these seeds. The "default" drying standard adopted by many genebanks and conservation seed banks is 15°C with 15% RH. The Center for Plant Conservation (CPC, 2019) recommends specific drying conditions depending on the storage temperature. Also shown are the conditions proposed here for two-stage drying. Again, darker shading indicates higher equilibrium moisture content.

In contrast with the FAO Genebank Standards, the Center for Plant Conservation (CPC), a nonprofit organization providing educational resources on plant conservation and responsible for conserving North America's most imperiled native plants through a network of botanical gardens and a coordinated metacollection, has standards in which the RH of the drying environment varies with both the temperature used for drying and the temperature at which the seeds will be stored (Figure 1). For example, if they are to be stored under conventional long-term conditions (−20°C), seeds could be dried at 25°C and 35% RH, 15°C and 35% RH, or 5°C and 32% RH (CPC, 2019). These standards assume that there is an optimum RH at which seeds should be stored (20%) which will be reached once the dried seeds have been hermetically sealed and equilibrated at the −20°C storage temperature. In other words, these standards assume that the water activity (a_w; where a_w is approximately equal to the RH of the equilibration environment divided by 100) of equilibrated seeds will decrease if the seeds are hermetically sealed and placed at lower temperatures and that the target moisture content will therefore vary with storage temperature (Vertucci & Roos, 1993). Indeed, a low-moisture-content

