Factors Affecting Tree Seed Storage

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Abstract: Seed storage is necessary to provide an annual supply of viable seed for reforestation and for preservation of germplasm for gene conservation, to mention only two purposes. Seed longevity is inherited and varies among species. Five storage behaviours are recognized: orthodox, sub-orthodox, temperate recalcitrant, tropical recalcitrant, and intermediate. Seed moisture content and storage temperature are the two most important factors contributing to storage success but the optimal values for these factors vary with tree species and their storage behavior. Hermetically sealed containers are necessary for maintaining viability of orthodox and sub-orthodox seeds but some air exchange is required for recalcitrant seeds which remain metabolically active and require oxygen for respiration.

Keywords: Longevity, storage behavior, storage condition, orthodox, recalcitrant

Introduction

Storage of tree seeds is necessary for sustainable forest management as many tree species produce good seed crops at irregular intervals. Sound sustainable forest management requires maintaining a seed inventory of major reforestation species for 5 to 10 years to meet continued demand for reforestation and afforestation purposes. Such a strategy is not only economic but also genetically and physiologically advantageous. Genetic diversity is being increasingly emphasized in sustainable forest management and must be incorporated into seed collection planning. This is especially true when purchasing seeds for planting programs where matching the seed source with planting sites and using seed of high genetic and physiological quality are important for plantation success. It should be remembered that forestry is a long-term investment and seed cost is typically less than 2% of the total cost of plantation establishment (Midgley 1990). Therefore, it pays to maintain an efficient and effective seed inventory for sustainable forestry programs.

An understanding of the major factors influencing the genetic and physiological quality of tree seeds is essential to maintaining this quality. In this paper we review the major factors such as seed longevity, seed quality, and storage conditions and discuss their effects on seed storage of temperate, sub-tropical and tropical tree species.

Seed Longevity

Seed longevity is inherited and varies among tree species and storage behaviour. The typical characteristics of the different types of storage behaviour are summarized in Table 1. Seeds of species with a high degree of tolerance to drying, sub-freezing temperatures and sealing, known as orthodox, can be stored for up to 75–100 years (FAO 1993) (Tables 1 and 2). Bonner (1990) sub-divided orthodox seeds into two groups: true orthodox and sub-orthodox. Sub-orthodox seed can be stored under the same conditions as true orthodox seed but for shorter periods due to high lipid content or thin seed coats. *Populus* seed was assigned to this category, however, recent research results showed that *Populus grandidentata* and *P. tremuloides* seeds can be successfully stored at -20°C for 32 and 29 years, respectively and therefore do not belong to this sub-orthodox group (Simpson et al. 2004) (Table 2).

In contrast, seeds classified as recalcitrant, cannot tolerate desiccation, sub-zero storage temperatures, or sealing, and therefore can only be stored for a relatively short period of a few weeks to a few years (Table 3). Again, Bonner (1990) subdivided recalcitrant seeds into temperate and tropical recalcitrant. In addition, there is another group of tree species whose seed storage behaviour is between the above two groups and is known as intermediate (Table 4). These artificially classified storage behaviours are not universal. For example, the intermediate seed storage behavior was not discovered until 1990 (Ellis et al. 1990) and more tree species with seeds of intermediate storage behavior have been found as seed research has expanded to tropical and sub-tropical species. In nature, the seed storage behavior of various tree species in different habitats has evolved in a continuous manner ranging from the most orthodox to the most recalcitrant (Farrant et al. 1988).

Hong and Ellis (1996) developed a simplified protocol for determining seed storage behavior of various plant species. They also developed a rough guide for classification of the three storage behaviors based on seed moisture content at maturity or shedding: orthodox seed, <20-50%; intermediate, 23-55%; recalcitrant, 36-90% (fresh weight).

