



Ecological insights into the coexistence of dormancy and desiccation-sensitivity in Arecaceae species

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Abstract

• **Key message** Mechanisms controlling germination of > 2600 Arecaceae species adapted to the tropical forests are not clearly understood. This contribution underpins the notion that the coexistence of dormancy and desiccation sensitivity in some Arecaceae species could significantly affect the germination ecology. Although the evolutionary and ecological significance behind this occurrence is unknown, these traits together could limit the germination from inappropriate depths and allow dispersal.

• **Context** Dormancy and desiccation sensitivity, i.e., recalcitrance, are considered as mutually exclusive traits that evolved to maximize seed survival after dispersal; the former by allowing seeds to spread germination risk temporally then synchronize germination with a favorable growing season, and the latter by allowing germination immediately. However, a few species from temperate ecosystems have been known to produce seeds that are both dormant and desiccation-sensitive, but little is known about such a relationship in the tropical forests.

• **Aims** To understand if desiccation sensitivity and dormancy can coexist in Arecaceae species, distributed predominantly in the tropical forests, and compare the seed traits found in Arecaceae species with other desiccation-sensitive species.

• **Methods** Information published in international peer-reviewed journals was reviewed and a database with records on seed dormancy and desiccation sensitivity was created and discussed.

• **Results** This literature survey has identified diaspores of 34 Arecaceae species that have both desiccation-sensitivity and an underdeveloped, small embryo, i.e., morphophysiological dormancy or morphological dormancy. In Arecaceae species, desiccation-sensitivity is neither confined to large-sized diaspores, nor all species adapted to dry ecosystems disperse diaspore during the wet-season; features reported to be prevalent in desiccation-sensitive species of other families. Endocarp is proposed to act as a mechanical barrier preventing water loss and also offer protection against physical damage; however, the extent of protection against water loss from internal structures is contentious.

• **Conclusion** The possible ecological significance of this unique relationship noted in Arecaceae is currently unknown, and this review puts forward “testable” hypotheses that call for more studies on germination ecology focusing on dispersal and burial.

Keywords Endosperm · Morphophysiological dormancy · Recalcitrance · Underdeveloped embryo · Wet ecosystem

1 Introduction

A ubiquitous survival mechanism evolved in the vast majority of angiosperm species is their ability to produce desiccation-tolerant (“orthodox”; Roberts 1973) seeds, which can lose a significant amount of water during maturation drying and are dispersed at c. 3–15% moisture content (on a fresh weight basis, fw) (Berjak and Pammenter 2008). While preserving viability after losing water to such a low level tends to be rare in most living organisms (Gaff and Oliver 2013), we still do not have a compelling

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understanding of its evolution and widespread occurrence in seeds. Due to decades of research, it is now well known that desiccation-tolerance favored the evolution of several dormancy mechanisms that synchronize germination with favorable growing seasons (Baskin and Baskin 2004; Willis et al. 2014). The reduction in seed mass as maturation drying occurs facilitates dispersal, especially by air (Fenner and Thompson 2005). Further, desiccation-tolerance promotes species persistence in adverse environmental conditions such as hot or cold climates, because seeds can potentially lose all “unbound” water, yet resume metabolic activities upon arrival of germination conditions (Roberts and Ellis 1989).

In contrast, c. 8–10% of the global plant species produce seeds that undergo no moisture reduction during maturation drying. They are dispersed at a high moisture content, often in the range of 25–40%, and remain metabolically active until they germinate or die (Berjak and Pammenter 2013). Such seeds labelled as desiccation-sensitive (“recalcitrant”; Roberts 1973) are killed even when there is a little moisture loss, which poses a significant problem for conservation in the form of seed storage. However, a small proportion of species can survive desiccation to some extent (“intermediate”; Ellis et al. 1990) but not to the levels of desiccation-tolerant species (Hong and Ellis 1996; Hong et al. 1998). Consequently, desiccation-sensitive seeds are at high risk mainly because of dry-spells that could desiccate and kill the seeds (Joët et al. 2016).

A suite of survival mechanisms has evolved in desiccation-sensitive seeds to maximize survival, including (i) germination almost immediately after dispersal often within a few days, thus a “seedlings bank” rather than “soil seed bank” is established (Berjak et al. 1984; Berjak and Pammenter 2013; Pritchard et al. 2004b); (ii) distribution restricted to a moist and aseasonal ecosystem, e.g., evergreen tropical rainforest, where water and appropriate temperature for seed germination occurs all-round the year, since immediate germination after dispersal requires a constant supply of water (Tweddle et al. 2003); (iii) dispersal of seeds during the wet season in seasonally dry ecosystems, which mimics the conditions of rainforests and favors immediate germination (Daws et al. 2005; Pritchard et al. 2004b); and (iv) morphological adaptations such as large seed size or conical shape (Dickie and Pritchard 2002; Hong et al. 1998; Singh et al. 2017) which provides some benefits to prevent water loss from the embryo; even if there is some drying, it affects only the surrounding storage tissues, e.g., seed coat, endosperm, or cotyledons and also by negating the need for imbibition (time) during germination (Wood et al. 2006).

Notably, some authors have postulated that dormancy in desiccation-sensitive seeds might be a redundant trait, because if present, it precludes immediate germination and the environments with a constant supply of water and appropriate temperature lower selective pressure for seed longevity and dormancy (Farnsworth 2000; Marques et al. 2018; Xia et al. 2012). At the same time, the coexistence of dormancy and

desiccation-sensitivity has been reported in a very few temperate species including *Asesculus hippocastanum* (Pritchard et al. 1996; Tompsett and Pritchard 1998) and probably some Fagaceae species of *Quercus* (Hawkins 2019, 2020; Hopper et al. 1985; Peterson 1983; Steele et al. 2001). Tweddle et al. (2003) treated the subject of dormancy and desiccation sensitivity thoroughly using a dataset of 886 trees and shrubs and found that approximately 10% of the dormant seeds are desiccation-sensitive. From their data, it is clear that physiological dormancy (sensu Baskin and Baskin 2004), the most abundant type of dormancy on earth resulting from hormonal imbalances was found only in 14% of all the desiccation-sensitive species. However, dormancy resulting from an impermeable seed coat, i.e., physical dormancy or combinational dormancy, wherein species have both physical and physiological dormancy (sensu Baskin and Baskin 2004) is completely absent in desiccation-sensitive species, because of the relationship between moisture loss and onset of impermeability during maturation drying. On the other hand, Tweddle et al. (2003) also found that the most common forms of dormancy in desiccation-sensitive seeds are (i) morphological dormancy (sensu Baskin and Baskin 2004), wherein the seeds have a small embryo (c. > 10% of the overall diaspore size) at the time of dispersal, and it requires suitable environmental conditions to grow inside the seeds, mature, develop and protrude the seed coat within 30 days and (ii) morphophysiological dormancy (Sensu Baskin and Baskin 2004), where seeds have both morphological dormancy and physiological dormancy, which germinate only when both forms of the dormancy have been broken. However, their analysis only included a handful of morphological or morphophysiological dormant species, thus warranting further attention.