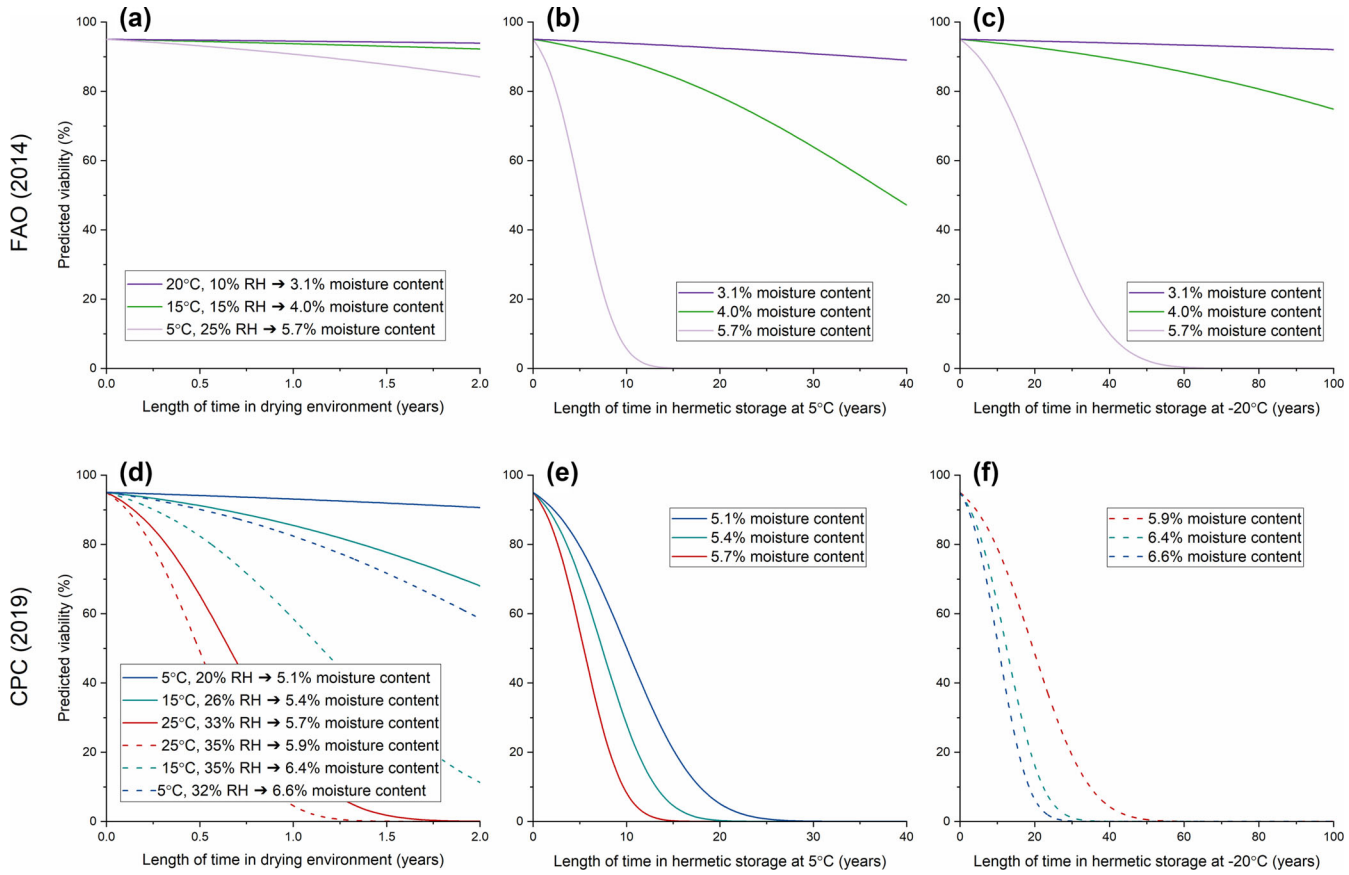

FIGURE 2 Predicted survival curves for *Digitalis purpurea* L. seeds showing the decline in viability (usually assessed through a germination test) under drying conditions—temperature and relative humidity (RH)—recommended by (a) FAO (2014) or (D) CPC (2019) and during storage at (b, e) 5°C or (c, f)—20°C after drying to equilibrium under the respective conditions: (B, E) FAO (2014); (c, f) CPC (2019). *Note: x*-axis scales in each column of graphs varies. Predictions were made using the *viability calculators* tools in the seed information database, assuming an oil content of 37.4% (SER, INSR, RBG Kew, 2023).

limit to the application of the viability equation has been reported for a number of species (e.g., Ellis et al., 1989) and shown to vary with storage temperature (Ellis & Hong, 2006). However, reducing seed storage moisture content below a low critical moisture value has often not resulted in a reduction in longevity (Ellis & Hong, 2006; HSBP, 2025; Kameswara Rao et al., 2017), whereas longevity will certainly be compromised above this critical value. The potential impact of the CPC recommendations for drying on longevity in storage as predicted by the viability equations is considerable (Figure 2e,f). For example, if stored at −20°C, seeds of *D. purpurea* are predicted to completely lose viability within 30 years if first dried to equilibrium at 15°C with 35% RH or at 5°C with 32% RH according to CPC guidelines but predicted to maintain viability >85% for more than 60 years when dried at 15°C and 15% RH (Figure 2).

3 | SEPARATING ACTIVE DRYING AND FINAL EQUILIBRATION

Seed development is typically divided into three phases: embryogenesis, when cells differentiate into the different structures of the seed; reserve deposition, when dry matter is accumulated; and maturation drying (Leprince et al., 2017). This last phase, when the developing cohort of seeds have all acquired desiccation tolerance and the seeds no longer have a vascular connection with the parent plant, is when there are considerable increases in the storage potential of the seeds, perhaps a consequence of a stress response to reduced water availability or the loss of vascular connection itself; removal of immature seeds from the parent plant is known to simulate the development of the ability to germinate (Dasgupta et al., 1982; Kermode et al., 1986). The accumulation of oligosaccharides and heat-stable proteins of low molecular weight (also known as late embryogenesis or chaperone proteins) during seed development and maturation are both associated positively with subsequent seed longevity, but the former precedes the latter such that variation in subsequent seed longevity correlates well with heat-stable proteins during late seed maturation (Sinniah et al., 1998). Moreover, the heat-stable proteins are known to be involved in coping with stress and damage (Bray, 1997). Hence, it is possible that the benefits to subsequent seed longevity from drying freshly-harvested seeds at warmer temperatures are due to increased production of heat-stable proteins but only while sufficient moisture remains available for such metabolic activity; that is, down

