Seeds and Pollen

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Introduction

Seeds of all of the species covered in this handbook must be stored for some length of time after harvest. Some seeds are used as food (for example, cereals and legumes) and stored before consumption, while others are stored to maintain viability and used to produce the next season's crop. This section describes basic procedures to maintain seed and pollen viability. More detailed descriptions or procedures to maintain seed viability for extended periods (for example, for genetic stocks) are published in Agricultural Handbook 506, *Principles and Practices of Seed Storage* (Justice and Bass 1978) or review articles (Priestley 1986, Hong and Ellis 1996, Walters 1998a).

Classification of Seed Storage Behavior

Mature seeds generally have higher tolerance for low moisture levels or temperatures than fresh fruits, vegetables, or flowers. They acquire this tolerance during maturation on the parent plant, presumably as a strategy to survive adverse climatic conditions such as drought and winter. The degree of tolerance varies among species, but three general categories exist: orthodox, recalcitrant, and intermediate.

Orthodox seeds are produced by most annual or biennial crops and horticultural species. Some examples are grains, pulse crops, vegetables, floral crops, and temperate tree fruit, as well as many temperate forest tree and shrub species. Orthodox seeds can survive complete water removal and can be easily stored for many years by drying and cooling.

Recalcitrant seeds are produced by herbaceous plants from aquatic habitats (for example, wildrice, watercress, and wasabi), perennials from tropical areas (examples include avocado, mango, coconut, cocoa, and jackfruit), and some deciduous forest trees from temperate areas (such as oak, chestnut, buckeye, and silver and sycamore maple). As the name implies, recalcitrant seeds are difficult to store and have shelf-lives usually <1 year unless they are cryopreserved.

Intermediate seeds are produced by perennials of tropical and subtropical origin (such as coffee, citrus, macadamia, and papaya) and by some tree nut species (for example, walnut, hickory, pecan, hazelnut, and pistachio). (Hazelnut and pistachio may belong to the recalcitrant category.) With proper handling and excellent quality seeds, the viability of seeds with intermediate storage behavior can be maintained for a few years. These seeds can be stored over a single winter with a stratification treatment, such as damp media at 5 °C (41 °F).

The best way to identify whether a seed is recalcitrant or not is to monitor survival while drying (Hong and Ellis 1996). Seeds that are recalcitrant lose viability within minutes of drying below

85 to 90% RH. Intermediate seeds lose viability within days of drying below 20% RH. Seeds that are orthodox can survive many months or even years when dried to 5% RH. The ability of orthodox seeds to survive drying is acquired during development, so seeds harvested prematurely will appear to be recalcitrant (Vertucci and Farrant 1995). Mature seeds must be dried sufficiently rapidly—within a few days—to avoid deterioration at intermediate water contents (Pammenter and Berjak 1999). Often drying experiments are inconvenient to perform, and growers resort to anecdotal information or guidelines (table 1) to identify storage behavior of their seeds. Guidelines exist to help identify seed storage behavior, but there are no hard and fast rules. A compendium listing storage guidelines for over 7,000 species is now available (Hong et al. 1996). Also, useful information on woody species grown in the United States can be gleaned from Agricultural Handbook 450 (Schopmeyer 1974).

Table 1. Guidelines to identify storage behavior of seeds

Trait	**Guideline**	**Some exceptions**
Growth habit	Most herbaceous plants produce orthodox seeds	Aquatic species
Habitat	Many aquatic species, tropical rainforest species, and temperate climax forest species produce recalcitrant seeds	Most native Hawaiian species, temperate conifers, some maples
Water content at harvest	Most orthodox seeds dry naturally on the parent plant	All immature seeds, Solanaceae, Cucurbitae
Seed size	Recalcitrant seeds are often large	Some aquatic species, Rutaceae, some Rubiaceae
Desiccation sensitivity	Orthodox seeds can survive complete water loss; recalcitrant seeds cannot	Orthodox seeds dried very slowly (for >2 weeks) can be severely damaged

Seed Storage Behavior and General Storage Principles

Because they are sensitive to drying, recalcitrant seeds must be stored at 92 to 98% RH. The best storage temperature depends on the chilling sensitivity of the species. Seeds from many tropical fruits (mango, avocado, cocoa, jackfruit) are sensitive to chilling and should be stored at ≥15 °C (59 °F). These seeds have the shortest potential shelf-life, remaining viable for 2 weeks to 3 mo. Seeds produced from temperate species such as oaks, buckeye, or chestnut can survive for 0.5 to possibly 2 years by storing them at 2 to 5 °C (36 to 41 °F). Microbial contamination is always a problem at high RH, and seeds often survive longer if a fungicide is applied. Storage in damp peatmoss is often beneficial. The RH required for safe storage of recalcitrant seeds often allows seeds to germinate. Once this has occurred, procedures for storage of seedlings should be adopted.

