

Seed Biology of Palms: A Review

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Seeds are a very important component of the life cycle of plants. They not only carry the necessary genetic variation required for evolutionary change, but they are quite often the only means of long-distance dispersal and long-term dormancy (Silander 1985). On the other hand, seeds are a valuable resource for the propagation and conservation of germplasm. Hence, the study of palm seeds remains a priority for future research.

The palm family (Arecaceae) comprises between 2200 (Johnson 1996) and 2600 (Jones 1995) species distributed throughout tropical and subtropical areas. Very little is known about the seed biology of most of these species. Scientific research has been carried out on a small number of species, mostly of economic value. Based on the reviews by Corner (1966), Tomlinson (1979), Moore and Uhl (1982), Uhl and Dransfield (1987) and others, our purpose is to summarize the most distinctive characteristics of seed biology of palms.

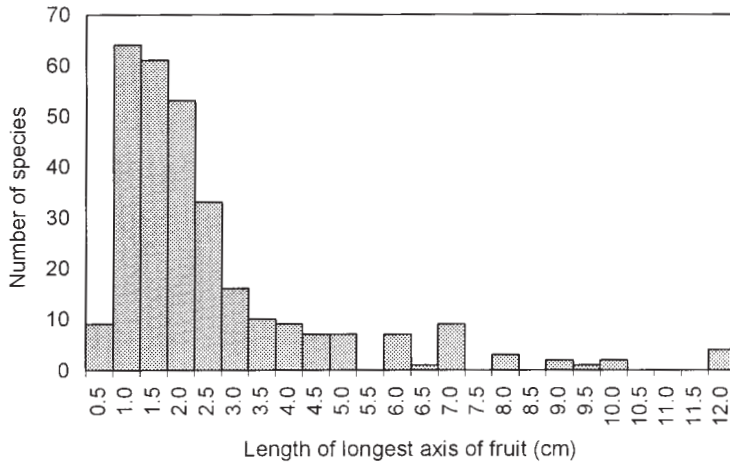
Palms are one of the most peculiar life forms among higher plants. These arboreal monocots share an assemblage of reproductive traits that are unique in many ways. Their propagules – nuts or seeds – are possibly the most characteristic feature, always containing part of the fruit (pericarp, exocarp, mesocarp and endocarp) (Corner 1966). Size of palm seeds ranges from the gigantic *Lodoicea maldivica* seeds (each weighs more than 20 kg and is about 50 cm long) to the very small seeds of *Roscheria melanochaetes* and *Chamaedorea elegans*, which are about 7 mm and 5 mm long, respectively (Sneed 1976, Moore & Uhl 1982, Jones 1995). The most common seed sizes in palms are between 1 and 12 cm (Fig. 1) (Jones 1995).

Morphology and anatomy

Anatomy and morphology of palm seeds have been useful bases for the definition of trends in

the evolution of the family Arecaceae. Generally, the gynoeceum develops only one seed (primitive character in palms) due to either the fact that only one of the three carpels is fertile, or that all three carpels are fertile, but two of them abort during fruit or seed development (Robertson 1977, Davis 1978, Padmanabhan & Regupathy 1981). Alternatively, all carpels that develop produce a seed surrounded by an endocarp (Siddiqi et al. 1991). Polyembryony – several embryos surrounded by the same endocarp – (Davis 1978, May et al. 1985, Clancy & Sullivan 1988), and parthenocarpic production of seeds (Shukr et al. 1988, Rohani et al. 1997) are also known among palms. Some species such as *Attalea phalerata* (as *Scheelea leandroana*), produce a single seed per fruit or multiseeded fruits with a variable number of seeds among fruits (Koebernik 1971, Moore & Uhl 1982). This fact has an ecological significance in palms like *Attalea butyracea* (as *Scheelea rostrata*); predators prefer fruits with a single mature seed, producing a negative selective pressure upon individual with this character (Bradford & Smith 1977).

Mesocarp and endocarp are commonly the most important structures remaining from the fruit. The mesocarp may vary from fleshy to very fibrous, whilst the endocarp may be differentiated into a hard stony structure as in *Cocos nucifera* and *Jubaeopsis caffra* (Murray 1973, Robertson 1977, Moore & Uhl 1982), or it may be papery or



1. Frequency distribution of palm fruit size (N = 298). The longest axis of the fruit was considered as the fruit size. This figure does not include species with the largest seed size, such as *Cocos nucifera*, whose fruit length is 22.5 cm (Zizumbo-Villarreal 1997) and *Lodoicea maldivica* whose fruit length is 50 cm (Uhl & Dransfield 1987).

an undifferentiated line of cells, as in *Caryota mitis* and *Mauritia flexuosa* (Murray 1973). Generally, the endocarp cannot be separated from the seed coat, which is poorly developed. At the time of dissemination, the endosperm may be solid, creamy, liquid or a combination of the three consistencies, as for example, in *Cocos nucifera*, *Jubaeopsis caffra* and *Attalea speciosa* (as *Orbignya martiana*) (Robertson 1977, May et al. 1985). Endosperm consistency also changes during the seed maturation process (Corner 1966). Endocarp classification can be found in Murray (1973).

