

Germination Characteristics of Tree Seeds: Spotlight on Southern African Tree Species

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ABSTRACT

Many tree species of economic potential are propagated by seeds, but seed germination information is limited due to inadequate research. This frustrates genetic conservation, ecosystem restoration, domestication and biodiversity efforts. Deforestation, floods, drought and other disasters are endemic to many countries of Africa and these have a negative impact on the availability of many tree species which have a significant contribution as food and income sources. This review takes stock of seed germination and storage behavior of some important southern African tree species. Recalcitrant and orthodox seeds are the two extreme seed germination behaviors distinctly discussed, but information on seed germination and storage behavior of many southern African tree species is limited. Furthermore, knowledge on seed dormancy of recalcitrant or orthodox tree seeds is limited. Orthodox seeds tolerate relatively long storage periods, and hence have inherent primary seed dormancy. Seed dormancy for many recalcitrant tree seeds is not well explained, but such seeds are sensitive to desiccation injury and have a short storage period. Seed germination and storage behavior of many southern African tree species are not fully established with respect to secondary metabolites, fruit pulp composition, growth hormones and physical impediments. In this review, seed germination and storage behavior and different germination barriers will be the main focus.

Keywords: hormonal balance, osmopriming, seed germination, seed testa

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INTRODUCTION

Tree seeds are stored as important genetic resources for species biodiversity, ecosystem restoration, conservation

and domestication (Berjak and Pammenter 2004). However, there has been little research on seed germination and storage behavior of many tree species, especially wild tree species of southern Africa. It is envisaged that reliable but

cheap seed storage technologies could reduce forest genetic resource erosion or extinction ravaging many countries of southern Africa. This review takes stock of the knowledge gaps on seed germination and storage behavior of some important tree species in southern Africa. Seed germination and storage behavior and aspects of seed germination barriers such as seed testa, pulp composition, hormonal balance and secondary metabolites (phenolic compounds) are discussed in this review.

IMPORTANCE OF TREE SPECIES

Biological diversity for tree species is now becoming a priority, and hence robust germplasm conservation programs are needed. According to Akinnifesi *et al.* (2007), one of the major challenges to widespread adoption of agroforestry and related technologies is the availability of high quality planting stock of priority trees. In southern Africa, trees such as *Pappia capensis*, *Parinari curatellifolia*, *Sterculia appendiculata*, *Schinziophyton rautanenii*, *Sclerocarya birrea*, *Uapaca kirkiana*, *Tamarindus indica*, *Ximenia caffra* and many others are vital sources of food and income. Some of these trees produce seeds rich in edible oils (Nerd *et al.* 1990; Mng'omba and du Toit 2006) and such vegetable oils could be utilized as potential alternative sources of bio-fuels (Mng'omba and du Toit 2006). Bio-fuels can be exploited as mitigation measures to reduce greenhouse gasses emitted into the atmosphere from fossil fuels. *Strychnos madagascariensis* and *X. caffra* seeds are high in fatty acids. The former contains about 68% oleic acid, while *X. caffra* seeds have about 59% oleic acid (Khumalo *et al.* 2002). Furthermore, the fatty acids from these two trees are potential starting materials for the production of cocoa butter equivalents. However, differences in the quantity of such fatty acids have been reported within these tree species. This has been attributed to provenance differences and possibly, the method used for fatty acid analysis. Fruits from several priority indigenous tree species in southern Africa such as *Adansonia digitata*, *U. kirkiana*, *P. curatellifolia*, *S. birrea*, *S. cocculoides*, *Ziziphus mauritiana* and *T. indica* contain edible pulp which can be processed into various products such as jam, juice, sweets, yoghurts, a variety of wines and concentrates (Akinnifesi *et al.* 2006; Mng'omba *et al.* 2007). Keegan and van Staden (1981) reported that *S. rautanenii* nuts are rich sources of protein (26%) and lipid (57%). According to Saxon and Chidiamassamba (2005) the use of *S. rautanenii* oil in preparing dishes (as oil or sauce thickener) offers a special taste that some oily (oleaginous) crop species such as groundnuts, sesame or sunflower do not possess.

Many wild trees of southern Africa can combat the problem of desertification ravaging or looming in many African countries. These wild trees of southern Africa grow on marginal land (Mng'omba and du Toit 2006). For example, *S. rautanenii* trees grow and survive on sandy and infertile soils that are of little use for agricultural crops (Saxon and Chidiamassamba 2005). The values of these wild trees for household consumption, medicine, ornamentals, timber and as sources of income generation are becoming evident in that many are now being spared during land-clearing for farming in many local communities of southern Africa (Packham 1993; Mng'omba and du Toit 2006). For instance, *U. kirkiana*, *S. birrea*, *Azanza garkeana*, *Vangueria* spp., and *P. curatellifolia* are some of the wild trees often spared on farmland during land clearing (Packham 1993; Akinnifesi *et al.* 2006). Many indigenous fruits from Miombo woodlands are important for the livelihood systems of both rural and urban dwellers in southern Africa, especially during periods of famine and food scarcity (Mithöfer and Waibel 2003; Mithöfer *et al.* 2006; Akinnifesi *et al.* 2006). However, efforts to conserve these important tree species of southern Africa either *in situ* or *ex situ* have been limited.