Seeds with intermediate storage behavior are more amenable to drying and consequently can be preserved for longer periods than recalcitrant seeds. RH of 40 to 60% appears to provide maximum longevity. Intermediate seeds survive 1 to 6 mo if stored at 25 °C (77 °F) and 2 to 5 years if stored at 5 °C (41 °F). These seeds rapidly lose viability if frozen (stored at -18 °C [0 °F]).

Seeds that exhibit orthodox behavior are easily stored by drying and cooling. The extent to which drying and cooling extends shelf-life is best described by Harrington's "Thumb rules" which state that the life of a seed is doubled for every 1% decrease in water content or every 5 °C (41 °F) decrease in temperature (Harrington 1963, Justice and Bass 1978). The "100s Rule" states that adequate longevity for commercial seed storage purposes (<5 yr) can be achieved by ensuring that the sum of the RH and temperature in °F during storage does not exceed 100.

These rules were developed as guidelines for commercial seed storage. They are not valid for extremely dry conditions, and their applicability at extremely cold temperatures has not been adequately tested.

A new rule is that seeds store optimally at 15 to 25% RH. Storing seeds with RH <15% will not increase shelf-life and may actually accelerate deterioration (Walters 1998b). Seed water content achieved at 15 to 25% RH varies from about 2 to 10%, depending on seed lipid composition and storage temperature.

Storage at -18 °C (0 °F) (the temperature of a standard freezer) enhances shelf-life 4- to 5-fold over that of seeds stored at 5 °C (41 °F) (Walters 1998a). Storage temperature should be dictated by the required longevity for the seed: Storage at 15 °C (59 °F) may be adequate for most species to maintain quality for 3 to 5 years; longevities of 5 to 10 years may require refrigeration at 5 °C (41 °F); while storage at -18°C (0 °F) is required if seeds are to be maintained for 15 to 20 years.

Seed Quality Factors Influencing Longevity of Orthodox Seeds

Harrington's rules are approximations and give relative, rather than absolute, longevities. Absolute longevity depends on initial seed quality. Seed quality is controlled by genetic and environmental factors such as seed structure and composition, maturity, dormancy, purity, mechanical damage, and initial viability and vigor (Justice and Bass 1978). Field conditions during seed development and harvest and postharvest treatment, such as drying temperature, cleaning procedures, and priming, affect overall seed quality and hence seed longevity (Walters 1998a). Infestations of storage fungi, insects, and rodents significantly curtail seed quality and lifespan. Reducing RH or temperature can ameliorate the deleterious effects of infestations. For example, insect activity is retarded at <10 °C (<50 °F) and almost ceases at 0 °C (32 °F). Exposure of seeds to -18 °C (0 °F) kills most insects and their eggs.

Numerous factors during seed development and maturation affect the potential longevity of seeds. Seeds harvested prematurely may have shorter shelf-life than seeds harvested fully mature (defined as having completed maturation drying). Shelf-life may be shorter because immature embryos are not fully tolerant of desiccation and are damaged when dried, or because maximum seed quality is acquired during the final stages of development on the parent plant. The high temperatures, >40 °C (>104 °F), frequently used to rapidly dry immature seeds can severely damage them. Some drying procedures call for exposure to 35 °C (95 °F) for several days. This treatment can initiate seed aging processes. An initial treatment that dries immature seeds slowly enhances seed desiccation tolerance (Vertucci and Farrant 1995, Pammenter and Berjak 1999) and potentially seed longevity. If seeds must be harvested prematurely, holding them for 2 to 5 days in their fruiting structures can simulate slow drying. Once immature seeds receive a slight and slow desiccation treatment, they can be threshed with less damage.