Arecaceae (the palm family) is one of the dominant plant families in the tropical and subtropical forests with > 2600 species of evergreen trees, shrubs, and lianas (Baskin and Baskin 2014; Corner 1966; Eiserhardt et al. 2011; Mabblerley 2017). The natural dispersal units of palm fruits are called berries (thin undifferentiated embryo) or drupes (thick rigid endocarp). Most species have only one seed per fruit but this can range up to ten seeds (Dransfield et al. 2008). Under the exocarp and a fibrous mesocarp, the fruits of some species contain a hard, thick endocarp, which is rich in lignin (Rencoret et al. 2018) and other phenolic compounds (Oliveira et al. 2013). The endocarp holds the endosperm and embryo, and this intact structure botanically called “pyrene” becomes the germination unit after the exocarp and mesocarp are eaten by dispersers or decompose over time. Germination of many Arecaceae diaspores (hereafter seeds) is slow, often takes months and completion may take years. Dormancy class in palms had remained confusing, until Pérez (2009) and then Baskin and Baskin (2014) reviewed available literature on Arecaceae diaspores and stated that all the species might have morphological or morphophysiological dormancy. The confusion continues to date, with studies concluding the occurrence of physiological dormancy, other forms of dormancy,

or non-dormancy in palm diaspores (see Jaganathan 2020). However, as articulated by Jaganathan (2020), those studies that concluded palm diaspores have other forms of dormancy, except morphological or morphophysiological dormancy, have utilized postmaturation storage mimicking conditions that would favour embryo growth leading to an erroneous description of dormancy class. The seeds can be desiccation-tolerant or desiccation-sensitive (Davies et al. 2009; Dickie et al. 1992), but the extent to which desiccation sensitivity occurs in Areaceae is currently not known. More specifically, whether desiccation-sensitive seeds have dormancy or they occur mutually exclusively is poorly understood and requires further investigation.

Understanding the relationship between dormancy and desiccation-sensitivity may provide critical cues about the distribution ecology of species, ecological niches, geographic range, and robust validation into the evolutionary drivers of various seed traits that aided the colonization of plants across the globe (Dickie and Pritchard 2002; Donohue et al. 2010). The current data display a disconnected pattern at the family level, with species having both dormancy and desiccation-sensitivity, but such information is considered to be the cornerstone in ecology and biogeography (Marques et al. 2018; Subbiah et al. 2019). Indeed, within Areaceae, a small number of studies have attempted to shed some light on the relationship between dormancy and recalcitrance (Moura et al. 2019; Porto et al. 2018; Silva et al. 2014). However, due to the imprecise treatment of dormancy, e.g., seeds of *Mauritia flexuosa* were described as dormant due to the constraint resulting from the operculum (Moura et al. 2019), or simply proposing the seeds have a fully developed embryo, therefore only physiological dormancy (see Jaganathan, 2020 for discussion), these studies have led to some confusions on the entry and exit of seeds in the soil (Jaganathan et al. 2019a). As such, there is a clear lack of understanding on the germination ecology of desiccation-sensitive seeds of Areaceae. Thus, the purpose of this review was to survey the literature on Areaceae in an effort to find answers to the following questions: (1) What is the relationship between desiccation-sensitivity and dormancy? (2) What similarities/differences exist between desiccation-sensitive palm seeds and those of other plant families? (3) Are there any seed structures offering protection during survival in the soil? (4) What are the ecological advantages for species having both dormancy and desiccation sensitivity in relation to seed survival in the soil? (5) Why does desiccation kill seeds?

2 Desiccation sensitivity and seed dormancy in Areaceae

Although there has been considerable interest in identifying the seed storage behavior of Areaceae species, available data represent only c. 7–10% of the species (SID 2020). In addition, some of the results are not conclusive due to the paucity

of explicit experimental evidence. For example, the seed information database (SID, Kew) lists 124 Areaceae species for which some information is available about their ability to survive drying. Of these, only 19 (12 orthodox and 7 intermediate) and 20 species most certainly have desiccation-tolerant and desiccation-sensitive seeds, respectively. For the purpose of this review, the latter group includes only ‘recalcitrant’ seeds, since the intermediate seeds may not undergo desiccation stress in the soil and hence are treated as desiccation-tolerant (Tweddle et al. 2003). Besides, 35 of the 124 species are labelled as uncertain, and 24 and 26 species probably have desiccation-tolerant and desiccation-sensitive seeds, respectively.

Despite the useful compilation of seed data for almost all angiosperm families in SID, information for Areaceae is neither complete nor up-to-date. Thus, a comprehensive literature search was conducted in Thomson’s Web of Science (WoS), and other search tools including “Science Direct” and “NCBI” using several string terms on the dormancy and storage of Areaceae seeds. Any new species not listed in SID was added to our list either by consulting the literature or by personal communication with researchers who study palms. They were grouped as either desiccation-tolerant or desiccation-sensitive (see Table 1; note that data on desiccation-tolerant species are not included). From the data given in SID (2020), I excluded the species listed with categories “uncertain” and also those in doubt, i.e., orthodox (?), orthodox p, recalcitrant (?), recalcitrant p, intermediate (?), and intermediate p. from SID, as their seeds are most likely to be desiccation-tolerant, regardless of being orthodox or intermediate, because they survived limited drying without any loss in viability. The species that are recalcitrant (?) and recalcitrant p. were also included as desiccation-tolerant, because they either survived desiccation to some level or survived storage for times typically longer than desiccation-sensitive species. However, when a species has received more than one classification, e.g., *Phoenix roebelenii* as highly desiccation-sensitive (Pritchard et al. 2004a) and orthodox (Prakash et al. 2019); *Archontophoenix alexandrae* as desiccation-sensitive (Martins et al. 2003) or able to tolerate mild desiccation (Wen 2019), I included these species showing incongruities under desiccation-sensitive, because at least one population is known to produce desiccation-sensitive seeds. However, it must be noted that for some of the species such as *Elaeis guineensis*, there has been more than one classification: orthodox (Grout et al. 1983), intermediate (Ellis et al. 1991), recalcitrant (Roberts 1973), and just as desiccation-tolerant (Aberlenc-Bertossi et al. 2003). Nonetheless, the earlier classification of recalcitrant by Roberts (1973) had no explicit experimental evidence, thus included under desiccation-tolerant.