Palm seeds contain small embryos relative to the seed size and a large amount of endosperm. In many cases, the different seed components are not completely developed at the time of dissemination. In several species such as *Cocos*

nucifera, the embryo initially consists of a simple disk of cells located near the operculum of a very large seed (Ginieis 1957, Corner 1966). Later, the cotyledon is differentiated into a tubular base, the petiole and the distal haustorium (Tomlinson 1990). The haustorium absorbs and assimilates nutrients from the endosperm, and during this process both the cotyledon and the embryo grow until they fill the entire nut cavity (DeMason 1985). However, the process of embryo development has been studied in detail for few palms, the best example being the date palm, *Phoenix dactylifera* (Lloyd 1910, DeMason 1984, DeMason et al. 1989).

In palms, the main storage resources for embryo development are lipids and insoluble polysaccharides (DeMason 1986, Chandra &

Table 1. Characteristics and adaptations of palm germination according to Rees (1960a) and Tomlinson (1960).

Type	Embryo	Plumule and radicle	Petiole and petiole	Ecological adaptation to the environment	Species-type
A	Straight	Along its main axis. Persistent radicle	Elongates, eligulate	dry	Phoenix-type
B	Straight	Obliquely to its long axis. Persistent radicle	Elongates, ligulate	dry	Washingtonia-type
C	Curved	Oblique. Non-persistent radicle	Scarcely elongates, ligulate	shaded and moist	Archontophoenix-type

DeMason 1988, DeMason et al. 1989). Many palm seeds contain very large amounts of lipids, e.g. the endosperm of the oil palm *Elaeis guineensis* contains 47% lipids and 36% insoluble carbohydrates in the form of galactomannan. During the early stages of germination, carbohydrates are metabolized more rapidly than lipids, but during seedling development the haustorium (cotyledon) actively converts triglycerides to carbohydrates (Alang et al. 1988). In other cases, the endosperm itself digests stored reserves, which are then subsequently absorbed by the haustorium, as in *Phoenix dactylifera* and *Washingtonia filifera* (DeMason et al. 1985).

Embryology

Differences are found in the form of the embryo, being either straight or curved. Germination is hypogeal (cotyledon below or on the soil surface) and cryptocotylar (cotyledon remains enclosed in the nut) (Pammel & King 1930). Nevertheless, there are four distinct variations in plantlet development in relation to the position of the plumule and radicle (oblique or along the main axis), persistence or loss of the radicle, degree of elongation of the cotyledon petiole, and presence or absence of a ligule (Tomlinson 1960). These differences have been related to establishment in

Table 2. Dispersal mechanisms among palms.

	Species	Dispersal agents	References
Primary dispersal	<i>Bactris baculifera</i>	birds	Bannister 1970; Trejo-Pérez 1976; Brown 1976a; Guix & Ruiz 1995; Matos & Watkinson 1998
	<i>Chamaedorea tepejilote</i>		
	<i>Euterpe edulis</i>		
	<i>E. globosa</i>		
	<i>Sabal palmetto</i>		
	<i>Syagrus romanzoffiana</i>		
Primary dispersal	<i>Acrocomia aculeata</i>	bats	Gardner 1977
	<i>Bactris</i> spp.		
	<i>Dypsis lutescens</i>		
	<i>Iriarteia exorrhiza</i>		
	<i>Livistona chinensis</i>		
Secondary dispersal	<i>Astrocaryum standleyanum</i>	monkeys	Oppenheimer, 1982
	<i>Bactris</i> spp.		
	<i>Desmoncus orthacanthos</i>		
	<i>Oenocarpus panamanus</i>		
	<i>Attalea butyracea</i>		
	<i>Socratea exorrhiza</i>		
Secondary dispersal	<i>Cocos nucifera</i>	water	Harries 1978; Smith et al. 1990; Matos & Watkinson 1998
	<i>Euterpe edulis</i>		
	<i>Attalea speciosa</i>		May et al. 1985
	<i>Euterpe globosa</i>		Bannister 1970
	<i>Astrocaryum</i> spp.	vertebrates (including rodents)	Glanz et al. 1982; Smythe et al. 1982; May et al. 1985; Eguiarte et al. 1993; Lott et al. 1995; Huch & Adler 1997; Brewer 2001
	<i>Normanbya normanbyi</i>		
	<i>Attalea speciosa</i>		
	<i>Bactris</i> spp.	ungulates	Bodmer 1991
	<i>Oenocarpus bataua</i>		
	<i>Mauritia flexuosa</i>		
<i>Syagrus romanzoffiana</i>	fish	Gottsberger 1978; de Souza-Steveaux et al. 1994	
<i>Astrocaryum jauari</i>			