Initial Seed Quality

Past research results have demonstrated that initial seed quality influences the storage life of tree seeds: the better the initial seed quality, the longer the seeds store (Willan 1985, Schmidt 2000, Simpson et al. 2004). Maximum genetic and physiological quality of seeds can be obtained and maintained when seeds are collected at maturity in good crop years, and properly handled and processed (Wang 1974, 1982; Schmidt 2000, Simpson et al. 2004). This is especially true for seeds requiring post-harvest ripening (e.g. *Abies procera, Picea glauca*) or artificial drying (e.g., *Shorea roxburghii, Shorea siamensis*) to complete their maturation (Rediske and Nicholson 1965, Caron et al. 1992, Panochit et al. 1984, 1986).

Seed Moisture Content

Seed moisture content is one of the most important factors for maintaining germinability and vigour of seeds in storage (Barton 1961, Harrington 1972, Wang 1974), especially for seeds in long-term storage. For agricultural seeds, Harrington (1972) developed a useful rule of thumb: when seed moisture content is between 5 and 14%, the longevity of seed storage is doubled for each percentage reduction of moisture content or for each 5°C decrease in storage temperature. Optimum moisture content for effective seed storage varies greatly with tree species and their storage behavior, storage condition and storage period because of the different morphological and physiological characteristics. Seeds with orthodox storage behavior (i.e., most conifers and small-seeded hardwoods), can be dried to a very low moisture content without injury (e.g., 0 to < 1%) (Joseph 1929, Schonborn 1964). The FAO/IPGRI (1994) recommended a low seed moisture content of 4–7 % for long-term storage of germplasm in gene banks.

For long-term storage of forest tree seed, the general guide for seed moisture content is below 10% (fresh weight). Willan (1985) recommended a moisture content of 4–8% for safe storage of most orthodox tree seeds. These criteria have been confirmed by results from a recent storage study in which the initial mean germination of 96% was maintained after 27 years for 24 seed lots of *Picea glauca* stored at -20°C with initial seed moisture content of 3.6–5.3%. Although seed moisture content increased 1.3–1.6% during storage in plastic bags it did not seem to have an effect on the maintenance of seed quality (Simpson et al. 2004). From these results, it seems that seed moisture contents of 4–7% are ideal for long-term storage of orthodox tree seeds.

For seeds with intermediate storage behaviour, the appropriate moisture content generally reported was 7–10% for those of tropical origin (Hong and Ellis 1996). In Thailand, Pukittayacamee et al. (1995) also found that 7% moisture content was the best for storing *Swietenia macrophylla* seeds in plastic bags at 10°C for 2 years.

For seeds with recalcitrant storage behaviour, the optimum moisture content varies between temperate recalcitrant and tropical recalcitrant tree species. A report from Daigle and Simpson (2003) demonstrated that when the moisture content of three single tree seedlots temperate recalcitrant *Quercus rubra* acorns dried from 37% to 32% (fresh weight) and stored in glass jars covered with parafilm or 0.1 mm thick poly bags at -2^0C, their germinability showed 86-95% after 6 months, 66-98% after 12 months, 30-83% after 18 months, 24-47% after 24 months, 15-46% after 30 months, nd 0-10% after 36 months. Bonner(1973) stored *Quercus falcate* var. *pagodaefolia* acorns of 35% moisture content at 3°C for 30 months with a loss of 6% viability. Bonner (1984) suggested storing acorns of the *Quecurs rubra* group at 35–45% seed moisture content and 1–3°C. He attributed the loss of viability to a rapid rate of seed respiration occurring at such conditions. Silver maple (*Acer succharinum*) seeds with 50% moisture content were successfully stored at -3°C for 18 months (Tylkowski 1984).

Seeds of some sub-tropical recalcitrant species, such as *Cyclobalanopsis gilva, C. morrii, C. glauca,* and *Quercus spinosa,* can be dried to moisture contents of 33-49% and stored in mixture with moist peat moss in cold stratification at 4°C for one year or more (Wang et al. 1995). Similarly, seeds of *Taxus celebica, Livistonia subglobosa, Palaquium formosanum, Roystonea regia, Areca catechu* and *Sassafras randaiensis* can also be moist stored in stratification at 4–5°C for 2–3 years or more (Wang et al. 1995). Dormant seeds generally store longer than non-dormant seeds. There is a need for more research on the storage behavior of sub-tropical tree species.