SIGNIFICANCE OF SEED GERMLASM

Seeds as vital propagules

Seeds are still important starting materials for propagation of many vital tree species. Furthermore, the use of seeds as propagules has been considered the easiest and cheapest, and the most common means for many agroforestry and timber tree species (Akinnifesi *et al.* 2007). Generally, this has been attributed to the fact that seeds are often easy to produce and handle (Black 1989). Comparatively, vegetative propagation methods such as grafting, budding and air layering require some skills and knowledge. However, many fruit trees are preferably propagated by grafting, budding, air layering or stem cutting methods in order to achieve early fruiting. For *U. kirkiana* trees, 80% graft-take has been achieved using seedlings as rootstocks (Akinnifesi *et al.* 2007). Therefore, seeds are important starting materials for tree propagation because many rootstocks are often raised from seeds (seedlings). This is because seedlings easily develop normal and functional roots unlike marcots or cuttings, and hence seedlings possess good root development (Mng'omba 2007). Moreover, such rootstocks are often used to rejuvenate the old fruit trees.

A seed is a juvenile plant material, and hence it is often easier to regenerate plants through micro-propagation (tissue culture) technique than from the mature plant tissues. *In vitro* propagation of many woody tree species is difficult due to low regeneration capacity, especially explants from mature plant tissues. Moreover, explants from mature plant tissues are often difficult to decontaminate. A few tree species of southern Africa have been cultured using explants derived from mature plant tissues. Mng'omba *et al.* (2007) reported that successful rejuvenation and pre-conditioning of grafted *U. kirkiana* trees were prerequisites for *in vitro* propagation. Because of a high loss of forest resources in many countries of southern Africa, micropropagation or tissue culture techniques can be employed for germplasm multiplication and selection of superior genotypes. In view of this, seeds are important starting materials for mass multiplication of tree planting materials as well as tree improvement through selection.

Seeds for genetic improvement

Seeds are important starting materials for tree breeding and genetic improvement. The use of seeds enables capturing the natural genetic variation (due to random mating or pollination) and this further enables selection and improvement of superior trees within a large population (Dawson and Were 1997). Through sexual hybridization, desirable genes could be gained cheaply unlike the use of modern biotechnology (cloning) which is often expensive. Although the genetic gains can be low for sexual hybridization (seeds), the genetic base is not narrowed (Kitzmilller 1990). Some tree and fruit traits requiring improvement for *U. kirkiana*, a priority fruit tree of southern Africa, include improved fruit load, size and taste and pulp content (Akinnifesi *et al.* 2007). It is envisaged that through sexual hybridization, new and superior genotypes could be developed. Moreover, *U. kirkiana* trees show wide genetic diversity and variations in geographical adaptation (Akinnifesi *et al.* 2004; Mng'omba 2007), and hence this genetic diversity can be exploited for improvement. Therefore, seeds are important starting materials for tree improvement.

Seeds for genetic conservation

In many farming communities in southern Africa, there is declining of tree genetic resources due to deforestation (Akinnifesi *et al.* 2007). Other catastrophes such as forest fires, drought and floods are also ravaging the region. According to Bewley and Black (1983), seed conservation has been the most reliable and widely used method for *ex situ* storage. Seeds are easily transported and stored in a small

space unlike the marcots, scions and cuttings. According to Akinnifesi *et al.* (2007), a participatory selection and propagation approach has been adopted by ICRAF for domestication of indigenous fruit tree species of southern Africa. Generally, it will be easier for many households to manage some tree seeds as germplasm conservation measure than the mother orchards due to land holding size limitations. In the wild, many trees regenerate from seeds and can be dispersed to different ecological sites. This will enable natural tree species perpetuation, and hence conservation of genetic resources.

Seeds for molecular farming

There are reports indicating that seeds could be important storage or hosts for specific proteins. This is because many seeds are already better storage organs for proteins, fatty acids and carbohydrates than leaves, tubers and other aerial plant parts (Moloney 2000). It is reported that novel proteins could be manipulated to accumulate in the seeds for therapeutic or industrial uses (Herman 2006). For instance, hirudin (blood anticoagulant) and avidin (protein with affinity for biotin) have been produced and stored in seeds through molecular technology (Moloney 2000). Furthermore, seeds could be utilised for long term and reliable storage of such special proteins. Therefore, seeds could be important vehicles in producing novel substances for human livelihood.

SEED GERMINATION AND STORAGE BEHAVIOUR

Seed germination is defined as the emergence of the embryo from the seed and the germination process is triggered by a variety of anabolic and catalytic activities (Bewley and Black 1983). Several reports indicate that there are three classes with respect to seed germination and storage behavior (Roberts 1973; Berjak and Pammenter 2004). These three classes are recalcitrant (intolerant to desiccation), intermediate or orthodox (tolerate desiccation and exhibit dormancy). Research data on seed germination are insufficient to classify many wild tree species of the southern Africa into these classes. According to Bonner (1990), tree seeds are better divided into four groups, namely (1) 'true orthodox'; (2) 'sub-orthodox'; (3) 'temperate recalcitrant'; and 'tropical recalcitrant'. The demarcating lines between these classes are often unclear, but a continuum of seed germination and storage behavior exhibited by many tree seeds support the existence of such subdivisions. This classification appears more appropriate for tree seeds than having an intermediate group. The issue on seed germination behavior to be categorized as either discrete or a continuum has been discussed by Berjak and Pammenter (2004).