moist or in dry environments. In *Sabal* and other palms of dry environments the cotyledon stalk develops into a tubular structure (remote ligular), which pushes the seedling below the soil surface protecting it from dehydration and giving ecological significance (Tomlinson 1960). In palms from shaded and moist habitats as *Archontophoenix* this characteristic is of no ecological advantage. A summary of the variations in embryo development and of the possible ecological constraints is shown in Table 1 (Tomlinson 1960, Rees 1960a).

Seed dispersal

Among palms hydrochory, barochory and zoochory are common, but anemochory is extremely rare. However, gravity is the most common dispersal mechanism of large and heavy seeds. Due to their size and to the fact that seeds in some species remain attached to the rachilla for a long time, other mechanisms are necessary for primary and secondary seed dispersal. For example, in *Cocos nucifera* (Harries 1978), and in *Reinhardtia gracilis* var. *gracilior* (Mendoza 1994) the action of strong winds plays an important role in seed dissemination (Brown 1976a). When mature seeds are not abscised or are trapped among leaf bases, they can germinate on the tree, but the seedling dies (Harries 1978, Clancy & Sullivan 1988).

Primary dispersal by different species of animals, mainly birds, has been reported in a review by Zona and Henderson (1989) for several palm species. Canopy characteristics of tropical forests and the behavior of animal dispersers can strongly influence seedling recruitment of some palms (Svenning 2001). Secondary dispersal is carried out by other mechanisms, such as water, and/or by vertebrates including rodents, ungulates and fishes (Table 2). Seawater dispersal of *Sabal palmetto* and *Cocos nucifera* requires the embryo to be tolerant to the dehydrating effect of salty water; this tolerance can be distributed differentially among cultivars and the natural population (Brown 1976a, Karunaratne et al. 1991).

Barochorous dispersal produces a clustered distribution of seedlings which leads to high seedling mortality. Only those seeds that are far away and isolated can survive; therefore, a random distribution among adults could occur (Sterner et al. 1986, Barot et al. 1999). This pattern does not differ from that proposed by Connell (1970) and Janzen (1970) for tropical species. In other cases, high seed mortality occurs below the parent plant due to predation, which is density-dependent (Janzen 1970). Seeds of *Attalea butyracea* (as *Scheelea rostrata*), *Euterpe globosa* and *Chamaedorea*

tepejilote are heavily predated by beetles on the soil; however, seeds removed rapidly by mammals could avoid predation, and germinate when they are forgotten in their burrows (Janzen 1971, 1972, Oyama 1991).

During dispersal fruit coats covering the seed have an important role to protect the embryo for a long time, while seeds are floating in water (as coconut and *Nypa*). Fibrous bundles of lignin in the mesocarp and/or the endocarp may also be a defense against seed predators, favouring dispersal by birds and mammals (Stocker & Irvine 1983, Bodmer 1991, Fragoso 1997). In contrast, predators damage seeds that do not have hard structures to protect the embryo, as in *Astrocaryum paramaca*. However, some of these seeds can survive, and thus predators can act as reliable dispersers (Forget 1991).

The coconut embryo develops in a way that presents a fascinating combination of adaptive traits for long distance sea water dispersal, germination and establishment in harsh environments on tropical sandy beaches (Edmonson 1941, Sento 1974, Sugimura & Murakami 1990). The fibrous mesocarp and stony endocarp allow flotation in salty water for long periods of time, thus preserving the viability of the seed. Embryo development remains practically isolated from any damaging effect of the external environment for several months, allowing long distance movement of the propagule. When the coconut arrives on a sandy beach, the heat of the sand accelerates the development of the embryo, and the plumule protrudes through the germinative pore. The plumule achieves photosynthesis, which allows the seedling to develop inside the coconut a strong rooting structure that escapes from the harsh conditions of the soil surface (Foale 1968).

Seed germination

Palms show an amazing diversity of developmental processes, timing and requirements for germination (Corner 1966). Protrusion of the embryo may take place as a result of the development of either the radicle or the plumule. Mechanisms of seed germination and dormancy are poorly understood processes for most palms. However, it is known that many species show rapid germination, such as *Jubaea chilensis* and *Sabal causiarum* that require only 13–20 and 12–22 days, respectively for full germination (Wagner 1982, Carpenter 1989), while others take more than five years to start germinating (e.g. *Chamaedorea seifrizii*) (Wagner 1982).