Table 1 Arecaceae species known to produce desiccation-sensitive seeds with evidence for dormancy

Species name	Adaptation	Dormancy	Dispersal time	Reference
<i>Adonidia merrillii</i> (Becc.) Becc	Tropical rainforest (Philippines, New Hebrides, Fiji)	Not known	Not known	Wood et al. (2006)
<i>Archontophoenix alexandrae</i> (F.Muell.) H.Wendl. & Drude	Rainforests of Australia, but planted worldwide now	Morphophysiological dormancy	All year	Ben Wen, Personal communication
<i>Areca catechu</i> L	Tropics (Africa, Asia, and Pacific)	Morphophysiological dormancy	Jan–Sep	SID
<i>Arenga westerhoutii</i> Griff	Rainforests (south China, Vietnam, Thailand, and Malaysia)	Not known	Not known	Davies et al. (2009)
<i>Bactris gasipaes</i> Kunth	Tropics (mostly south and central America)	Morphophysiological dormancy	Rainy	Lima et al. (2014)
<i>Borassus flabellifer</i> L	Tropics (south and southeast Asia)	Morphophysiological dormancy	Late dry/wet	Jaganathan, unpub
<i>Calamus manan</i> Miq	Tropics (south China to Australia)	Morphophysiological dormancy		SID (2020)
<i>Calamus shendurunii</i>	Tropics (only Western Ghats)	Morphological dormancy	Rainy	Jacob et al. (2016)
<i>Caryota mitis</i> Lour	Tropics (humid, sometimes dry)	Morphophysiological dormancy		Ellis et al. (2007)
<i>Caryota urens</i> L	Tropics (mostly India and Sri Lanka)	Morphophysiological dormancy	All year	Prakash et al. (2019)
<i>Chamaedorea alternans</i> H.Wendl	Mexico	Morphophysiological dormancy	Rainy	Rodríguez et al. (2000)
<i>Chamaedorea tepejilote</i> Liebm	Tropics (moist and wetlands of Central and South America and Hawaii)	Morphophysiological dormancy	Late dry/wet	SID (2020)
<i>Coccothrinax fragrans</i> Burret	Tropics (warm climate, native of Cuba)	Morphophysiological dormancy	Late dry/wet	Mattana et al. (2019)
<i>Cocos nucifera</i> L	Tropics	Morphophysiological dormancy	All year	Jaganathan, unpubl
<i>Dyopsis decaryi</i> (Jum.) Beentje & J.Dransf	Tropics (Madagascan rainforest)	Morphophysiological dormancy	Not known	Batista et al. (2016)
<i>Dyopsis lutescens</i> (H.Wendl.) Beentje & J.Dransf	Tropics (Madagascan rainforest)	Morphophysiological dormancy	Not known	Batista et al. (2016)
<i>Dyopsis pinnatifrons</i> Mart	Tropics (Madagascan rainforest)	Morphophysiological dormancy	rainy season	Ellis et al. (2007)
<i>Euterpe edulis</i> Mart	Tropical rainforest (South America)	Morphological dormancy		Panza et al. (2004)
<i>Euterpe oleracea</i> Mart	Tropical rainforest (South America)	Morphophysiological dormancy or morphological dormancy	Dry season	Lima et al. (2014)
<i>Euterpe precatoria</i> Mart	Tropical rainforest (South America)	Morphophysiological dormancy	Dry season	Lima et al. (2014)
<i>Jessenia bataua</i> (Mart.) Burret	Tropical rainforest (South America)	Morphophysiological dormancy	Not known	Dickie et al. (1992)
<i>Livistona chinensis</i> (Jacq.) R.Br. ex Mart	Sub tropical and warm temperate	Morphological dormancy	Not known	Wen Ben, Personal Communication
<i>Livistona muelleri</i> F.M.Bailey	Sub tropical	Morphophysiological dormancy	Not known	Wood et al. (2006)
<i>Livistona rotundifolia</i> (Lam.) Mart	Sub tropical	Morphophysiological dormancy	Not known	Sanjeevani et al (2013)
<i>Mauritia flexuosa</i> L.f	Tropical (South America)	Morphological dormancy?	Dry/rainy season	Lima et al. (2014)
<i>Oenocarpus bacaba</i> Mart	Tropical (South America)	Morphophysiological dormancy	Dry season	Lima et al. (2014)

Table 1 (continued)

Species name	Adaptation	Dormancy	Dispersal time	Reference
<i>Oenocarpus mapora</i> H.Karst	Tropical (South America)	Morphophysiological dormancy	Dry season	Lima et al. (2014)
<i>Oenocarpus minor</i> Mart	Tropical (South America)	Morphological dormancy?	Dry/rainy season	Lima et al. (2014)
<i>Ravenea dransfieldii</i> Beentje	Tropics (Madagascan rainforest)	Morphological dormancy (or non dormant)	Not known	Rakotondranony et al. (2006)
<i>Ravenea glauca</i> Jum. & H.Perrier	Tropics (Madagascan rainforest)	Morphological dormancy (or non dormant)	Not known	Rakotondranony et al. (2006)
<i>Ravenea rivularis</i> Jum. & H.Perrier	Tropics (Madagascan rainforest)	Morphological dormancy (or non dormant)	Not known	Rakotondranony et al. (2006)
<i>Ravenea xerophila</i> Jum	Tropics (Madagascan rainforest)	Morphological dormancy (or non dormant)	Not known	Rakotondranony et al. (2006)
<i>Roystonea borinquena</i> O.F.Cook	Tropics (South America)	Morphophysiological dormancy or Morphological dormancy	Not known	Mattana et al. (2019)
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Tropics (South America)	Not Known	Not known	Pritchard et al. (2004a, b)
<i>Syagrus schizophylla</i>	Tropics (South America)	Not Known		Beltrame et al. (2018)
<i>Thrinax radiata</i> Lodd. ex Schult. & Schult.f	Tropics (South America and Mexico)	Morphophysiological dormancy	Not known	Davies et al. (2009)
<i>Trachycarpus latisectus</i> Spanner. H. J. Noltie & M. Gibbons	Littoral woodlands of NE India	Not known	Not known	Wood et al. (2006)