Seed drying is used to group seeds into either recalcitrant, intermediate or orthodox, but faulty seed drying often lead to incorrect classification (McDonald 2004). For example, *Citrus limon* (lemon) seeds were initially identified as recalcitrant, but recent revelation shows that the seeds exhibit orthodox germination behavior upon removal of the seed testa (Chin 1995). According to Bonner (1990), lemon seeds are classified as 'sub-orthodox' based on storage behavior. However, it is unclear whether this classification was made after seed testa removal or not. According to Bewley and Black (1994), the seed testa protects the embryo, and may contain some phenolics. The composition of such compounds may change with time. Since seed germination is complex due to a number of factors involved, there is a need for more research studies to elucidate the significance of seed testa on seed classification. Such information could be useful in seed classification and post harvest handling of tree seeds. At present, our knowledge is limited to make a concise recommendation as to whether seed classification should be based on seed with or without seed testa.

Generally, classifying seeds into an intermediate group might not provide enough information, especially to indicate whether such seeds are closer to recalcitrant or ortho-

dox behavior. Therefore, use of sub-classes, such as true-orthodox or sub-orthodox, is more informative in that it could aid handling and storage of such seeds. Classifying recalcitrant seeds into either tropical or temperate (Bonner 1990) is based on tree species as already discussed by Berjak and Pammenter (2004).

Recalcitrant seeds

Many tropical and subtropical tree species are known to produce recalcitrant seeds (Berjak and Pammenter 2004), but there is still limited knowledge on the germination and storage behavior of such tree seeds, especially wild tree species. Recalcitrant seeds have high moisture content, estimated to be in the range of 30-70% at maturity and such seeds include rubber, cocoa, coconut, mango, and jack fruit (Chin 1995). Recalcitrant seeds germinate rapidly when sown fresh, but are sensitive to desiccation and freezing (Berjak and Pammenter 2004; McDonald 2004). This makes them difficult to store and some recalcitrant seeds perish at 26% moisture content or when stored at 15°C temperature or below. According to Chin (1995), *Hevea brasiliensis* (rubber) seeds die when stored at 15% to 20% moisture content, while *Theobroma cacao* seeds die at 26% moisture content. Death of recalcitrant seeds due to loss of moisture is mainly attributed to the loss of membrane integrity and nuclear disintegration (Chin 1995).

Intermediate seeds

These seeds are known to have relatively high water content at harvest and are able to withstand substantial dehydration. *Azadirachta indica* (neem) seeds exhibit variations in storage behavior which varies from orthodox through intermediate to recalcitrant (Berjak and Pammenter 2004), while Gaméné *et al.* (1996) described neem seeds as intermediate. This germination behavior has been linked to a function of provenance. Bonner (1990) classified neem seeds as 'tropical recalcitrant'. Furthermore, tropical and temperate recalcitrant seeds only differ in that the former group of seeds is sensitive to low temperatures. Tropical recalcitrant seeds include many tropical fruit trees and other trees such as *Theobroma cacao* and *Shorea* spp. (Bonner 1990). *S. cocculoides* seeds are said to be intermediate, but significant differences between provenances and storage temperatures (at room temperature and 4°C below zero) have been reported (Mkonda *et al.* 2003; Akinnifesi *et al.* 2007). As mentioned before, this intermediate group lacks adequate information. Sub-divisions of orthodox and recalcitrant seeds would be more informative. Perhaps, this is the reason that many reports do not dwell much on this group compared to the two extreme seed germination behavior (orthodox or recalcitrant). There has been insufficient scientific research on tree seed germination and storage behavior. Consequently, several seed germination reports tend to classify tree seeds based on observations. In addition, the storage conditions are not uniform, and hence it is difficult to verify that particular seeds belong to the recalcitrant, intermediate or orthodox group.

We hypothesize that there should be 'true recalcitrant' and 'sub-recalcitrant' classes, especially for tree seeds. The 'sub-recalcitrant' class means seeds exhibiting germination and storage behavior close to the 'true recalcitrant'. Many tree seeds are often wrongly classified as recalcitrant because they exhibit variations in seed germination behavior. For instance, *U. kirkiana* seed viability is short-lived (Ngulube *et al.* 1997) and such seeds have been described as recalcitrant. These seeds also germinate readily within the first three months (Mwamba 1995). There has been no desiccation study to confirm whether *U. kirkiana* seeds are really recalcitrant. Observations clearly show that *U. kirkiana* seeds are short-lived and are sensitive to desiccation, but they might not be 'true recalcitrant' seeds. The appropriate class is most likely to be 'sub-recalcitrant'. However, research is needed to confirm whether these seeds belong to

true recalcitrant or sub recalcitrant group. Since recalcitrant seeds are more difficult to handle and store than orthodox seeds, sub-classes of recalcitrant seeds are, therefore, important to determine or estimate a reasonable storage period for a particular plant species. For instance, Hans (1981) reported that *U. kirkiana* seeds can be stored for a maximum period of four months, but some true recalcitrant seeds can be stored for a maximum period of only a few weeks.