According to Tomlinson (1971) *Nypa fruticans* shows vivipary, an extreme case of palm seed

germination in which seeds germinate on the mother plant. This probably occurs as in other viviparous species because seeds do not dehydrate during seed maturation (Kermode 1995, Vertucci & Farrant 1995). Seeds have enough water to germinate on the tree and do not show a clear period of quiescence or dormancy; therefore, embryo development is continuous. However, *Nypa* can be dispersed ungerminated in the fruit. When mature fruits are collected from the tree and the seeds are extracted, seed germination begins 4–5 days after sowing in a moist substrate and is completed by 22 days, showing a brief period of rest, the duration of which is widely spread among the seed population (Siddiqi et al. 1991).

There is also wide variation in germination time among palms (Koebernik 1971, Basu & Mukherjee 1972, Wagner 1982, Endt 1996), including those from the same environment (Braun 1968, Jordan 1970). In a seed cohort, synchrony of seed germination can be from immediate and almost simultaneous to very delayed and/or sporadic. Seeds of *Metroxylon warburgii* and *M. vitiense* germinated almost simultaneously after falling to the ground (Doren 1997), while in *Ceroxylon ceriferum* (as *C. klopstockia*), *Chamaedorea elegans*, *Elaeis guineensis*, *Gronophyllum ramsayi* and *Pelagodoxa henryana*, germination is erratic, and several years may be required for all seeds to germinate (Hussey 1958, Poole & Conover 1974, Braun 1976, Wagner 1982, Braun 1984, Clarke 1988, Phillips 1996). This delayed or sporadic germination has been linked with different factors such as seedling escape from predation (Braun 1968). It has also been related to the extent of the period of dryness in savannas and forests. Different germination peaks from the same seed cohort could occur in several subsequent years during each wet season (Rees 1962, Carvalho et al. 1988, Ataroff & Schwarzkopf 1992, Harms & Dalling 1995, Olvera 1997).

Germination rates and germination capacity among seeds from different populations (cohorts and individuals of the same species) may differ considerably, as has been demonstrated for coconut and other species. These differences are mainly due to environmental and genetic factors in natural populations and/or to selection during domestication, or different handling techniques in cultivated species (Whitehead 1965, Robertson 1977, Al-Madeni & Tisserat 1986, Broschat & Donselman 1986, Clement & Dudley 1995, Rohani et al. 1997, Zizumbo-Villarreal & Arellano-Marín 1998).

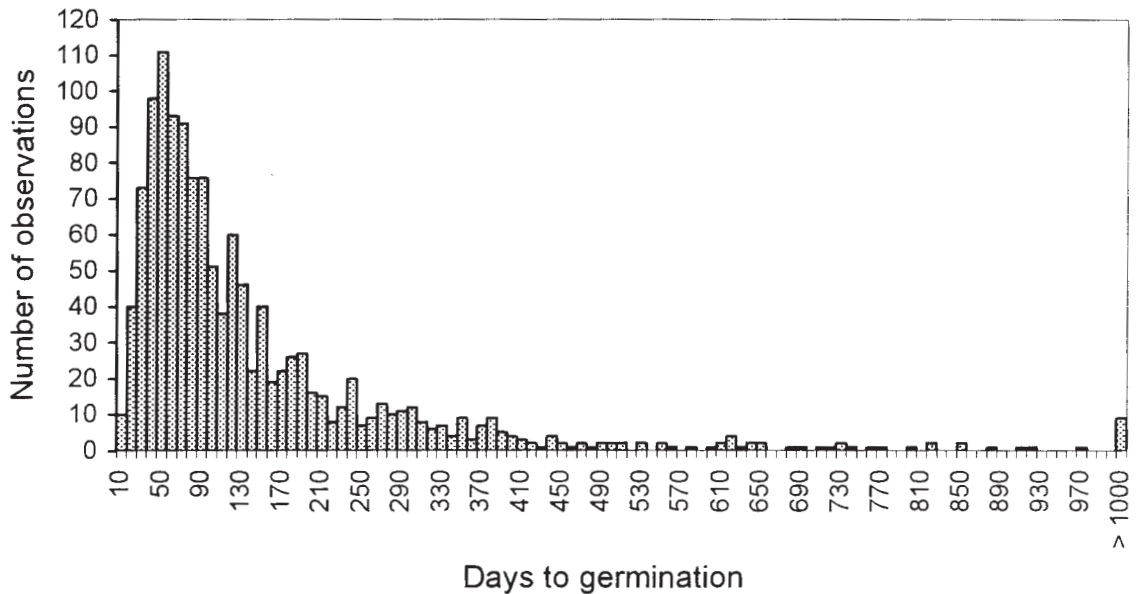
Variation in germination rates and germination capacity has also been related to different degrees