To evaluate the presence of dormancy in species with desiccation-sensitive seeds, I used the compilation presented by Baskin and Baskin (2014) and assigned each of the species to a dormancy class: morphological dormancy or morphophysiological dormancy, or not known. This survey resulted in 37 species that are certainly desiccation-sensitive at least in some populations (Table 1), and 32 species that have both dormancy and desiccation-sensitivity; the dormancy status in the other five species is not known. Information about seed dispersal time and species distribution ecology are all taken from the primary literature, SID, personal communication, or personal observation (see Table 1 for details). The literature search revealed that most of our knowledge about the seed biology of Arecaceae is restricted to species occurring in the neotropics, with the Afrotropics and Indo-pacific tropics receiving little attention, but interest in these geographic locations is increasing (see Table 1).

3 Desiccation-sensitive seeds of Arecaceae differ from those of other families

Some desiccation-sensitive seeds of Arecaceae do not seem to comply with the generalized adaptations of desiccation-sensitive seeds. First, desiccation-sensitive seeds of many families are widely agreed to be larger [1000 seed weight,

total seed weight (TSW) above 500 g; Hong and Ellis (1996)] than those that are desiccation-tolerant. Seed size has even been proposed as a useful indicator for predicting desiccation response in many families (Daws et al. 2005; Dickie and Pritchard 2002), including Arecaceae (Lan et al. 2014). However, seed size varies several orders of magnitude in Arecaceae with species like *Lodoicea maldivica* and *Cocos nucifera* having an individual seed mass of ~30 and 2 kg, respectively, and those of *Chamaedorea tepejilote* with an individual seed mass of only 0.15 g. Although the storage behavior of *L. maldivica* seeds is still unknown, they most likely are desiccation-sensitive; seeds of *C. nucifera* and *C. elegans* are desiccation-sensitive (Table 1). According to the details presented in SID (2020), there are some desiccation-sensitive Arecaceae species with an individual seed mass of less than 1 g, e.g., *Caryota mitis* (0.37 g), *Dypsis lutescens* (0.76 g), and *Chamaedorea elegans* (0.21 g), indicating that desiccation sensitivity is spread across all seed sizes of Arecaceae.

Second, it has been suggested that desiccation-sensitive seeds invest little in physical defense, mainly because of rapid germination after dispersal, even before the predators can find the seeds using sight, smell, or touch (Curran and Webb 2000; Dalling et al. 2011; Paulsen et al. 2013). This is similar to the strategy used by physically dormant species, which also invest little in physical defense because their impermeable seed coat protects the seed during persistence in the soil, and rapid germination following dormancy break obviating predatory

pressure. Paulsen et al. (2013) claimed that “desiccation sensitivity” and “physical dormancy” are two different routes seeds use to deal with the problem of predation in different types of climates. In seasonal environments, species with physical dormancy might delay germination, but seeds cannot be found easily due to the lower emission of volatile substances. On the other hand, in aseasonal ecosystems, recalcitrant seeds provide ecological benefits by immediate germination. Seed defense theory suggests that physiologically dormant seeds invest in both chemical and physical defenses, whereas non-dormant seeds do not invest in these defenses, with survival being determined by the interaction with soil microbes (Dalling et al. 2011). However, most desiccation-sensitive seeds of Arecaceae also have morphological or morphophysiological dormancy (Table 1) and require a considerable period in the soil for embryo growth to occur. Thus, seeds are close to the soil surface and subjected to numerous pressures including predation (Brewer 2001; Galetti et al. 1992; Mendes et al. 2016); microbial attack (Carlile et al. 2012); insect or beetle damage (de Almeida and Galetti 2007), while dormancy-break is occurring.

Third, knowledge on the distribution pattern of Arecaceae species shows that palms are well adapted to humid tropical landscapes including rain forests and swamplands, with very few species inhabit in the dry habitats of savannas or deserts (Baker and Couvreur 2013; Blach-Overgaard et al. 2010). While records of some date palms and coconuts growing in desert conditions imply the widespread adaptation of palms, there is no concrete evidence for the adaptation of desiccation-sensitive species in the dry tropics, except from a few mentions of species from Africa and South America for which climate data or information about desiccation-sensitivity is unknown (Plotkin and Balick 1984). It appears that when seed size, restriction to a moist climate, and immediate germination fail to explain the distribution of a desiccation-sensitive species, relating the time of seed dispersal to the wet season tends to be the best potential explanation for desiccation-sensitive species surviving seasonally-dry habitats (Pritchard et al. 2004b). However, the evidence is growing that desiccation-sensitive species disperse seeds during the dry season which remain viable in the soil until the arrival of the wet season, e.g., *Swartzia langsdorffii* in Brazil (Vaz et al. 2016). In palms, desiccation-sensitive seeds of *Oenocarpus bataua*, *O. mapora*, *Euterpe oleracea*, and *E. precatoria* matured in the Amazon region are dispersed only during the dry season (Lima et al. 2014). Similarly, some of the desiccation sensitive species of Arecaceae adapted to drylands are known to disperse seeds throughout the year, e.g., *Cocos nucifera* and *Areca catechu*, which disperses seeds from January through September (Jaganathan, unpublished). These records indicate that desiccation-sensitive seeds of palms are not necessarily restricted to moist environments or dispersal with the wet season. However, more detailed field studies are required from

dry areas that produce desiccation-sensitive seeds to understand the survival mechanisms. More specifically, information about dispersal timing and the ecological parameters such as rainfall, (soil and air) temperature, relative humidity data might help understand the adaptive behavior of palm seeds.

