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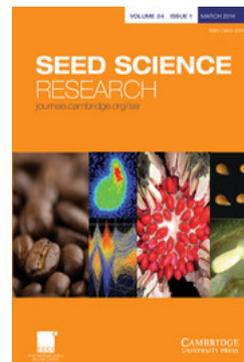
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RESEARCH OPINION

What kind of seed dormancy might palms have?

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Abstract

Palm diaspores are reported to have various kinds of dormancy. However, (1) the embryo is underdeveloped; (2) the endocarp is water permeable; and (3) the diaspores take a long time to germinate. Thus, we conclude that the diaspores of the majority of palm species have morphophysiological dormancy (MPD). The ones that do not have MPD are morphologically dormant.

Keywords: Arecaceae, embryonic axis (inside cotyledonary petiole), endocarp germination pore ('eye'), haustorium (cotyledonary blade), hypogeal germination, morphological dormancy, morphophysiological dormancy, operculum, underdeveloped embryo

Introduction

The palm family (Arecaceae) includes about 2400–2600 species of evergreen trees, shrubs and lianas, most of which occur in the tropics and subtropics (Corner, 1966; Moore and Uhl, 1973; Uhl and Dransfield, 1987; Tomlinson, 1990; Mabberley, 2008). Various kinds of dormancy have been assigned to the diaspores (seeds or fruits) of this family, including physical (Carpenter *et al.*, 1993; Moussa *et al.*, 1998), non-absolute physical (Neves *et al.*, 2013), physiological (Ribeiro *et al.*, 2011), non-profound physiological (Ribeiro *et al.*, 2012b; Neves *et al.*, 2013; Megalhães *et al.*, 2013), non-deep physiological (Junior *et al.*, 2013; Schlindwein *et al.*, 2013), morphological, morphological combined with chemical, morphological combined with mechanical, morphological combined with both mechanical and

non-deep physiological (Nikolaeva *et al.*, 1985), mechanical exogenous (Fior *et al.*, 2011) and morphophysiological (Perez *et al.*, 2008). Thus, it seems that much confusion exists concerning the kind(s) of diaspore dormancy in the Arecaceae. The purpose of this opinion paper is to evaluate the literature on palm seeds and their germination in order to determine to which dormancy class(es) (*sensu* Baskin and Baskin, 2004) they might belong.

Results and discussion

Palm fruits are berries or fibrous drupes with up to ten seeds. However, in many species there is only one seed per mature fruit, although the ovary is tricarpellate. The fruits exhibit a wide range of sizes, the largest being that of the double coconut *Lodoicea maldivica* (c. 45–50 cm long and weighing 36 kg), which has the largest seed in the plant kingdom. Generally, the fruit wall (pericarp) consists of the exocarp, mesocarp and endocarp. The endocarp or 'shell' may be thick and stoney (drupe) to thin, papery or fleshy (berry); in some taxa, it is undifferentiated (Corner, 1966; Harper *et al.*, 1970; Moore and Uhl, 1973; Uhl and Dransfield, 1987; Tomlinson, 1990; Dransfield and Uhl, 1998).

The seed consists of an achlorophyllous embryo and endosperm surrounded by a thin (usually) seed coat and sometimes a sarcotesta (fleshy outer seed coat). In most species, the embryo is small and linear, but in some species, e.g. *Nypa fruticosa* (see figure B.51 in Tomlinson, 1986), the only palm that is a 'strict or true mangrove species', it is shaped like a cylinder, being flat on one end and tapering to a point on the other end. In general, the embryo (E):seed (S) length (E:S) ratio is low, i.e. <0.10 to c. 0.30–0.40. However, in a few genera the embryo is large, e.g. E:S ratio of c. 0.70 in *Oenocarpus* and c. 0.85 in *Jessenia* [E:S ratios determined by measuring lengths of seeds and embryos from drawings in Uhl and Dransfield (1987)].

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The embryo may occupy <1% of the total seed volume, and its position can be basal (micropylar end), apical (other end), lateral or some variation thereof, e.g. subapical. In seeds with thick endocarps, such as those of coconut palm and oil palm, the embryo is located adjacent to an endocarp germination pore ('eye') (Fig. 1a). Seed storage behaviour can be orthodox or non-orthodox (intermediate or recalcitrant) (Corner, 1966; Yakovlev and Zhukova, 1980; Janzen, 1982; Uhl and Dransfield, 1987; Tomlinson, 1990; Ellis *et al.*, 1991; Orozco-Segovia *et al.*, 2003; Panza *et al.*, 2004; Pritchard *et al.*, 2004; Von Fintel *et al.*, 2004; González-Benito *et al.*, 2006; Perez *et al.*, 2008; Ribeiro *et al.*, 2011, 2012a, b; Jose *et al.*, 2012).

In whole-view (Fig. 1a), the embryo can be divided into two regions: cotyledonary petiole located adjacent to the operculum [portion of endosperm (micropylar endosperm) and seed coat covering the proximal end of embryo that may be demarcated by a zone of weakness] and cotyledon blade, which remains inside the seed. The endosperm is homogeneous or ruminant, and in some species it contains a cavity that is dry or filled with liquid, e.g. coconut 'milk' in *Cocos nucifera*

(Hussey, 1958; Corner, 1966; Robertson, 1977; DeMason, 1985; Uhl and Dransfield, 1987; DeMason *et al.*, 1989; Aguiar and de Mendonça, 2002; Neves *et al.*, 2013). The cotyledonary blade or apical portion thereof acts as a haustorium and absorbs and metabolizes products of hydrolysis from the endosperm; however, see Panza *et al.* (2004), who concluded that the endosperm of the recalcitrant species *Euterpe edulis* is inactive, i.e. no storage metabolism. Histologically, the embryo consists of a single cotyledon and a short plumular–radicular axis (epicotyl with leaf primordia and root apex) located in the proximal end of the cotyledonary tube (Fig. 1b) (Dassanayake and Sivakadachchan, 1973; Robertson, 1976; Haccius and Philip, 1979; DeMason, 1988a; Aguiar and de Mendonça, 2003; Panza *et al.*, 2004; Henderson, 2006; Ribeiro *et al.*, 2012a; Nazario *et al.*, 2013; Neves *et al.*, 2013).