While a brief period of slow drying of <5 days at 20 °C (68 °F) enhances quality of prematurely harvested orthodox seeds, prolonged exposure of fully mature seeds to RH >75% promotes deterioration, encourages microbial infection, and at RH >95% allows precocious germination (Pammenter and Berjak 1999). Seeds may be exposed to high RH in the field if harvest is delayed by rain or if, after harvest, there is inadequate RH control. Generally, exposure of seeds to high RH first results in a reduction of seed vigor (slower germination) and then a reduction in germination percentage. The higher the RH or temperature, the faster seeds deteriorate (refer to Harrington’s rules). Germination percentages of vegetables and grains may decline to 0% within 3 to 6 mo of storage at 20 °C (68 °F) with 90% RH. It is generally assumed that reduction in seed quality leads to a reduction in shelf-life once seeds are placed under more favorable storage conditions. Preharvest and postharvest treatments may explain the variability in longevity among seed lots of the same cultivar (Walters 1998a).

Seed priming is a procedure used to accelerate germination rates of planted seeds. Seeds are usually held at <10 °C (<50 °F) with water potentials close to -1 MPa for a few days. While this treatment gives the appearance of improving seed vigor—seeds germinate faster or more uniformly—it exposes mature seeds to high RH and likely reduces their shelf-life if they are redried and then stored (Walters 1998a).

Anecdotal evidence suggests that seeds harvested from the wild have a shorter shelf-life than seeds harvested from cultivated plants. There are numerous possible explanations. Through agricultural practices, humans may have selected for seeds with superior quality. Cultivated plants may have received optimum growth conditions—irrigation, fertility, and pest management—and are therefore more robust. Seeds collected from the wild are often highly immature because maturation of uncultivated seeds is less uniform and mature fruits often dehisce.

Seed dormancy is often linked to seed longevity. Seeds with hard seed coats store longer (Justice and Bass 1978), probably because the seed coats restrict the movement of air and water. Seeds of Leguminosae and Malvaceae have a tendency toward hard-seededness. The linkage between embryo dormancy and longevity is difficult to verify since seed dormancy confounds measurements of viability for longevity tests. Clearly, dormant seeds survive longer in the soil, but this is more likely because they fail to germinate under moist conditions than because they have more efficient mechanisms to survive in the dry state.

Given similar storage and harvest conditions, seeds from orthodox species exhibit different inherent longevities. For example, lettuce and onion seeds are fairly short-lived, whereas tomato and barley seeds show substantial longevities. Generally, orthodox species from Leguminosae and Malvaceae are long lived, while many species in Asteraceae or Umbelliferae produce short-lived seeds. Longevity of seeds from annual crops is better described than that from herbaceous or woody perennials. Sample longevities of different seed species are listed in table 2. More exhaustive species lists and detailed storage conditions can be found in Justice and Bass (1978) and Priestley (1986).

Table 2. Approximate longevities for various seed storage behaviors and seed species

Storage type	Species	Optimum RH	Optimum moisture content of seed[1]	Time to 50% loss in viability[2]
		%	g H_2O per g dw	
Recalcitrant	Tea *(Camellia sinensis)*	95 to 98	0.6 to 0.8	2 weeks to 2 mo
	Buckeye *(Aesculus hippocastanum)*	95 to 98	0.5 to 0.7	6 to 8 mo
	Trifoliate orange *(Poncirus trifoliata)*	90 to 95	0.5 to 0.7	6 to 14 mo
	Wildrice *(Zizania palustris)*	90 to 95	0.35 to 0.45	9 to 18 mo
Intermediate	Coffee *(Coffea arabica)*	40 to 60	0.10 to 0.13	2 to 4 years at 5 °C; damage at <0 °C
	Papaya *(Carica papaya)*	40 to 60	0.09 to 0.11	3 to 6 years at 5 °C; damage at <0 °C.
	Hickory (*Carya* spp.)	80 to 90		3 to 5 years
	Citrus *(Citrus limon)*			6 to 18 mo
Orthodox	Lettuce *(Lactuca sativa)*	20	0.04 to 0.05	>4 years at 5 °C, >20 years at -18 °C
	Onion *(Allium cepa)*	20	0.06 to 0.08	>4 years at 5 °C, >20 years at -18 °C
	Peanut *(Arachis hypogeae)*	20	0.04 to 0.05	>4 years at 5 °C, >20 years at -18 °C
	Soybean *(Glycine max)*	20	0.07 to 0.08	>5 years at 5 °C, >20 years at -18 °C
	Sunflower *(Helianthus annuus)*	20	0.03 to 0.04	>6 years at 5 °C, >25 years at -18 °C
	Corn *(Zea mays)*	20	0.07 to 0.09	>8 years at 5 °C, >25 years at -18 °C
	Chickpea *(Cicer arietinum)*	20	0.07 to 0.08	>8 years at 5 °C, >25 years at -18 °C
	Pea *(Pisum sativum)*	20	0.09 to 0.12	>10 years at 5 °C, >25 years at -18 °C
	Barley *(Hordeum vulgare)*	20	0.09 to 0.12	>10 years at 5C, >25 years at-18C
	Tomato *(Lycopersicum esculentum)*	20	0.05 to 0.06	>12 years at 5 °C, >25 years at -18 °C