4 Endocarp protects the internal seed structures

After dispersal, the endocarp plays a crucial role in protecting the internal structures of the seeds. In most of the palms, although endosperm, endocarp, and mesocarp are well developed at the time of dispersal, physiological and metabolic changes of the embryo continue to occur even after dispersal (de Melo et al. 2017; Dickie et al. 1992; von Fintel et al. 2004). At the cellular level, however, seeds of desiccation-sensitive species differ considerably from those of desiccation-tolerant species. For example, Pérez et al. (2012) found that embryos of *Pritchardia remota* undergo progressive changes in sugar accumulation just at the time of dispersal but dry matter accumulation in the embryo is delayed until seed germination, which happened 170–250 days after dispersal. In *Livistona chinensis*, soluble sugars and heat-stable proteins increased at the beginning of seed development then decreased during maturation (Wen et al. 2012). Similarly, lipid reserves did not accumulate in the highly vacuolated endosperm and embryo until dispersal in the seeds of *Mauritia flexuosa* collected from Brazil (Silva et al. 2014) and *Euterpe edulis* grown in Argentina (Panza et al. 2004), explaining the high water content of the seeds even after maturity. This is in contrast with the developmental patterns observed in desiccation-tolerant seeds of *Butia capitata*, where the endosperm contains large protein and lipid reserves with starch present in the embryo (Oliveira et al. 2013).

Despite the difference in metabolic changes during seed development between desiccation-sensitive and desiccation-tolerant species, both groups of diaspores seem to have high water content at the time of dispersal due to the large amounts of water in the fibrous mesocarp and large endosperm. Consequently, unlike seeds from other desiccation-tolerant families that are dispersed at a low water content, seeds of many Arecaceae species that can withstand desiccation when dried empirically (only orthodox) are shed at a relatively high moisture content (when tested in the lab), e.g., 10% in *Attalea speciosa* whole seeds but 25% in the embryo (Saleh et al. 2017); 22% in *Acrocomia aculeata* (Ribeiro et al. 2012); 24% in *Livistona muelleri*, 14% in *Sabal minor* Var. *louisiana*, 29% in *Wallichia disticha* (Wood et al. 2006); 19% in *Livistona cochinchinensis* (Ellis et al. 2007); 12–13% in *Sabal mexicana* and *Washingtonia filifera* (Dickie et al. 1992); 36% in *Phoenix rupicola*, 25% in *Phoenix sylvestris*, 18% in *Phoenix theophrasti*, 20% in 27% in *Syagrus botryophora*, 38% in *Syagrus flexuosa* and 40% in *Syagrus yungasensis* (Pritchard

et al. 2004a). Desiccation-sensitive (and intermediate) seeds also are shed at a high moisture content (Davies et al. 2009; Dickie et al. 1992; Ellis et al. 2007; Rakotondrany et al. 2006) or sometimes lower than those of desiccation-tolerant species, e.g., 19% in *Phoenix roebelenii* and 25% *Syagrus schizophylla* (Pritchard et al. 2004a).

From empirical desiccation studies, it is apparent that for pyrenes dried in silica gel (c. 5% RH) it takes several days to lower the water content (von Fintel et al. 2004), indicating external structures, particularly the endocarp, provide resistance for water loss. In the natural environment, seeds do not dry to such low moisture levels as those obtained for ex situ storage. However, regardless of whether seeds are present in the lab or the field, drying could harden the endocarp, a process that begins during seed development but halts during dispersal when seeds equilibrate with the atmospheric humidity and likely continues when the humidity drops further (Morton 1988). Morpho-anatomical studies in *Attalea microcarpa* showed that during seed development, the endocarp was soft in young fruit and gradually hardened in a basipetal and centrifugal pattern (de Melo et al. 2017). A completely hardened endocarp protects against fungi, insects and other stresses, including desiccation and high temperature during persistence in the soil. Broschat (1998) reported that seeds of *Butia capitata* from North America from which the endocarp was removed rotted when placed in moist sphagnum peat in polyethylene bags at 40 °C due to fungal attack, but seeds with the endocarp present germinated successfully. In the Cerrado biome of Brazil, the endocarp plays a vital role in protecting the embryo of *Acrocomia aculeata* from high temperatures during episodes of fire (Rodrigues-Junior et al. 2016).

In an 8-year ongoing study to understand the germination ecology of desiccation-sensitive fruits of *Borassus flabellifer* from Tamil Nadu, India, I found that the water-permeable endocarp is important in maintaining viability during the dry season. Near the field collection site in 2013, 2014, and 2017, a series of plots were established (8×7×3 feet; l×b×h) and fenced with tight-netted steel mesh to exclude predators but allowing gas and water exchange. Pyrenes were extracted from the fruits collected during their natural dispersal time (late June to late July) by ripping the mesocarp open with a surgical knife or saw after placing them in an “engineers vice” and returned to the soil on the same day (Fig. 1). For 2013 and 2014, 42 pyrenes (two replicates of 15 each and one replicate of 15) had a 0.3 mm hole drilled into them using an electric drill, after which they were placed in plots containing natural soil. In separate plots, 45 intact pyrenes (three replicates of 15; each replicate placed in one plot) were used. The pyrenes were visually inspected weekly for 11 months. In 2017, the experiment was repeated with 45 (three replicates of 15 each) and 60 (three replicates of 20 each) pyrenes, drilled and intact, respectively. In all cases, the endosperm in pyrenes with a hole drilled in the endocarp dried within a few days. This was evident from the significant

decrease in the mass of the drilled pyrenes. When all pyrenes were cracked open with a hammer after 3 weeks, the endosperm and the embryo were completely decayed in the drilled pyrenes. In contrast, intact pyrenes had germination of between 36 and 59% across different years (Jaganathan, unpublished).