of maturation among seeds. Immature fruits of apparently full size could remain on the tree for a long time (Tomlinson & Soderholm 1975); therefore, occasionally it is difficult to identify seed maturation from the external appearance of the fruit (Holmquist & Popenoe 1967, Manokaran 1978, Broschat & Donselman 1988, Kheong 1992, Phillips 1996). It is necessary to identify maternal effects that could induce different degrees of maturation in the same infructescence during palm seed development. In Asteraceae and other flowering plants the position of seeds in the infructescence can produce polymorphism in seed requirements for germination (Baskin & Baskin 1998). This type of maternal effect could be related to erratic germination e.g. seeds from the same infructescence of *Arenga engleri* can germinate over a period of 515 days (Koebernik 1971). Maternal effects could also explain differences in germination requirements among batches, individuals, populations or years of seed production.

Several studies summarize germination data on palms (e.g. Braun 1968, Koebernik 1971, Basu & Mukherjee 1972), but the information is not uniform, and data about treatments are not always included. The criterion to define time for germination is also expressed in several ways, producing misunderstanding of the information: i) time to start germination, ii) time for full germination, iii) time for 50% of germination, iv) the interval between the start and the end of germination. The distribution of "time for germination" of 457 species is shown in Figure 2, which was taken from 1281 published records. From all the data reviewed it is possible to show that it is common for palms to begin germination within 120 days after planting. However, due to the heterogeneity of information it is difficult to conclude anything with certainty about the time necessary for completion of germination, especially for species that show delayed and/or sporadic seed germination.

Seed dormancy and germination requirements

According to the most widely accepted concept of germination – defined as the moment when the embryo protrudes through the seed covers – palm seeds do show a period of quiescence or dormancy. Some authors state that dormancy does not exist in palms because in most cases the embryo is immature at the time of dispersal and keeps developing while germination is arrested (Corner 1966). This is common among dormant seeds of flowering plants. Consequently, morphological dormancy related to anatomical features of embryo, and/or physical dormancy related to



2. Frequency distribution of "time for germination" of 457 species taken from 1281 published records. Data taken from the last twelve observations show that time for germination in some species took from 1021 to 1941 days.

features of the surrounding structures (coat, endosperm, etc.) have been proposed for palms that show delayed germination (Baskin & Baskin 1998). Germination delay after dissemination may have different causes among palms, varying from seed dormancy to unsuitable environmental factors for germination and/or the interaction between them.

Anatomical embryo immaturity is frequent in palms, but very little is known about other causes of morphological dormancy. Sometimes embryos in culture are capable of growing immediately, but germination of nuts is delayed because of a hormonal imbalance (physiological dormancy) (Hussey 1958, Robertson & Small 1977, Yuri 1987). Therefore, treatments with gibberellins and other hormones may promote germination percentage or increase germination rate in dormant seeds of several species (Nagao et al. 1980, Odetola 1987, Chin et al. 1988).

Moisture. Moisture balance between seeds and the surrounding environment determine the progress of germination. Conditions such as radiation, soil moisture and atmospheric humidity may affect this balance (Hussey 1958, Robertson & Small

1977, Ferreira & Santos 1992). Seeds gaining moisture will germinate faster than those that take up little or no water at all. Contrary, excess of moisture may also become an obstacle to germination due to improper ventilation for the physiological process of germination, or because it can promote the development of pathogenic fungi (Rees 1960a, b, 1963, Robertson & Small 1977, Fullington 1978).

From the physiological point of view it has not been demonstrated that lack of oxygen induces dormancy (Bradbeer 1988). Nevertheless, it has been proposed that oxygen is required to break chemical dormancy caused by substances in the endocarp that inhibit or delay seed germination (Hussey 1958, Robertson & Small 1977). In order to remove chemical inhibitors in palm seeds, the most common treatment is to soak the seeds for a period of 12–72 hours or more. However, prolonged soaking could be required only to break down the hard seed covers or to increase water uptake making germination more uniform and/or faster (Kheong 1992, Chalita et al. 1996, Davies & Pritchard 1998a, Doughty 1988, Moussa et al. 1998), as occurs in the field during flooding (Kitzke

1958). Due to the general practice of removing the fleshy parts of the fruits and washing the seeds before germination (Yocum 1961, Rees 1963), and in the absence of adequate experimental procedures to test the presence of chemical inhibitors, there have been few studies of the effects of soaking on germination that have been sufficiently documented (Kitzke 1958, Robertson & Small 1977, Ehara et al. 2001).