[1] For orthodox seeds, the lower value in the water content range is more appropriate for 5 °C (41 °F) storage, and the higher value approximates optimum water contents for constant storage at -18 °C (0 °F). Water content on a percentage dry weight or fresh weight basis are often used in

the seed industry. To calculate percentage water content on a dry weight basis, multiply water contents in the table by 100.

[2] Values for approximate longevity are given for 5 °C (41 °F) storage for all species except *Camellia sinensis*, which is chilling sensitive and should be stored at 15 °C (59 °F).

While species have characteristic longevities, variability among cultivars and among lots of the same cultivar may be so great that it precludes prediction of shelf-life. For example, germination of sesame seeds with initial germination rates of 70 to 80% ranged from 0 to 80% after 18 years storage at the National Center for Genetic Resources Preservation. Similar results were obtained for potato, pepper, sorghum, onion, and tomato: initial rates of germination from 90 to 100% and rates after 18 years of 0 to 100%. The source of this variability is unknown. Suppliers should monitor seed viability periodically to ensure quality.

Additional Storage Factors Affecting Shelf-Life

In addition to RH and temperature, the gas composition of the storage environment may be important, but evidence for a clear relationship is lacking. Low O_2 should enhance longevity since aging reactions are either oxidative or linked to respiration. Storage under higher O_2 tensions causes rapid deterioration (Ohlrogge and Kernan 1982), but the converse has not been demonstrated. Freeze-drying or vacuum packaging may be beneficial (Woodstock et al. 1976, Justice and Bass 1978, Ellis et al. 1993), but it is not clear whether these treatments control moisture level or O_2 level. Reducing the RH is a far more effective method of limiting respiratory processes than lowering O_2. The time and expense of using low O_2 is probably not worthwhile for short-term storage of orthodox seeds.

Exposure to light, even at low intensities, appears to damage dry seeds. Seeds intended for nursery stock should not be dried under the sun and should not be stored in a lighted room without a protective container.

Procedures to Dry Orthodox Seeds

At storage temperatures >0 °C (32 °F), seed water content or RH are the most important factors determining seed longevity. Seed producers must consider two factors when drying seeds: the rate at which seeds are dried and the level to which they are dried. With the exception of immature seeds that benefit from a short, slow, drying period, orthodox seeds with high water content, >18%, should be dried to about 12% as rapidly as possible. Temperatures >35 °C (95 °F) can be damaging, so lower temperatures and high air flow are recommended. Seeds should be spread out in a thin layer to allow air to circulate through the seed mass and gently mixed daily to ensure even drying.

In temperate or cold climates, no special storage conditions are required if seeds are to be planted the next season, that is, within 6 mo. Storage of dried seeds in open bins with no RH control is called "open storage," and the water content of the seed will fluctuate according to the RH and temperature in the warehouse. Open storage is not recommended in warm humid regions or if seeds will be planted several years after harvest.

The water content of seeds must be controlled if seeds are to retain high quality for >2 years. This is easily accomplished by placing seeds at a known RH once they have been dried to a safe water content of <12%. There are two strategies: Dried seeds can be packed in moisture-permeable bags and stored in rooms where the RH is controlled, or they can be equilibrated at the desired RH and then packaged in moisture-impermeable containers (for example, glass, foil laminate, or aluminum cans). The RH in the moisture-proof containers is a function of the water content of the seeds and the temperature at which they are stored.

A RH of 20 to 25% produces optimal seed water content for storage of most orthodox species (Walters 1998a,b). The equilibrium water content varies among seeds according to lipid composition and storage temperature. For example, peanut seeds with 45% lipid will contain 2 to 5% water, while pea seeds with 2% lipid will contain 8 to 12% water. When RH during storage is controlled, water content of seeds need not be monitored. The simplicity of this method may cause some producers to use it exclusively; however, constant dehumidification, especially in conjunction with refrigeration, may be prohibitively expensive (Walters-Vertucci and Roos 1996). Depending on volume of seeds handled and risk of mechanical failure, it may be safer and more cost-effective to store seeds in moisture-proof containers.