For tropical recalcitrant seeds, seed moisture content for safe storage varies from little to no tolerance for drying For example, seeds of the mangrove tree species such as *Avicennia marina* (probably also *Rhizophora apiculata, Rhizophora mucronata*) are highly recalcitrant and can withstand very little drying either before or after shedding (Farrant et al. 1992), conversely, *Hopea hainanensis*, with a lowest safe moisture content (LSMC) of 30% (fresh weight), can survive 365 days in optimum storage (Tompsett 1992). Of the most tropical recalcitrant seeds, the LSMC for optimum storage was found to be 30–74% and storability of 15–365 days (Tompsett 1992). Berjak and Pammenter (2002) discussed storage behaviour of orthodox and recalcitrant seeds and concluded that the loss of viability of recalcitrant seeds is likely due to the consequences of unbalanced metabolism during dehydration and desiccation damage occurring when non-freezable moisture is removed. They also stressed the importance of rapid drying rates in safely achieving lower moisture levels. In spite of recent extensive research on tropical recalcitrant seeds, optimum storage of this category is still limited to very short term of 365 days.

Storage Temperature

Storage temperature is another critical factor that influences tree seeds in storage. It interacts closely with seed moisture content. The effect of temperature on seed storability varies with tree species, storage behaviour, seed moisture content, type of containers, and frequency and carefulness of seed withdrawal. The impact of temperature on tree seed storability has been reported by many investigators (Holmes and Buszewicz 1958; Barton 1961; Wang 1974; Bonner 1984, 1990; Stanwood and Bass 1981; Stanwood 1985; Willan 1985; FAO 1993; Schmidt 2000). The general relationship between storage temperature and seed moisture content, can be summarized as follows: for a given seed moisture content, the higher the storage temperature the faster the rate of seed deterioration within the limits of storage temperature; the lower the storage temperature, the greater tolerance of seeds to higher moisture contents (less than 7–8%) (Barton 1961).

Sub-freezing storage temperatures have been studied and found to be more advantageous than near or above freezing temperatures for the long-term storage of orthodox tree seeds, and the lower the temperatures below freezing, the better its benefits (Barton 1961, Stanwood and Bass 1981, Stanwood 1985, Wang et al. 1993; Simpson et al. 2004). Based on results from many years of research, the protocols established for long-term storage of germplasm recommended by FAO/IPGRI (1994) are 4–7 % seed moisture content and -18°C or lower temperature. So far, these storage recommendations remain unchanged. However, some gene banks have adopted cryopreservation with temperatures of -145 to -196°C for long-term storage of their valuable germplasm (Stanwood and Bass 1981, Stanwood 1985). Stanwood (1985) grouped seeds of different species into three categories based on their tolerance to liquid nitrogen(LN_2): desiccation-tolerant and LN_2-tolerant; desiccation-tolerant and LN_2-sensitive; and desiccation-sensitive and LN_2-sensitive. Crypreservation of tree seeds has primarily been experimental to evaluate its feasibility and effectiveness. Five years of cryo-storage of black spruce (*Picea* mariana), white spruce (*Picea glauca*), and lodgepole pine (*Pinus contorta*) seeds has shown no superiority of using liquid nitrogen of – 196^{0}C to –20^{0}C at a given moisture level of 3–4%, 5–7%, and 15–20% (fresh weight) (Beardmore and Wang 2001).

With advancements in tissue culture, a new technique known as cryo-storage of excised embryo axes was developed with promising results (Krishnapillay and Marzalina 1994, Hong and Ellis 1996, Pence 1990). This technique is especially important for extending the longevity of large-sized recalcitrant seeds such as butternut (*Juglans cinerea*) (Beardmore et al. 2002) and many tropical recalcitrant seeds and for saving storage space.