Seed covers. Dormancy has been attributed to a hard or water-impermeable seed cover (physical dormancy, Baskin et al. 2000), such as a fibrous mesocarp and/or a stony endocarp, which are very common among palms (Holmquist & Popenoe 1967, Robertson & Small 1977, Daquinta et al. 1996). In fact the hardness of many palm nuts has prompted their use for handicrafts (Bernal 1988, Doren 1997). However, in species such as *Jubaeopsis caffra* it has been demonstrated that parts of the seed (stony endocarp and hard endosperm) are permeable to water and oxygen (Robertson & Small 1977). After removing the hard shell of *Acrocomia aculeata* (as *A. mexicana*) and *A. sclerocarpa*, germination time was reduced from 440 and 878 days to 138 and 373 days, respectively (Koebernik 1971). Also, the endosperm by itself could be a barrier for germination that may delay germination for more than 150 days (Koebernik 1971, Murray 1973).

An extreme case of dormancy imposed by a hard coat has been described for *Chamaerops humilis* from the Mediterranean area; germination takes about a month to initiate, but a treatment of 4.5–7 hours of concentrated sulphuric acid to weaken the coat, allows germination after only 7 instead of 35 days (Merlo et al. 1993). It should be emphasized that seed covers only delay water absorption and probably oxygen diffusion (Robertson & Small 1977). Then, sooner or later the embryo itself will break the seed covers when it becomes more vigorous and/or when the germination process is initiated after imbibition (Baskin & Baskin 1998). Seed covers in palms act mainly as a mechanical obstacle for germination contrary to the impermeable hard coat of legume seeds (Vázquez-Yanes & Orozco-Segovia 1994).

Temperature. Most palm seeds are thermophilous, since optimal temperatures for germination are between 30–40°C (Odetola 1987, Addae-Kagyah et al. 1988, Carpenter 1988, Muñoz et al. 1992, Broschat 1998, Ehara et al. 1998). Soil temperatures above 38°C, but below 42°C can reduce the time required for germination of seeds of *Elaeis guineensis* from years to weeks (Rees 1960b, 1962). However, some species from subtropical areas do not require such high

temperatures, and a few even require a period of cool temperature (cold stratification at 5°C) to reach the highest germination percentage. For example, several cold-tolerant *Sabal* species and *Rhapidophyllum hystrix* require cold stratification and have their optimal temperatures for germination in a temperature range that is relatively low for most palms (21–25°C, Clancy & Sullivan 1988, Carpenter 1989). *Sabal palmetto* additionally requires daily fluctuating temperatures to reach high germination percentages, while constant temperatures are suboptimal for germination (Brown 1976b).

Heating at 38–40°C for several days is a common practice to induce germination of palm seeds (Addae-Kagyah et al. 1988). However, knowledge of the morpho-physiological role of high temperature on dormancy and seed germination is based on only few rigorous studies carried out on *Elaeis guineensis* (Hussey 1958, Rees 1962). The time of exposure to high temperatures required to induce germination can be as long as two months or more. This can be considered as a stratification treatment because high temperatures are necessary to break dormancy, but not necessarily needed for germination. The effect of this treatment is retained during seed storage.

In other plant families an optimal warm stratification commonly occurs at lower temperatures than in palm seeds (25–30°C), accelerating the growth rate of embryos (e.g. *Jeffersonia diphylla*, Podophyllaceae, Baskin & Baskin 1989, 1998). Nevertheless, in *E. guineensis* the effect of warm stratification has not been directly related to the embryo growth rate, but it has been reported that gibberellic acid can substitute the effect of heat in accelerating seed germination (Nagao et al. 1980). In this species high temperature seems to be related to: 1) changes in the physiological ability of the embryo to modify the characteristics of the abscission layer of the operculum, promoting its rupture, 2) changes in the characteristics of the endosperm reducing the constraint to the embryo growth, 3) modifications of the embryo, which can make efficient use of the endosperm. In fact, the main problem for germination of *E. guineensis* seeds is the presence of the operculum; once it is abscised, the embryo germinates (Hussey, 1958).

Germinating palms at constant high temperatures is not always adequate. In some cases this treatment induces germination as in *Coccothrinax argentata* and *Acoelorrhapha wrightii* (Carpenter 1988). Nevertheless, these temperatures are deleterious for other species, and germination percentages are higher when high daily

temperatures are followed by a period of relatively low temperature, e.g. in coastal dunes, deserts and other sunny environments (Rees 1962). On the other hand, non-dormant seeds of species that can germinate at relatively low constant temperature (25°C) can also germinate at fluctuating temperatures that include high temperatures during the diurnal period (e.g. 25–35°C, Carpenter 1989). It has been shown that germination temperatures are related to the lipids melting point. This relationship is crucial to understand adaptive evolution and biogeographic distribution of angiosperms (Linder 2000). Then, future research is necessary to understand the effect of high temperature on the liquefaction of lipids in the seeds and its relation to palm seed germination.