According to Berjak and Pammenter (2004), there are striking differences in seed germination characteristics among species. For instance, *Coffea liberia* (coffee) seeds are recalcitrant, while *C. canephora* (robusta coffee) seeds are said to be intermediate. Furthermore, *C. arabica* seeds are less sensitive to desiccation than orthodox seeds, but they are sensitive to chilling. This example shows that classifying the behavior of coffee seeds into either 'true recalcitrant' or 'sub-recalcitrant' would not be totally wrong, and hence coffee seeds would be better handled or stored as true or sub-recalcitrant rather than true or sub-orthodox seeds.

Orthodox seeds

Orthodox seeds can be dehydrated to low moisture content without drastic effect on germination unlike recalcitrant seeds (McDonald 2004). They are deliberately dried to very low moisture content to enhance storability and longevity. The true orthodox seeds are known to withstand sub-freezing temperatures for long periods when dried to 10% moisture content (Bonner 1990). *Acacia*, *Gmelina* and *Eucalyptus* trees are some of the examples of 'true orthodox' seeds found in the tropics. Generally, many exotic crop varieties produce orthodox seeds and, therefore, can be stored for a year or more. *A. garckeana*, *Flacourtia indica*, *S. birrea* and *P. curatellifolia* have orthodox seeds (Akinifesi *et al.* 2007), and hence they can be stored for a year or more (Teichman *et al.* 1986). Although this classification might be based on observations (without any seed drying tests), such seeds seem to clearly belong to the orthodox. Comparatively, there is a lot of information on the seed germination behavior and optimal storage conditions for most of the agricultural crops (exotic crops) compared to the wild tree species.

Seed viability in storage

Seed viability under storage conditions is known to vary from species to species and depends on many factors. The seeds of some Miombo fruit trees are known lose viability during storage at room temperature (20-25°C) or in the cold room (7-10°C) (Prins and Maghembe 1994). This low seed viability contributes to the poor seed germination of many wild fruit tree species, such that it is difficult to obtain sufficient propagules (Akinifesi *et al.* 2007). According to Dawson and Were (1997), some fruit tree species such as *U. kirkiana* produce recalcitrant seeds (i.e. seeds that do not tolerate low temperatures) which lose their viability if stored for any length of time, even under conditions that are normally conducive to seed longevity. As mentioned before, *U. kirkiana* seed viability is limited to a maximum of four months after removal from the fruit and viability can drop from 80% to 20% within four months. This is attributed to the high moisture content of the seed (48% fresh weight of sun-dried seeds). *U. kirkiana* seeds have no dormancy period and normally germinate as soon as the fruit ripens (Prins and Maghembe 1994).

SEED DORMANCY

Seeds are classified into recalcitrant, intermediate, orthodox groups and/or including the sub-classes as outlined by Bonner (1990). Regardless of the seed class, seed dormancy is an important factor that can affect germination of each group at any stage. Several reports on germination behavior of tree seeds indicate that seed dormancy is prevalent amongst the orthodox seeds compared to recalcitrant seeds.

However, both primary and induced (secondary) seed dormancy could exist in many tree seeds.

Desiccation tolerance and seed dormancy are known to be acquired traits. Seed dormancy is defined as the failure of viable seeds to germinate when conditions are favorable for seed germination. Ecological significance of seed dormancy is that seeds only germinate when conditions are favorable and this ensures plant species survival. Seed germination failure is attributed to the presence of either exogenous or endogenous factors. The latter could be due to the presence of the hard seed testa (morphological seed dormancy) or germination inhibitors present in the capsules or endosperm (Hilhorst *et al.* 2006), while exogenous seed dormancy (i.e. outside the embryo) is caused by physiological factors (Yang *et al.* 2007). However, some seeds exhibit both endogenous and exogenous seed dormancy (Bewley and Black 1994). Often, seed dormancy in some seeds can be established by a close examination of seeds, especially for exogenous seed dormancy. However, it was reported that the hard seed testa does not restrict embryo expansion and seed germination of *S. rautanenii* (Keegan and van Staden 1981). Furthermore, seed dormancy induced during seed handling or storage can hardly be noted by this method.

Primary seed dormancy

Some tree seeds have inherent seed dormancy known as primary seed dormancy, which is mainly caused by maternal tissues. For example, this could be due to embryo immaturity at harvest, inhibition of water uptake, restriction of embryo expansion and the absence of leaching of inhibitors (Hilhorst *et al.* 2006). In this case, such seeds do not germinate despite presence of favorable germination conditions. *P. curatellifolia* seeds are associated with immature embryo, and hence the seeds require after-ripening process to take place before they are successfully germinated. In this case, seed storage is required to allow the after-ripening process to occur. According to Amen (1968), the balance between growth promoters and inhibitors may play a key role in controlling embryo maturation, and hence the seeds are dormant at harvest. With progress in storage time, the hormonal balance shift in favor of the growth promoters, and hence the primary seed dormancy is then broken to enable the seeds to germinate.