In addition to mechanical protection, the endocarp also prevents asynchronous germination resulting from the sporadic rainfall events that might provide false cues for germination by restricting the water entry into seeds during seed persistence in the soil, particularly in the dry season. This restriction allows germination to occur only during a continuous supply of water, i.e., the growing season. In Cerrado biomes of Brazil, seeds of *Attalea vitrivir* having more likely morphophysiological dormancy due to the underdeveloped embryo and the restriction of embryo growth due to the endocarp, germinate only during the favorable time of the year, i.e., from February to April of the second year following dispersal (Neves et al. 2013). In the same region, fruits of *Caryocar brasiliense* (Caryocaraceae) are dispersed late in the rainy season (January–March), but the following dry season delays the germination until the arrival of the rainy season in September (da Silva Sousa et al. 2017). Similar arguments can be found in the literature on other families, e.g., Lauraceae (Jaganathan et al. 2019b), Rosaceae (Chen et al. 2007), and Empeteraceae (Baskin et al. 2002). However, the precise role of endocarp in regulating the germination timing of Arecaceae diaspores requires more critical studies.

5 Ecological significance of dormancy in desiccation-sensitive Arecaceae seeds

Given that palm species have been in the tropics for the past 80 million years or so, they have been subjected to serious environmental pressures leading to the evolution of numerous adaptive traits (Onstein et al. 2017; Svenning 2001). Ecological studies have largely focused on seed germination in the soil, with dormancy breaking often being the central goal. The ecological significance of having desiccation-sensitive and dormant seeds in many Arecaceae species is not clear, at present. Interestingly, some studies on temperate ecosystems have shown that species such as *Aesculus hippocastanum* (Pritchard et al. 1996, 1999) and some oaks (Bonner 1987; Joët et al. 2016; Pritchard 1991) produce seeds that have both physiological dormancy and desiccation sensitivity, are dispersed in the late autumn, but overwinter before germinating in the following spring, thus establishing a soil seed bank of a few months. Despite evidence showing that the development of dormancy in the desiccation-sensitive species is tightly under the control of parental environmental conditions (Obroucheva et al. 2016), recently Joët et al. (2016) reinforced that dormancy in desiccation-sensitive seeds of the temperate zone is an important mechanism to preclude autumn germination immediately after shedding, thereby avoid seedling

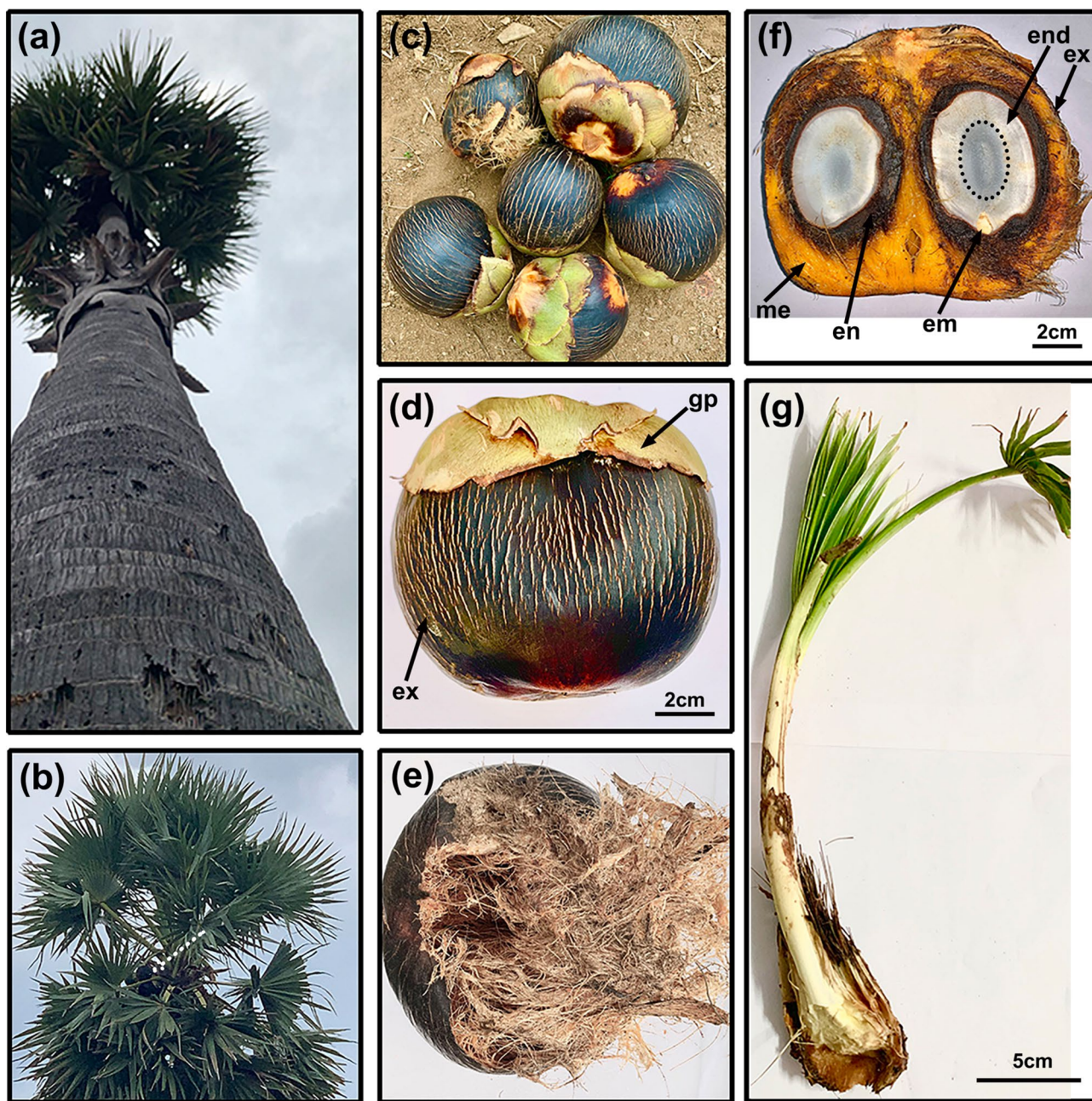


Fig. 1 A 20–25-year-old *Borassus flabellifer* tree approximately 15 m tall (a); close up of the tree top showing pinnate leaves and matured fruit (indicated with a dashed white arrow) ready for dispersal. This is evident from the dark black exocarp (b); fruits recently fallen to the ground (c); a single fruit showing all external parts (d); mesocarp eaten fruit (e); transverse section of a single fruit showing half liq-

uid-to-solid endosperm that is still soft but outside this soft area the endosperm matured and is hard and cannot be cut with a knife (f) and seedling from an endocarp buried 2 years ago under the mother plant (g). en endocarp end endosperm, em embryo, pe pericarp, me mesocarp, ex exocarp, gp germination pore

death during winter, hence synchronizing germination with the spring conditions. Consistent with this proposition, a tentative hypothesis for the coexistence of dormancy and desiccation-sensitivity in palms with distributional limitation in the tropics may be that dormancy prevents immediate germination in seeds of some desiccation-sensitive Arecaceae species dispersed

during the dry season (see Table 1). However, this explanation does not answer the question of why dormancy is present in desiccation-sensitive seeds of species adapted to moist climates (see Table 1).