Light. It has been documented that light may act as a germination inhibitor in *Sabal palmetto* (negative photoblastism, Brown 1976b). Germination of seeds covered by soil suggests that most seed palm species are indifferent to light, although the effects of light on germination have not been properly studied. For example, in *Calamus manan*, Aminuddin and Siti (1990) tested seed germination in the open and beneath the canopy, but not in the darkness. To identify positive or negative photoblastism or indifference to light it is necessary to test seed response to darkness, white light and far red light, either beneath the canopy, or using special filters. Some positively photoblastic seeds germinate in far red light but not in darkness (Smith 1982).

Biotic interactions. In some cases primary and secondary animal dispersers promote germination

as in *Pinanga insignis*, *Caryota rumphiana* and *Attalea speciosa* (as *Orbignya martiana*) (May et al. 1985). Sometimes transit through the guts of birds and mammals removes the sarcotesta and/or the mesocarp, which accelerates germination of species like *Attalea speciosa* (as *Orbignya martiana*) and *Washingtonia filifera* (Bullock 1980, Stocker & Irvine 1983, May et al. 1985). In other cases, seeds are deposited in safe sites that correlate with the best conditions for germination and establishment, as *Astrocaryum mexicanum* and *A. murumuru* (Cintra & Horna 1997, Martínez-Ramos & Samper 1998).

Handling. Palm seeds collected and transported to places away from sites of production are often very difficult to germinate. Part of the problem may be partial dehydration during handling. In seeds of *Chamaedorea alternans*, even a small degree of desiccation induces hysteresis and rehydration is not completed; therefore, germination is inhibited (Rodríguez et al. 2000). On the other hand, there are palm seeds in which germination is improved by partial dehydration at the end of seed maturation. This partial dehydration may take place before or during dissemination (Robertson & Small 1977, Kheong 1992, Daquinta et al. 1996, Zizumbo-Villareal 1997).

Field germination. Several studies have documented conditions for germination in the field (Fullington 1978, Velez 1992), e.g. for *Caryota mitis* and *Prestoea acuminata* (as *P. trichoclada*) (Raich & Gong 1990, Bonilla & Feil 1995, Bonadio 1998, Matos & Watkinson 1998). However, there is a deficiency of experimental studies designed to document

Table 3. Types of storage behavior among palms.

Species	Seed moisture content (%)	Habitat	Storage behavior	References
<i>Bactris gasipaes</i>	-			Ferreira & Santos 1992, 1993; Hong et al. 1997; Andrade 2001
<i>Calamus manan</i>	67	tropical	recalcitrant	
<i>Chamaedorea tepejilote</i>	40	humid		
<i>Euterpe precatoria</i>	-			
<i>Euterpe edulis</i>	-			
<i>Mauritia flexuosa</i>	-			
<i>Coccothrinax argentata</i>	-			
<i>Phoenix dactylifera</i>	34	dry	orthodox	Hong et al. 1997
<i>Sabal mexicana</i>	12–13			
<i>Washingtonia filifera</i>	-			
<i>Acoelorrhaphe wrightii</i>	-	tropical		Rees 1960b; Grout et al. 1983; Chin et al. 1984; Hong et al. 1997
<i>Attalea crassispatha</i>	57	brackish		
<i>Roystonea regia</i>	50	swamps	intermediate	
<i>Adonidia merrillii</i>	45	or seasonal		
<i>Elaeis guineensis</i>	21–30	areas		

field germination. It is necessary therefore, to carry out laboratory and field experiments to provide more information about the factors that break dormancy and/or induce germination, and to improve techniques for propagation of palms from seeds. Currently there is much useful anecdotal information, but it contributes little to the biological knowledge of palm seed germination. Many manuals and papers directed to horticulturists working on palm propagation in nurseries or botanical gardens describe a variety of treatments for germination. However, these treatments cannot be applied as a rule for all the species; seed characteristics and the habitat of each species need to be taken into account (Rees 1963, Doughty et al. 1986, Hodel 1992).

Seed longevity

One of the first classifications of palm seed longevity was that of De Leon (1961), who was able to test viability of seeds coming from all over the world at the Fairchild Tropical Garden. He classified them in three groups: a) short lived seeds, which lose viability after only 2 or 3 weeks of storage – most of these were species from tropical humid origin; b) an intermediate group with viability of 4 to 6 weeks, also of tropical origin; and, c) long-lived seeds characteristic of species of subtropical and/or very seasonal climates with viability of two to three or more months. Hong et al. (1997) questioned the validity of this classification. These authors based their classification on the initial seed moisture content, tolerance to dehydration and low temperatures, while De Leon's classification ignores storage and handling conditions.