In contrast, the appropriate storage temperature for temperate recalcitrant seeds is 2 to -3°C with seed moisture contents of 35–50% depending on tree species (Bonner 1990). For tropical recalcitrant seeds, the optimum temperature for storage varies greatly from 2–16°C depending on tree species and storage period (Bonner 1990, Schmidt 2000). However, seeds of some *Dipterocarpus* species were killed by the storage temperature <14°C, while *Shorea ovalis* seeds stored best at 21°C (Willan 1985).

For seeds with intermediate storage behaviour, Hong and Ellis (1996) had an updated review of the temperature effect on their storability. The optimum temperature for storing intermediate seeds varied greatly depending upon whether the species was adapted to temperate or tropical environments. For example, papaya (*Carica papaya*) seeds with moisture content of 9–10% can be stored at 10°C for 6 years (Bass 1975 quoted by Hong and Ellis 1996), while *Swietenia macrophylla* seeds with about 7 % moisture content can be stored for 2 years at 10°C in air-tight plastic bags (Pukittayacamee et al.1995). When seeds with intermediate storage behaviour are stored at temperatures lower than 10^{0}C, those of the tropical origin deteriorate more rapidly (Hong and Ellis 1996). Although reports exist of failures in cryopreservation trials of the whole seeds with the intermediate storage behaviour, there were successful examples of cryopreservation of excised embryos of intermediate storage species including *Citrus sinensis, Coffea arabica, Corylus avellana* (Hong and Ellis 1996).

Storage Method and Seed Withdrawal

The efficiency of a storage container is largely determined by its intrinsic permeability characteristics and method of sealing (Freire and Mumford 1986). Past experience has positively proved that hermetic sealing or airtight storage of orthodox and sub-orthodox tree seeds is critical for long-term storage (Huss 1967, Wang 1974). Airtight storage has the advantages of maintaining constant moisture content and of protecting seeds from insects and diseases. Of the various containers used for tree seed storage, moisture-proof, laminated foil packets are used for long-term storage of small quantities of genetic material in gene banks, while custom-made plastic bags in various capacities, are commonly used for operational seed stores. In Canada, orthodox tree seeds used for reforestation are stored in high-density plastic containers in the provinces of New Brunswick, Nova Scotia, Ontario, and Québec while 0.13–0.15 mm thick plastic bags with all excess air expelled and placed into waxed cardboard boxes at -18°C in the provinces of Alberta and British Columbia (Altmann and Lafleur 1982, Kolotelo et al. 2001). Plastic bags should be checked periodically to ensure there are no cracks or leakage problems (Donna Palamarek, Alberta Tree Improvement and Seed Centre, personal communication). Small quantities of seed are stored at the National Tree Seed Centre in glass jars with screw cap lids.

Although recalcitrant seeds are stored at reduced seed moisture content and temperature, they remain metabolically active and need oxygen for respiration. Plastic bags of 0.05–0.10 mm thickness were found suitable to allow some gas exchange and to prevent excessive moisture loss. Schmidt (2000) and Wang et al. (1995) reviewed moist storage with media of both temperate and tropical recalcitrant seeds and found that many species benefited from moist storage with media such as sphagnum, coconut dust, sawdust, or perlite.

Since the proportion of the empty space in storage containers will affect storability, the container should be completely filled. When the volume of seeds is reduced in the container due to withdrawal, seed should be transferred to containers with smaller capacities to minimize air space. Another critical factor for seed storage life is disturbance from seed withdrawal if proper precautions are not strictly observed (Simpson et al. 2004). To minimize the ill-effects of disturbance from seed withdrawal, precautions must be exercised to ensure that the seeds in the container have come to equilibrium with room temperature and that the withdrawal is completedin the shortest time possible.