to about −15 MPa (Roberts & Ellis, 1989) or a water activity of roughly 0.85. This water activity tallies with the results of Whitehouse, Hay, and Ellis (2018) and Jawad et al. (2025) where the drier, and so more mature seed samples, did not benefit from warmer-temperature drying.

Accordingly, seeds should ideally be harvested when they have dried in situ, as far as possible. However, in some environments, ambient RH may never be very low, and seeds will not be able to dry to low moisture content in situ. For example, Whitehouse et al. (2015) recorded a wide range of harvest moisture contents from 13% to 29% for rice seeds produced in the humid tropical climate of the Philippines. Whitehouse et al. (2015) also found that when seed harvest moisture content was high, there was an improvement in subsequent longevity in experimental storage if seeds were initially intermittently dried at a higher temperature (45°C) for a few days compared with immediately drying in the genebank drying room (15°C). In further experiments, the response seemed to be related to the drying temperature rather than drying rate or humidity (Whitehouse et al., 2017). The greatest benefit of initial drying at a higher temperature on subsequent seed longevity, measured as the percentage increase in the time for seed viability to reach 50% during experimental storage, was more than 370% (Whitehouse, Hay, & Ellis, 2018). Such improvements in longevity will translate into more effective conservation of diversity in seed (gene) banks, reducing the requirement to recollect or regenerate fresh seeds. Note that while seeds in fleshy fruits do not dry down greatly as they mature, they also improve in quality (and subsequent seed longevity) after the end of seed filling over a similar time scale to cereal seeds (Demir & Ellis, 1992).

Similar, positive effects of two-stage drying—initial high temperature drying followed by cool final equilibrium drying—on subsequent seed longevity have also been found for other crops produced in a tropical environment, although a relationship with harvest moisture content could not be established (Whitehouse, Owoborode, et al., 2018; Salvador et al., 2025). More importantly, initial drying at the high temperature either did not have a negative effect on longevity for any seed lots (Whitehouse et al., 2015) or reduction in longevity was only seen for a relatively low proportion of seed lots (Whitehouse, Owoborode, et al., 2018; Salvador et al., 2025). Hay (1997) considered the impact of leaving seeds in a car in Niger to