Seed longevity and storage behavior are closely related. Therefore, any discussion about this subject should be based on Hong & Ellis (1996). Seeds with low moisture content that are tolerant to low temperatures (below 0°C) and have a long viability are classified as orthodox; those with high moisture content, no tolerance to dehydration or to temperatures are classified as recalcitrant; these seeds have a short viability. Finally, those seeds that are tolerant to dehydration, but not to low temperatures (0°C and -20°C) were classified as intermediate. The viability of these seeds can be prolonged by dehydration.

Generally, palm seeds have high seed moisture content at the time of dissemination; however, even within a genus, species can differ in their storage behavior (Hong et al. 1997). As expected some palm seeds from tropical humid environments are classified as "recalcitrant" due to their high moisture content (Table 3). Nevertheless, other palms from tropical humid,

brackish swamps or more seasonal areas are intermediate, while others from seasonally dry climates or dry environments show the orthodox storage behavior and can be maintained viable in cold dry storage (Table 3).

On the other hand, lack of information about seed physiology could lead to a wrong classification of storage behavior. *Elaeis guineensis* has been classified as recalcitrant due to its high moisture content, later was classified as orthodox due to its favorable seed response to cryopreservation, and finally as intermediate after more detailed studies (Grout et al. 1983, Chin et al. 1984, Hong et al. 1997). This could explain why 30% of its seeds remained viable after 33 months when kept under bare soil in natural conditions (Galt 1956, cited in Rees 1960b).

Cryopreservation. According to the definition, intermediate and recalcitrant seeds cannot survive cryogenic storage. However, it has been possible to keep frozen seeds or embryos of *Elaeis guineensis* (intermediate), *Calamus manan* and *Cocos nucifera* (recalcitrant) viable for a considerable period of time (>15 months) (Grout et al. 1983, Chin et al. 1989, Engelmann et al. 1995, Hong et al. 1997). Amazingly, tropical seeds of *Ptychosperma macarthurii* and other species germinated after 1 hour in liquid nitrogen (Al-Madeni & Tisserat 1986). Cryopreservation of the excised embryos, either by encapsulation or vitrification may solve the difficulties of germplasm conservation of palms in the future. More research on palm tissue culture should be performed.

Handling. Responses of palm seeds to dryness may cause confusion with regard to how long they can be stored. In some cases, dryness may induce a long lasting dormancy that might be misinterpreted as loss of viability; germination might be delayed for such a long time that seeds have been declared dead too soon (De Leon 1958, Kitzke 1958, Rees 1962). After dissemination, seeds of *Geonoma membranacea* and *Acoelorrhaphe wrightii* normally germinate within 48 and 90 days, respectively. However, previously dehydrated seeds developed a very retarded and erratic germination pattern (up to three and fifteen months, respectively) (Koebernik 1971, Dickie et al. 1993). On the other hand, chemical treatments (benomyl, methomyl, etc.) used for seed disinfections, and applied before germination tests, can cause an important germination reduction as in *Bactris gasipaes* (Coates-Beckford & Chung 1987). At the moment, storage behavior and seed viability of most palm species is uncertain or ought to be confirmed taking into account handling and storage of seeds from collection

(Hong et al. 1997, Davies & Pritchard 1998a, b). Several techniques to prolong viability of entire recalcitrant seeds have been developed, including suitable handling, transportation, the use of fungicides, keeping seeds in moisture and warm storage, etc. A temperature of 23°C has been shown to be suitable for *Dypsis lutescens* (as *Chrysalidocarpus lutescens*) (Broschat & Donselman 1986).

Ecological longevity. Longevity of palm seeds may differ considerably between field and controlled storage conditions. Recalcitrant seeds of *Attalea speciosa* (as *Orbignya phalerata*) survived for 9 months in the field, but less than 3 months in controlled conditions (Carvalho et al. 1988). In spite of expecting rapid germination from recalcitrant seeds, it has been reported that seeds of *Chamaedorea alternans* survived in the natural soil seed bank for 290 days (Moreno-Casasola 1976). Seeds of this species may require a long time to germinate under controlled conditions (Rodríguez et al. 2000), unlike other recalcitrant or short-lived seeds, which germinate quite quickly (Jordan 1970, Manokaran 1979, Hong et al. 1997). Thus, a relatively long viability in the moist soil of the forest might be favorable for those seeds requiring after-ripening. However, very little information is available on this subject.

Because palms are an important component of tropical and subtropical forests, are the world's third most useful plant family (Johnson 1996), and generate great interest among collectors, fans, horticulturists and scientists, we urge to make a greater effort to increase our knowledge on the biology of these species. Any contribution will enhance our ability to propagate, use, manage, and preserve this extraordinary and important plant family.

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