Secondary seed dormancy

Induced (secondary) seed dormancy occurs after the seeds are harvested and may exist to either recalcitrant, orthodox seeds or the sub-classes. Furthermore, this type of seed dormancy seems to affect many plant species and it is mainly a function of the prevailing environmental conditions such as temperature, moisture, chemicals, light and many others. Therefore, poor seed handling and storage can bring about secondary seed dormancy. In this case, such environmental conditions play a key role in this type of seed dormancy. For instance, prolonged seed exposure to moist and anaerobic conditions can induce seed dormancy (Totterdell and Roberts 1979). Higher temperatures can also induce seed dormancy for the imbibed seeds that require after-ripening process. Therefore, there is need for research to gather adequate information on proper handling and storage of a particular tree seed to avoid the induced seed dormancy. Currently, information is insufficient, especially for the wild tree species unlike exotic plant varieties that have received a lot of attention in research and development.

Induced seed dormancy can make recalcitrant (non-dormant) seeds to be dormant under unfavorable conditions despite the fact that recalcitrant seeds show rapid germination when sown. This induced seed dormancy may be too long for recalcitrant seeds to germinate rapidly. Furthermore, induced seed dormancy is known to reduce the germination rate, even after exposing such seeds to favorable conditions for germination. In this case, induced seed dormancy shows

remarkable difference between recalcitrant and orthodox seeds in that the orthodox could attain an optimal germination rate upon removal of seed dormancy.

Variations in seed germination within a plant population, provenance or species are often found for non-dormant seeds. Narbona *et al.* (2006) reported significant differences in germination percentage of *Euphorbia nicaeensis* seeds, non-dormant, from different populations and within individuals. It was, therefore, concluded that seed germination studies based on one population must be interpreted with caution since differences in environmental conditions can impose differences in seed germination capacity. Such factors that may impose variations in seed germination could be pre-harvest and post-harvest seed characteristics. According to Basu (1995), pre-harvest, harvest and post-harvest environmental conditions affect seed viability. This is because such environmental conditions could impose differences in seed quality. Pre-harvest conditions include the quality of the initial seed, soil fertility, temperature and photoperiod, soil moisture and herbicides/pesticide application (Basu 1995).

Soil fertility is regarded as a key factor because it can cause abnormal seeds. Temperature influences seed development and ripening and consequently, high temperatures may be undesirable while low temperatures adversely affect the ripening process due to freezing injury. On the other hand, soil moisture can affect seed viability in that drought induced at flowering period can interfere with fertilization, seed weight and decreases seed size (Basu 1995). However, several research reports on the effects of seed size on germination remain contradictory.

CHEMICAL COMPOSITION

The process of seed germination involves an active participation of a whole complex synthetic machinery of the cell and these include enzymes, other factors and co-factors, plant hormones, nucleic acids and energy provision (Basu 1995). It is known that disruption of such activities of one component may cause germination failure. Presence of inhibitors in the endosperm can cause chemical dormancy (Hilhorst *et al.* 2006).

Recent findings show that both moisture content of the embryo axes and chemical composition modify seed germination behavior. According to Berjak and Pammenter (2004), the embryo axes are sensitive to water loss. Furthermore, hormonal imbalance in many orthodox seeds, without visible signs of maturity, may cause seed dormancy. Orthodox seeds require after-ripening process since they are immature embryos at harvest and require storage after harvest. However, optimal storage conditions and duration to attain full germination potential are not yet established for many tree seeds.

Some seeds easily germinate in fruits or pods and this germination behavior has been noted in *X. caffra* (Mng'omba *et al.* 2007). According to Doijode (2006), mature fruits are congenial conditions for seeds storage, especially for a short-term preservation. Furthermore, such storage is ideal for seeds that cannot germinate in the fruits or pods because this type of storage induces seed dormancy. Fruit storage has been known to retain quality for relatively longer periods (Doijode 2006). However, some seeds start to germinate inside the fruits and such seeds are not ideal to be stored in their fruits. van Staden *et al.* (2000) reported that many seeds that are stored in the plant canopy do not often show seed dormancy when released from storage. Observations show that *Moringa oleifera* tree species tend to retain their seed pods on the trees for several months after seed maturation. Furthermore, we have observed high seed germination percentage (>85%) in our trials for one-year old stored seeds or those seeds stored in the tree canopy.

Fruit pulp

X. caffra fruit pulp has a sour taste, while *U. kirkiana* pulp

is sweet when ripe (Mng'omba and du Toit 2006). One is tempted to think that *U. kirkiana* pulp decay faster than *X. caffra* due to high concentration of sugars favorable for microbial growth. However, we observed that *X. caffra* pulp is also easily overgrown by unidentified fungi. This indicates that sour pulp composition may not totally hinder pathogen infestation. Pathogens, especially fungi are known to enhance seed deterioration or decay and some produce toxins that degrade seeds. In this case, degraded seeds could result in low germination rate.

Removal of fruit pulp has been effective in promoting seed germination of *F. indica* (20%), *Diospyros mespiliformis* (80-87%) and *Ziziphus* spp., *T. indica* and *Bridelia cathartica* (93-100%) (Maghembe 1995; Akinnifesi *et al.* 2007). This could be attributed to some germination inhibitors presence in the fruit pulp. The work by Barnea *et al.* (1993) indicated that secondary compounds are present in the pulp, but not in the seeds. Therefore, removal of fruit pulp can also remove seed germination inhibitors in certain tree seeds.