Silva et al. (2014) noted that in swampy habitats of the Cerrado biome, Brazil, the dominant occurrence of *Mauritia*

flexuosa is due to the presence of dormancy and desiccation sensitivity. Dormancy would favor seed dispersal leading to population expansion, but desiccation sensitivity restricts the species to moist environments. One possible reason for the presence of dormancy in desiccation-sensitive Arecaceae seeds can be ascribed to the fact that a wet soil surface alone does not ensure germination success. Seeds also have a high-temperature requirement (c. 25–40 °C, with 30 °C being optimal for many species) to germinate, and this temperature range occurs in the tropical rainforest all year (Broschat 1998; Hussey 1958; Rees 1962; Visscher et al. 2020). However, soil temperature increasing to 40–60 °C is a common occurrence, and such “erratic” high temperatures on the soil surface have a risk of drying the seeds. Besides, seeds may dry during drought but be wetted during aseasonal rainfall events, which will lead to severe stress (Gonçalves et al. 2020; Wen 2019). In *Butia capitata*, embryo survival from water stress resulting from drier conditions is related to their abundant protein reserves, SOD activities, and high ABA content (Gonçalves et al. 2020). Thus, as a ‘risk-reduction’ mechanism to ensure that seeds are in a ‘safe place’ to germinate, many palm species germinate better when buried in the soil and those that are on the bare soil have a higher risk of mortality. Microclimates under leaf litter or tree shade, could minimize the desiccation stress for some seeds resulting from high temperature (Ali et al. 2007) and also fast hydration which is known to kill Arecaceae seeds (Gonçalves et al. 2020).

The second advantage of delayed germination is that it allows species to disperse to other sites within the same ecosystem. Both dispersal to other sites and burial, protect the seeds of Arecaceae from predatory pressure and desiccation imposed damage, thereby enhancing the number of seeds able to successfully germinate (Carlile et al. 2012; Silva and Tabarelli 2001). Most Arecaceae species do not have specialized dispersal structures for assisted dispersal, i.e., wings for air dispersal; therefore, they fall mostly under the parent plants. Thus, the secondary movement of seeds by rodents is important for germination success and to avoid seedling competition (Galetti et al. 2006). However, studies have indicated that seeds are not moved over long distances, perhaps due to the large fruit size (Galetti et al. 2006; Pimentel and Tabarelli 2004), or because of a complex network of events, such as rodents consuming the exocarp which might lead to fungal growth in the mesocarp, making it less attractive for further dispersal by rodents (Pereira et al. 2014). However, if predators consume most of the mesocarp which is rich in nutrients and also packed with an attractive smell in some species, e.g., *Borassus flabellifer*, they reduce the overall size of the dispersal unit (Jaganathan, personal observation). This allows whole small seeds and the individual pyrenes to be dispersed by bats, birds, reptiles, insects, land mammals, and very rarely fishes (Muñoz et al. 2019; Zona and Henderson 1989). Muñoz et al. (2019) recently showed that there are 750

unique diaspore-disperser interactions in 126 palm species, most of which are predated by more than one dispersor.

Dormancy in desiccation-sensitive seeds provides some survival advantages by spreading the risk of germination. The seeds in the soil could be dispersed to different microsites or different soil depths that result in various establishment strategy for palm species. For example, desiccation-sensitive seeds of *Mauritia flexuosa* collected during the natural dispersal time and buried at 10 cm depth in the soil under three different microenvironment showed that seeds germinated and establish seedling banks in dry climates, but were maintained in a seed bank for at least one year in humid and wet locations (Porto et al. 2018). Palms adapted to seasonally dry (and moist) ecosystems are known to undergo primary and secondary dispersal after shedding from plants (Lopez-Toledo et al. 2013). Desiccation-sensitive seeds benefit if they are moved to wet soil or under a canopy. In contrast, if they are moved to dry landscapes, dormancy ensures no germination. Likewise, desiccation-tolerant seeds could be moved from moist to dry land. In this case, dormancy allows seeds to reach a suitable site for germination. This is particularly true because regardless of desiccation tolerance ability, most of the Arecaceae seeds do not form soil seed banks exceeding 3 years and rarely up to 5 years (Mengardo et al. 2012).

6 What causes viability loss during desiccation in Arecaceae seeds?

Desiccation tolerance quantifies the amount of water lost from the whole seeds without any loss in viability (Berjak and Pammenter 2007). If the dispersal unit is a fruit, the outer coverings are removed manually and the stony endocarp, i.e., pyrene in Arecaceae is desiccated. In palms, the endosperm is inside the endocarp, and it occupies up to 98% of the total diaspore (Baskin and Baskin, 2014; also see *Borassus flabellifer*, Fig. 1). An interesting feature emerging from a plethora of palm storage studies is that whole seeds do not tolerate moisture loss to < 10–15% when dried using silica gel. However, excised embryos can withstand drying to < 10% moisture range and can survive storage at low temperature (Dias et al. 2015; Engelmann 2004; Grout et al. 1983; Jacob et al. 2016; Shao et al. 2009; Wen et al. 2012). These studies highlight that drying of the embryo is not necessarily lethal for many desiccation-sensitive palm species. However, explicit experiments are required on a range of species within Arecaceae to confirm this at family level.