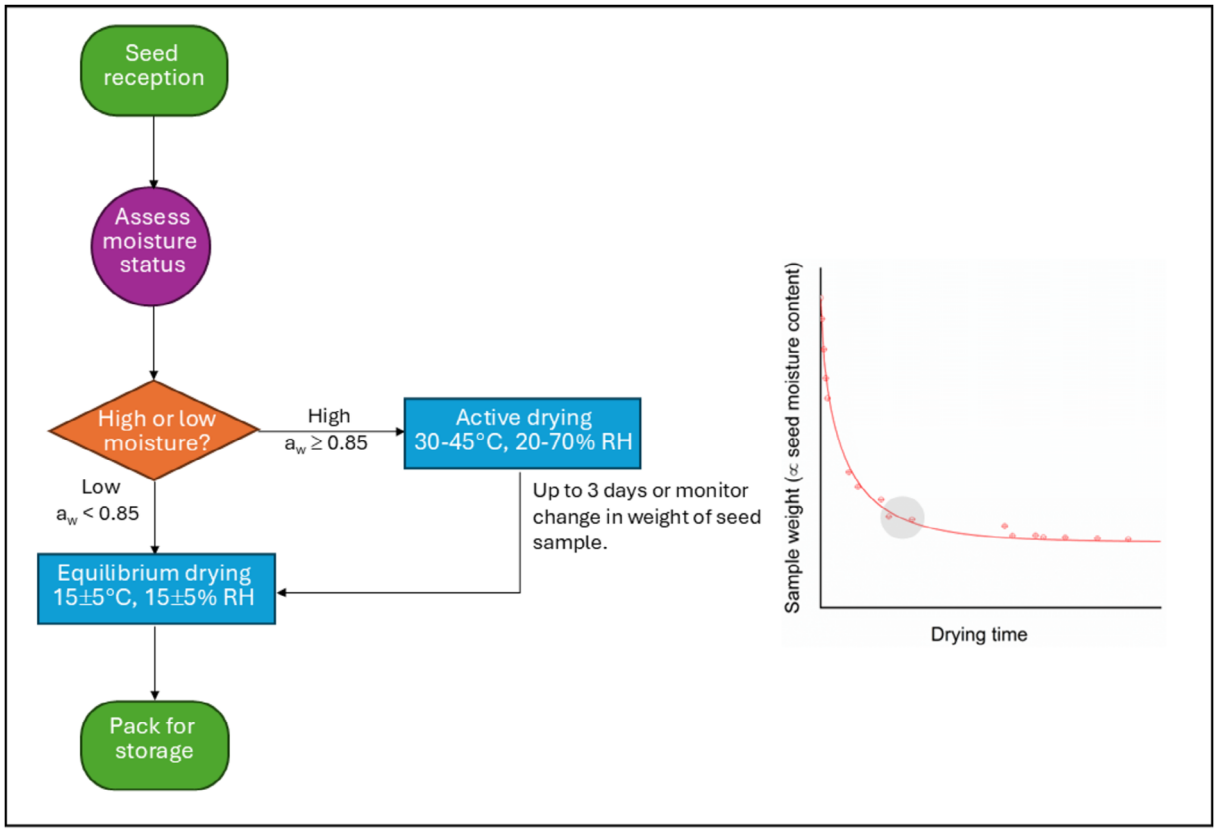

FIGURE 3 Flow chart summarizing two-stage drying. Two-stage drying may improve the subsequent seed storage longevity, in particular for seeds which have not yet dried on the plant. Moisture status could be checked by measuring seed water activity (a_w) or determining the relative humidity (RH) to which seeds have already dried using, for example, humidity indicator paper/cards (Guzzon et al., 2024). The graph on the right shows a typical drying curve (based on real data in Rezaei, 2023). The initial active drying stage (at 30°C–45°C and 20%–70% RH) should not exceed 3 days or beyond the time when most of the moisture has been lost and the equilibrium moisture content is being approached (shaded circle in graph). Note, for very immature seed lots, it is recommended to hold seeds at a higher humidity for a few days before drying (Probert et al., 2007).

simulate what might happen during a seed collecting trip, perhaps particularly of native seeds harvested directly from the plant; the subsequent longevity was significantly greater for seeds left in a car than for seeds immediately dried at 15% RH and 15°C, an effect attributed to the higher temperature (25.4°C–33.6°C). Similarly, Jawad et al. (2025) found an advantage to longevity from initial drying at a higher temperature (30°C) for less-developed seeds, but in that research, the most mature seeds showed greater longevity after cool temperature (15°C) drying. In response to the results for rice, the International Rice Genebank at the International Rice Research Institute (IRRI) now has two drying rooms: the first drying room running at 40°C, 30% RH and the final, equilibrium drying room running at 15°C, 15% RH. Seeds are initially dried at the higher temperature for 3 days and then transferred to the second drying room for final equilibration before packing, ideally within 1–3 months. Initial drying at a higher temperature may more closely simulate the environmental conditions seeds would experience on the plant, at least in terms of temperature, though it should be noted that seeds will be cooler than 40°C when there is active moisture loss due to evaporative cooling (Fernández Marín et al., 2019). In fact, some national genebanks, particularly in low- and middle-income countries in the tropics, do dry at a higher temperature, at least initially, perhaps also because they do not have access to a purpose-built and effective drying room. Simple heated-air, desiccant or sun-drying, or application of other traditional drying methods where seeds may be exposed to much higher temperatures than 10°C–25°C may be good for the subsequent quality of the seeds—perhaps not surprising given this is what farmers have been doing for crop species for millennia. Certainly, genebanks in resource-limited locations should not view cool drying in a purpose-built drying room as the only option for effectively drying conservation seed lots if other practical solutions are available. Similarly, wild species seed collectors may actively air-dry seeds in the field during a collecting trip (Royal Botanic Gardens Kew, 2022b), often at temperatures >15°C.