Plant hormones

Seeds or fruits contain plant hormones which can either promote or inhibit seed germination. Abscisic Acid (ABA) is an example of a hormone (endogenous) which inhibits seed germination, while gibberellic acid (GA₃) is known to promote seed germination (Rehman and Park 2000). These two plant hormones are found in many seeds and the concentration ratio of ABA to GA₃ plays a vital role in seed germination. This concentration ratio varies with seed developmental stages. This explains why an external application of GA₃ to some seeds has promoted seed germination (Rehman and Park 2000). Several reports suggest that this hormonal balance (ABA/GA₃) controls seed dormancy. According to Bewley and Black (1994), ABA prevents precocious embryo or seed germination, but genetic mutations, 'viviparous mutants', enable precocious germination. The genetic mutations override the activity of ABA even with the external application of ABA. Differences in ABA concentration between recalcitrant and orthodox seeds have not been established. However, precocious seed germination is prevalent in recalcitrant seeds, but there are inadequate scientific findings to conclude that recalcitrant seeds have higher ABA concentration than orthodox seeds or that the genetic mutations are more prevalent in recalcitrant than in orthodox seeds. Despite numerous research studies on seed germination, there is still need for more work in order to elucidate key factors controlling seed germination in different seed categories or classes. Moreover, a few studies have been carried out on many important wild tree species of southern Africa.

Phenolic compounds

Many tropical plants produce seeds containing high concentrations of secondary metabolites (phenolic compounds) and phenolic oxidases (Chin 1995). Plant phenols are known to form a barrier to water loss, diffusion and pathogen attack (McCue *et al.* 2000). Furthermore, they can function as antioxidants. It has been hypothesized that high phenol concentrations increase seedling vigour and greater lignification. Phenolic compounds are compartmentalized within cell walls and released when cell membrane is damaged due to desiccation (Loomis and Battaile 1966). They are oxidized and form protein/phenol complexes responsible for the loss of enzyme activity (Loomis and Battaile 1966), but there has been limited research work on this subject to elucidate the impact of phenolic compounds on seed germination, despite the fact that many tropical tree species accumulate a lot of secondary metabolites in their cells. According to Basu (1995), accumulation of a number of phenolic compounds was implicated in rice seed viability. Phenolic compounds are important at post germination process for lignification of seedlings. To our knowledge, the role of

Table 1 Seed pre-treatment used to promote germination of some Southern African tree species.

Tree species	Seed pre-treatments	Germination (%)	References
<i>Pappea capensis</i>	seed testa removal	70-90	Mng'omba 2007
<i>Parinari curatellifolia</i>	nicking seeds or complete seed coat removal	17-30	Prins and Maghembe 1994; Swai <i>et al.</i> 2004
<i>Schinziophyton rautanenii</i>	Ethrel - 48 hr at 2.1 cm ³ .dm ⁻³	100	Keegan and van Staden 1981
<i>Sclerocarya birrea</i>	operculum removal for 14-23 months, soaking in potassium hydroxide (1 mol) for 24 hr	80	Teichman <i>et al.</i> 1986
<i>Strychnos spinosa</i>	soaking in water for 12 hr	80	Prins and Maghembe 1994
<i>Uapaca kirkiana</i>	1. soaking in water for 12 hr 2. seed testa removal	93 100	Prins and Maghembe 1994
<i>Vangueria infausta</i>	nicking	40	Prins and Maghembe 1994
<i>Tamarindus indica</i>	pulp removal	100	Prins and Maghembe 1994
<i>Ximania caffra</i>	soaking in water for 24 hr	90	Mng'omba <i>et al.</i> 2007
<i>Zizyphus mauritiana</i>	fruit pulp removal	100	Prins and Maghembe 1994
<i>Strychnos cocculoides</i>	Cleaning and soaking in water for 24 hr	91%	Swai <i>et al.</i> 2004
<i>Flacourtia indica</i>	removing fruit pulp	17%	Prins and Maghembe 1994

many phenolic compounds on seed germination has not been clearly established.

SEED DETERIORATION

There are many factors that cause seed deterioration and these include genetic and mechanical damage, seed moisture, pathogens and many others (McDonald 2004). Furthermore, relative humidity and temperature are important factors affecting seed deterioration since they influence many other factors. It is always difficult to control or stop seed deterioration, but seed deterioration rate can be reduced. Therefore, several reports focus on reducing seed deterioration rather than stopping it. In view of this, seed handling and storage conditions are of paramount importance in reducing this seed deterioration rate. According to McDonald (2004), the events that cause physiological seed deterioration remains incomplete and several reasons and mechanisms of seed deterioration have been well elaborated. For detailed information on this, refer to McDonald (2004).