While it is often assumed that failure of germination in a specified period is due to embryo death, it is tempting to propose that the endosperm in Arecaceae species plays a critical role in assisting embryo growth by providing nutrition to the slowly elongating cotyledonary petiole and haustorium, as the importance of the endosperm in many species is increasingly becoming apparent (Yan et al. 2014). Hence, excessive

drying of palm diaspores or pyrenes leads to endosperm cell damage, which might result in germination failure, as the elongated embryo cannot penetrate the endocarp, which requires exceptional strength supplied by the nutrition from the endosperm. This explains the higher survival percentage of embryos after drying to low moisture content and cultured only in nutrition-rich medium. More generally, consumption of endosperm by predators did not inhibit palm seed germination, as the embryo did not have to protrude through the hard endocarp, but too much endosperm loss resulted in seed death (Pérez et al. 2008).

In many other desiccation-sensitive families, the drying of the “dispersal unit”—usually the embryo, endosperm, and other covering structures—results in loss of water molecules to the surrounding humidity (Gold and Hay 2014). This process keeps the structure of the endosperm and embryo intact as only cells lose water. Whereas in most palms, the endocarp prevents water loss from the endosperm, and thus, the underdeveloped embryo also remains in a moist state during desiccation. However, continuous desiccation leads to structural changes in the endosperm and/or loss of volume, which means a loss of nutrients for the embryo’s growth when rehydrated. One compelling piece of evidence for this claim comes from the fact that the diaspores of some species of palms which have liquid endosperm, e.g., *Cocos nucifera* (Child and Nathaniel 1950); *Borassus flabellifer* (Davis and Johnson 1987); *Attalea princeps* and *Astrocaryum ayri* (Plotkin and Balick 1984) the process of hardening happens after shedding, during which the seeds are also dispersed to other environments. The exocarp, water-rich mesocarp, and a hardened endocarp further protect the endosperm from water loss. After the liquid endosperm matures into a tough solid endosperm, the embryo differentiates and grows internally before protruding the endocarp and mesocarp, if present. Thus, when freshly dispersed seeds are collected and subjected to drying, it results in loss of endosperm and not just the structural changes which can be resumed after hydration in seeds of many other families.

However, palm species producing berries have a very thin endocarp and are dispersed with fleshy endosperms (Corner 1966; Tomlinson 1990). Drying these berries results in water loss from the endosperm, and upon continuous desiccation, the endosperm loses its structural integrity, which corresponds with seed death when tested for germination, e.g., *Trachycarpus fortunei* and *Phoenix dactylifera* (Jaganathan et al., in prep). In some temperate-zone species such as *Anemone nemorosa* (Ali et al. 2007) and *A. ranunculoides* (Mondoni et al. 2009) of Ranunculaceae; *Galanthus nivalis* and *Narcissus pseudonarcissus* of Amaryllidaceae (Newton et al. 2013), which have a small undeveloped embryo, the seeds are dispersed at a high moisture content ($\geq 40\%$), a feature unusual for desiccation-tolerant species, but their ability to withstand drying maximizes just before or within a few days after seed dispersal. The acquisition of

desiccation tolerance can occur in a matter of a few days. That is, seeds collected and tested immediately after dispersal showed desiccation sensitivity, but those tested few a days after collection are desiccation-tolerant (Ali et al. 2007; Newton et al. 2013). For the berries of Arecaceae, survival during desiccation is dependent on the characteristics of the endosperm and its accumulated reserves which are determined by several environmental and genetic factors. To this end, the relationship between hard endocarp in drupes and papery endocarp in some berries controlling the water loss must be a subject worth considered for future studies.

Indirect evidence supporting the fact that endosperm damage might affect the survival of the embryo during germination when allowed to germinate as one unit comes from germination studies conducted in species of other families. In coffee, the ultrastructural analysis showed that endosperm damage occurs during drying, but whether this results in seed death was not determined (Borém et al. 2008). Allen et al. (2000) reported that when 12 h imbibed seeds of *Hordeum vulgare* were subjected to moderate drying, the water from the endosperm moved into the shoot meristem, radicle, and scutellum of the elongating embryo, but water from the embryo never moved into the endosperm. Variation in moisture content between different seed parts have been reported both during desiccation (Chandel et al. 1995; Pritchard 1991; Pritchard and Prendergast 1986; Walters 2000; Xia et al. 2014) and imbibition (Egli and TeKrony 1997). However, whether such variation affects the survival of seeds, particularly in a family with a hard endocarp such as Arecaceae, is poorly understood (but see Grout et al. 1983). The proposition that endosperm could act as the critical tissue and drying results in irreversible damage to the endosperm cells leading to absence of germination in Arecaceae may seem counterintuitive, but this proposal requires careful experimental investigation.

7 Conclusion

This contribution highlights the fact that associations between seed desiccation sensitivity and dormancy are more common in palms than previously thought. Given that desiccation-tolerant species also shed seeds with high moisture content and low mass, ability to survive drying (at least) in Arecaceae can neither be predicted based on the moisture content of the seeds at the time of shedding nor based on the 1000-total seed weight. Furthermore, it is suggested that not all desiccation-sensitive seeds germinate immediately. Seeds of some species of Arecaceae could persist in the soil until dormancy is broken, which allows a proportion of seeds to be dispersed to other microclimates or environments. The unique features present in seeds of Arecaceae might challenge researchers working ex situ in the laboratory to identify their survival ability after drying

to low moisture content and classifying them as desiccation-tolerant or sensitive with development of appropriate storage protocols, but those features provide some benefits to the seeds under ecological conditions. Thus, the evolutionary and ecological benefits of species having both dormancy and desiccation sensitivity require in-depth attention. Our knowledge gap in understanding the ability of Arecaceae diaspores to survive desiccation provokes the need for critical investigations channeled to gain more insights into the information on water contents from specific tissues. More specifically, information about the survival ability of seeds to the lowest water content during embryo growth within the diaspores are deemed useful. Further morpho-anatomical and molecular studies could reveal whether drying hardens the endocarp in such a way that it acts as a barrier for water loss from the endosperm and embryo. Such studies on a range of species are expected to advance the theoretical framework that the endosperm is a critical tissue in Arecaceae by focusing on specific seed structure water loss during drying. Most investigations of palm seed germination concerning radicle elongation, do not take into account if the embryo elongation failed to occur because of embryo death or because the endosperm was incapable of providing nutrients for embryo growth. More advances in these areas will emerge through specific studies dealing with various aspects for a better understanding of palm seed biology and also serve as useful information for the conservation of palm species in the face of climate change.

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