When seed producers opt to store seeds in moisture-proof bags, they increase the complexity of water content adjustments but also the flexibility in choosing drying and storage conditions. The interested reader may refer to more in-depth literature on water sorption isotherms of seeds (Walters 1998a,b). The guiding principle is that 20 to 25% RH provides optimum storage. However, since RH is a function of temperature, both the drying and storage temperature need to be considered. Generally, seeds are dried at ambient temperatures or slightly higher to speed up the drying process and to reduce refrigeration costs (Walters-Vertucci and Roos 1996). The greater the temperature differences between drying and storage temperatures, the higher the allowable RH for drying. For instance, if seeds are dried at 25 °C (77 °F) and stored at 15, 5, or -18 °C (59, 41, or 0 °F), they should be equilibrated to about 30, 38, or 45% RH, respectively. Table 3 gives a brief summary of recommended drying conditions for given storage temperatures. To date, these guidelines have proven reliable for all species tested.

Table 3. Recommended drying conditions for seeds subsequently stored in moisture-proof containers at various temperatures
[The given drying temperature and RH combinations give storage RH of 20 to 25% at the indicated storage temperature.]

Drying temperature	Drying RH for storage at—		
	15 °C (59 °F)	5 °C (41 °F)	-18 °C (0 °F)
°C		*%*	
25	30	38	45
15	22	30	38
5	15*	22	30

* Drying seeds at temperatures less than the storage temperature is not cost-effective and therefore strongly discouraged; dehumidification is more difficult at lower temperatures and the refrigeration costs used during drying might be more effectively spent during storage.

Cost-Benefit Analyses

Drying and storage conditions used by seed producers and suppliers largely depend on a balance between the cost of seed preservation and the necessity to maintain high quality seeds for a certain period. The three main questions should be considered when deciding appropriate storage conditions:

- What is the required longevity of the seed?
- What is the volume of seed to be produced, processed, and stored?
- Are the resources available?

The answer to the first question is the major determinant of seed storage procedures.

Maintaining seed quality for ≥5 years usually requires storage at ≤5 °C (41 °F). Refrigeration is expensive, but only moderately so if the quality of the seed would be destroyed by substandard storage conditions. Generally, dehumidification requires less energy than refrigeration, making controlled RH environments a less expensive alternative to refrigeration for the short term (Walters-Vertucci and Roos 1996). However, because there is a limit to beneficial effects of drying at 20 to 25% RH, extended longevity can only be achieved through refrigeration (Walters 1998b). Moisture-proof packaging may be expensive, but it may be more cost-effective over the long term than constant dehumidification in a warm, humid climate. Seeds equilibrate faster at ambient temperatures, allowing more seeds to be processed in a shorter period if labor is available to package seeds for low-temperature storage. Alternatively, seeds can be equilibrated at lower temperatures, thereby increasing energy costs but allowing a longer processing period without compromising quality.

Assessing Changes in Seed Quality

No storage procedure guarantees that seeds will remain viable forever. Seeds eventually lose vigor and then viability with time. The extent to which aging occurs can be monitored with initial and subsequent germination assays. Different seed species have different germination requirements that are cataloged in Rule Books published by the Association of Official Seed Analysts (1999). Assessments of seed vigor are more difficult than assessments of germination percentage but usually provide an early warning of deterioration.

Pollen

Pollen can be stored for facilitating seed production and breeding. Pollen from some families is desiccation-tolerant—Liliaceae and Solanaceae, for example—and fairly easy to store, but pollen from other families is desiccation sensitive and is more difficult to store—for example, Cucurbitaceae, Gramineae (Poaceae), and Compositae (Asteraceae) (Hanna and Towill 1995, Hoekstra 1995, Barnabas and Kovacs 1997). As with seed, the major factors affecting longevity are water content, storage temperature, and storage atmosphere. Desiccation-tolerant pollens are best stored at moisture levels of ≤10%, obtained by either air -drying or by equilibration at known RH. Greater longevities occur at lower temperatures, with more than 2 years often feasible with -18 °C (0 °F) storage. Cryogenic storage at -80 to -196 °C (-112 to -320 °F) greatly increases longevity.

Storage in a vacuum or with a N_2 atmosphere also enhances longevity.

Storage of desiccation-sensitive pollen is more problematic, but some can be desiccated to 10 to 15%. Reports of storage at 4 °C (39 °F) and -20 °C (-4 °F) are sparse, and the expected longevities are short: from hours to a few days. If the pollen is not over-dried, cryogenic storage is possible.

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