Conclusions

1. Seed longevity in storage is affected by its genetic and physiological quality. Therefore, as much efforts as possible should be made to attain and maintain maximum seed quality from collection through handling and processing to storage and withdrawal.
2. Based on current knowledge and experience, the storage life of true orthodox tree seeds has been extended to at least 50 years when seeds are optimally handled and stored with 4–7% seed moisture content (fresh weight) in sealed or airtight containers at -18 to -20^{0}C. Cryopreservation has the potential to extend longevity of true orthodox tree seeds to 100 years or more.
3. To minimize the impact of disturbance on long-term stored tree seeds, several smaller containers should be used for each seed lot to avoid impacts from frequent withdrawals from large containers.
4. To minimize the impact of disturbance on stored seeds, containers should be only be opened after they have come to equilibrium with the ambient temperature and withdrawal should be completed in the shortest time possible. With current international research efforts on recalcitrant and intermediate seeds, it is hopeful that suitable techniques will soon be developed for extending the seed storage life of those species.

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Table 1. Characteristics of the various seed storage behaviours.

Storage behavior	Maturity drying	Desiccation tolerance	Seed moisture content (% fw)	Storage Temperature (°C)	Longevity (years)	Storability
True orthodox	yes	very high	2–6	2 to -196	75–100	long-term
Sub-orthodox	yes	high	< 10	-1 to -40	< 12	medium term
Temperate recalcitrant	yes	low	> 35	2–4	2–4	short term
Tropical recalcitrant	yes/no	very low	> 45	4–15	up to 1 year	very short
Intermediate	yes	high	9–10	10	2–6	medium

Table 2. Some selected tree species with orthodox seed storage behavior

Species	Moisture content (% F.W.)[1]	Storage temperature (°C)	Maximum storage time (years)	Germination (%)[2]	References
Abies balsamea	4.1	-20	21	73	Simpson et al. 2004
Betula alleghaniensis	5.8	-20	28	85	Simpson et al. 2004
Picea glauca	7.9	-20	33	92	Simpson et al. 2004
Picea mariana	6.5	-20	30	95	Simpson et al. 2004
Picea rubens	7.4	-20	45	80	Simpson et al. 2004
Picea sitchensis	5.1	-20	31	92	Simpson et al. 2004
	6.0	-18	32	84	Kolotelo et al 2001
Pinus banksiana	8.9	-20	40	87	Simpson et al. 2004
Pinus contorta var. *latifolia*	10.7	-20	33	90	Simpson et al. 2004
Pinus palustris	6–9	-18	20	75	Barnett and Pesacreta 1993
Pinus resinosa	7.3	-20	42	83	Simpson et al. 2004
Pinus strobus	7.4	-20	23	97	Simpson et al. 2004
Populus grandidentata	9.3	-20	32	63	Simpson et al. 2004
Populus tremuloides	9.5	-20	29	72	Simpson et al. 2004
Pseudotsuga menziesii var. *menziesii*	7.0–8.3	-18	31	92–94	Kolotelo et al. 2001
Thuja plicata	8.0	-18	31	52	Kolotelo et al. 2001

[1] fresh weight basis
[2] germination after the number of years in storage

Table 4. Tree species with intermediate storage behavior.

Species	Moisture content (% F.W.)	Storage temperature (°C)	Maximum storage time (months)	Germination (%)	References
Azadirachta indica	9–13	20	2+	75+	Gaméné et al. 1996
Cinnamomum camphora	6.7	5 or 15	12	77[1]	Chien and Lin 1999
Carica papaya	7.9–9.4	15	12	95+[1]	Ellis et al. 1991
Coffea arabica	10	15	12	90+[1]	Ellis et al. 1990
Lindera Communis	50.8[2]	4	24	35	Chien et al. 2004
Lindera megaphylla	47.8[2]	4	18	62	Chien et al. 2004
Swietenia macrophylla	7	10	24	80+	Pukittayacamee et al. 1995

1 Estimated value from the original graph

2 Moisture content in moist storage equivalent to cold stratification

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