Similar responses to drying at a higher temperature have also been found for seeds of different crops produced in a temperate environment. In recent studies on oilseed rape, pea, wheat, barley, and oat produced in the south of Sweden, drying to equilibrium with 30°C and 19% RH resulted in greater or no significant difference in subsequent seed longevity compared with drying at 16°C and 11% RH (Rezaei, 2023). In these experiments, seeds were dried entirely at the higher temperature, with the RH adjusted (increased) such that the seeds would in theory reach the same equilibrium moisture content at the higher temperature as the seeds dried at 16°C and 11% RH. However, extended periods at the higher temperature would in theory result in a higher rate of aging compared with 16°C. Furthermore, in practice, many seed (gene) banks use the drying room as a temporary storage place for seeds where they are kept until staff are available for further processing and packing. Hence, we still recommend placing seeds at a lower temperature and humidity for final equilibrium drying. As to when to transfer seeds from the warm temperature drying environment to cooler dry conditions (e.g., 15°C and 15% RH), we suggest when the rate of loss of moisture is starting to slow—which can be followed by recording the weight of drying samples—or up to a maximum of three days (Figure 3). In the case of plant species adapted to very cold conditions, we still suggest that drying at a higher temperature would be beneficial, although perhaps not as high as 45°C, but this is a research gap that still needs to be addressed.

Introducing two-stage drying at the International Rice Genebank has helped to move seed lots through all the seed processing operations more efficiently, which may also contribute to overall improved seed quality at the time seeds are placed into genebank storage. Initial drying at a warmer temperature also offers greater energy efficiency. At the higher temperature, water will more readily move from the seeds to the air and then be expelled from the drying environment, whereas at cooler temperatures, the dehumidification system will need to work harder to remove the water and maintain the low humidity.

4 | CONCLUSION

Overall, given the increasing evidence that immediate drying at 15°C may compromise seed longevity, particularly for seeds harvested before full maturity, we recommend that seed genebanks and conservation seed banks adopt a two-stage drying protocol for fresh seed lots (Figure 3). This involves an initial phase of active drying at a higher temperature (30°C–45°C) for a few days, followed by final equilibration at a cooler temperature (15°C ± 5°C) and lower relative humidity (15% ± 5% RH). The initial drying phase should maintain sufficiently low RH (e.g., 20%–70%) to ensure effective moisture loss. We urge that this approach be considered in future revisions of the Genebank Standards. In the meantime, seed conservation practitioners may need to adapt their protocols where evidence supports improved outcomes. Adopting two-stage drying, especially for seeds with high harvest moisture content, offers the potential for significantly enhanced longevity and more efficient processing, ultimately reducing the need for regeneration and enabling greater focus on broader conservation goals.

AUTHOR CONTRIBUTIONS

Fiona R. Hay: Conceptualization; visualization; writing—original draft; writing—review and editing. **Richard H. Ellis, Dustin Wolkis, Katherine J. Baum**: Conceptualization; writing—original draft; writing—review and editing. **Charlotte Lusty, Olorunnisola Salvador, Olaniyi Oyatomi, Michael F. Lyngkjær**: Writing—review and editing. All authors have read and agreed to the published version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

No conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

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