Genetic damage for seeds may occur during seed storage (Bonner 1990). Seed organelles and micro-molecules can be damaged during poor seed storage. According to Basu (1995), the damages could be a broken plasmalemma structure, contraction of plasmalemma from cell wall, fragmented endoplasmic reticulum and organelles devoid of poly-ribosomes. Such physiological and biochemical damages or DNA lesions become cumulative. Temporary lesions might be repaired during hydration prior to seed germination (Basu 1995), but harsh storage conditions might accelerate seed damage beyond repair. It is likely that damage to seed organelles due to harsh storage conditions might be confused with seed dormancy, especially for temporary lesions. This is more so with non-dormant seeds stored under such harsh storage conditions and developing dormancy with or without any temporary lesions. Seed priming has been used to repair seed damage, but the exact time to achieve the benefits of priming remains unresolved question (McDonald 2004).

SEED PRE-TREATMENTS

Many savanna tree seeds are known to be dormant and this is attributed to the presence of physical dormancy (Baskin and Baskin 1998). Physical impediments (physical seed dormancy) such as hard seed testa hinder seed germination. Furthermore, some fruits are indehiscent at maturity, and hence require physical abrasion or other mechanisms to release the seeds. According to Baskin and Baskin (1998), fire and other chemicals released during burning are important factors in seed germination of many plant species in the tropical savanna areas. Fires are prevalent in savanna areas and southern Africa is not an exception.

Some seed pre-treatment methods used experimentally to promote seed germination of selected tree species are

presented in **Table 1**. Seeds of some fruit trees do not require any special pre-treatment. For instance, Prins and Maghembe (1994) reported up to 80% seed germination from *S. spinosa* (**Table 1**), *S. cordatum*, *U. kirkiana*, *Zizyphus abyssinica*, and *Z. mauritiana* by just cleaning and soaking (24 hrs) the seeds. Furthermore, less than 20% germination was obtained from *F. indica* and *P. curatellifolia* seeds with different pre-treatments (**Table 1**). Nicking *A. garckeana* resulted in 100% germination (Maghembe 1995), while *Zizyphus* spp., *T. indica*, *Parkia filicoides* and *Bridelia cathartica* seeds resulted in 93-100% germination by just removing pulp (Maghembe 1995). Complete removal of seed coat resulted in 70-100% germination for *U. kirkiana* seeds (Hans 1981; Maghembe 1995), but also cleaning followed by soaking in cold water for 24 hours resulted in 90-100% (**Table 1**) (Maghembe 1995).

Seed scarification

Pterocarpus angolensis seeds have a tough seed testa which impedes water imbibition. Fire has been used to rupture the tough seed coats (Banda *et al.* 2006), but can also cause high seed mortality. According to Baskin and Baskin (1998), fire plays a key role in regeneration of many savanna species. It exerts a shock directly on the seed coats, and hence rupturing or cracking the seed coats. Chemical components such as ethylene, ammonia and nitrogen oxides and ash are also released during burning and some of these chemicals are known to stimulate seed germination (van Staden *et al.* 2000). Ethylene has been implicated in seed germination (van Staden *et al.* 2000; Hilhorst *et al.* 2006). Furthermore, leachate from charred wood promotes seed germination and some seeds respond positively to smoke pre-treatment.

Smoke has been reported to enhance seed germination in many plant species and fynbos species that respond to smoke are mostly non-sprouting (van Staden *et al.* 2000). Furthermore, plant seeds that can be stored in the soil respond more to smoke than species with canopy stored seeds. A hypothesized mechanism that makes smoke effective in seed germination has been that active compounds in smoke trigger enzyme activity that controls growth rate (van Staden *et al.* 2000). In the wild, fire also plays a vital role for the buried seeds. The fire can burn a big proportion of the seed coat without damaging the seed embryo, and hence enabling seeds to imbibe water and trigger the germination process. However, many times the seed embryo can be severely damaged, and hence it might be difficult to establish the role of fire to germination of some tree species.

Hot water, sulphuric acid, filing and abrasion pre-treatments have been used to scarify the hard seed coats. However, optimal levels and methods of scarification vary among plant species, and hence they must be determined for each species. We observed that *P. curatellifolia* seed testa is difficult to remove and the use of sulphuric acid (98%) easily damaged the seed embryos, especially for seeds col-

lected from the ground. It seemed that beetles perforated the seed testa, and hence the acid penetrated the weaker part of the seed testa to reach the embryo. Furthermore, the use of a nut cracker proved ineffective and not strong enough to completely remove the tough seed testa of *P. curatellifolia*. Filing and abrasion were rather difficult. We hypothesize that use of concentrated sulphuric acids on *P. curatellifolia* seeds directly collected from the trees could be an option to avoid seed embryo damage.

Fang *et al.* (2006) reported a high seed germination percentage (98%) for 'sweet tea tree' (*Cyclocarya paliurus* (Batal) Iljinjakaja) after the seeds were scarified in concentrated sulphuric acid for ten hours. In the tropics, some seeds have responded positively to sulphuric acid scarification and these include *Acacia nilotica*, *Proposis juliflora*, *Sapindus trifoliatus* (soapnut) and *Annona senegalensis* seeds (Naidu *et al.* 1999). However, such seeds should be collected direct from trees to ensure absence of holes prior to acid pre-treatment.

Bridelia macrantha seeds require just soaking, while *Strychnos spinosa* and *U. kirkiana* require removal of mesocarp and soaking (Prins and Maghembe 1994). Seedling entrapment in sclerotesta has been the main cause of *U. kirkiana* seedling mortality (Ngulube *et al.* 1997). Different scarification methods have been used to remove the seed coats. In the wild, other seed scarification methods include seed trampling by hoofed animals, uncompleted predation by animals, seed damaged by fungi and soil micro-organisms, through an animal's digestive tract passage and extreme changes in temperature (Todd-Bockarie and Duryea 1993). According to Nichols (2005), *S. birrea* (marula) and *Syzygium cordatum* seeds are subjected to digestive juice in the guts of wild animals. This process is said to remove any seed germination inhibitors, and hence enables the seeds to germinate.

Partial removal of seed testa has also improved seed germination of some tree species. According to Prins and Maghembe (1994), *A. garkeana*, *Carithiaum foetidum* and *P. curatellifolia* required nicking of seed testa. Abrasion method of scarification has been effective in promoting germination emergence of *Tylosema esculentum* seeds (Travlos *et al.* 2007).

Phytohormones

Exogenous plant hormones have been used to break seed dormancy in some tree seeds. For example, Keegan and van Staden (1981) reported that *S. rautanenii* seeds with or without seed testa were germinated after pre-treating with Ethrel (used as a source of ethylene). They reported that *S. rautanenii* seeds are dormant and possess a hard testa, but this does not restrict water uptake. This is because these seeds have large and continuous pores (Keegan and van Staden 1981). However, no seed germination was observed after water imbibition for untreated seeds. Furthermore, the hard testa does not restrict embryo expansion during germination, and hence no seed dormancy imposed by the testa. Effective treatments that improved seed germination were only GA₃ and ethylene (Keegan and van Staden 1981). From their work, the main cause of seed dormancy in *S. rautanenii* seeds remained unclear despite the breakthrough in seed germination using ethylene.

Osmopriming

Generally, seeds with low vigour are known to respond positively to osmopriming because DNA repair process can occur at certain water potential to allow metabolism to occur and triggers seed germination. Osmopriming or osmoconditioning is defined as a pre-sowing hydration treatment often used to accelerate seed germination (McCue *et al.* 2000). KH₂PO₄ and KNO₃ solutions are commonly used for seed osmopriming. Mng'omba *et al.* (2007) reported that exogenous application of GA₃ to the stored *X. caffra* seeds was more effective in improving germination. However,

soaking these seeds in water was necessary to achieve high germination of fresh seeds. This indicates that some seeds have specific requirements to improve germination at a particular stage. Research data on seed priming for tree seeds are limited unlike agricultural crops.

STORAGE TECHNOLOGIES

Recalcitrant seeds

Typical recalcitrant seeds are short-lived and can be viable from days to a few weeks and are difficult to store. Some reported potential storage methods include *in vitro* gene banks and embryogenic axes storage as described by Chin (1995). About 60% germination of rubber seeds (recalcitrant) was achieved by immersing these seeds in water for a month. Some reports recommend storing these seeds in moist sawdust and charcoal and sand. Furthermore, storing seeds at 7°C prevents early seed germination, and hence this moist storage has been used for a number of crops including rubber. Inhibitors of seed germination such as natural juice from the aril or pulp of trees have also been used (Chin 1995). Abscisic acid, coumarin, tannins and other phenolic acids have been some of the common seed germination inhibitors (Bewley and Black 1994).

Partial desiccation technique has been used for recalcitrant rubber seeds (Chin 1995). This technique involves surface drying of seeds with fungicide treatment before air-drying at 25°C. The seeds are cleaned before soaking in 0.3% Benlate, drained and surface dried to 20% moisture content. They are stored in perforated plastic bags at 20 ± 3°C. With this technique, rubber seeds have been viable and more than 50% seed germination has been achieved after one year in storage. Cocoa seeds are partially dried to 35% moisture content and dusted with 0.2% w/w Benlate thiram mixture. The seeds are packed in batches of 500 seeds in thin (0.5 mm) perforated plastic bags. They are stored closely in a closed box in air-conditioned room. With this method, more than 50% seed germination has been achieved for cocoa seeds stored for more than six months (Chin 1995). Controlled atmosphere and cryogenic storage methods have been evaluated for the storage of recalcitrant seeds, but with no success. For rubber seeds, cryogenic storage resulted in damaged or cracked seeds (Chin 1995).

Orthodox seeds

Generally, orthodox seeds are cheap and easy to store compared to recalcitrant seeds. This is because many orthodox seeds can be dried to a certain level of moisture content before storage. Many seeds can be stored for a year or more. Liquid nitrogen (-196°C) has been used to store orthodox tree seeds for years without deterioration. Cryogenic seed storage holds the potential to extend the storage life of orthodox tree seeds without genetic damage unlike the conventional storage (Bonner 1990).

CONCLUDING REMARKS

Seed germination involves a number of complex cell activities and both genetic and environmental factors play a key role in modifying tree seed germination and storage behavior. However, seed germination and storage behavior of many tree seeds of southern Africa are yet to be classified. Forest trees of southern Africa are under enormous deforestation pressure and many other catastrophes, and hence more research work is warranted to enhance germplasm multiplication and domestication programs. Furthermore, more research work is needed to determine proper handling and storage of tree seeds, especially recalcitrant seeds which are difficult to store.

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