In some palms, the natural dispersal unit is a drupe with a hard, thick endocarp from which the seeds can be removed only by physically cracking it (Robertson and Small, 1977; Broschat, 1998; Davies and Pritchard, 1998; Moussa *et al.*, 1998; Ehara *et al.*, 2001; Perez *et al.*, 2008; Myint *et al.*, 2010; Ribeiro *et al.*, 2011; Neves *et al.*, 2013).

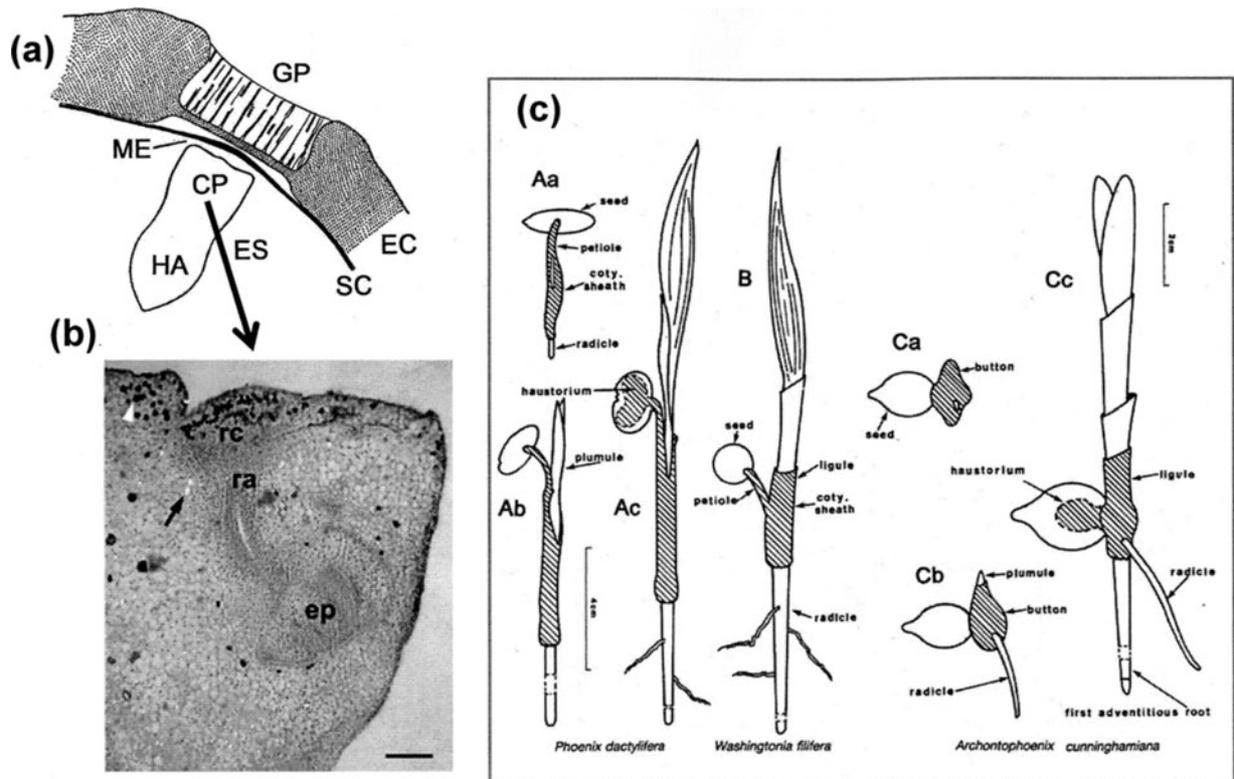


Figure 1. (a) Longitudinal section of a palm fruit showing embryo with cotyledonary petiole adjacent to the operculum (micropylar endosperm + seed coat) under the germination pore of a drupe of a palm. The embryo is about 3 mm long (from Hussey, 1958). (b) Median longitudinal section of proximal region of cotyledonary petiole showing embryonic axis (ep, ra, rc) that is enclosed within it. Scale bar is 0.20 mm (from Panza *et al.*, 2004). (c) The three primary morphological types of seedlings (germination) commonly recognized in palms (from Tomlinson, 1960). Aa, Ab, Ac, remote-tubular; B, remote-ligular; Ca, Cb, Cc, adjacent-ligular. CP, cotyledonary petiole; EC, endocarp; ep, epicotyl; ES, endosperm; GP, germination pore with fibrous mesocarp tissue; HA, haustorium; ME, micropylar endosperm (endosperm cap); ra, radicle; rc, root cap; SC, seed coat. Figures reproduced with permission.

In most cases, presence of a hard endocarp inhibits seed germination. Thus, isolated seeds (removed from endocarp) germinate better, often much better (higher percentage/rate), than those with the pericarp intact (Broschat, 1998; Moussa *et al.*, 1998; Ferreira and Gentil, 2006; Perez *et al.*, 2008; Ribeiro *et al.*, 2011). As such, claims have been made that the fruit is water impermeable, thus accounting for the 'physical dormancy' of the diaspore, i.e. drupe (Carpenter *et al.*, 1993; Moussa *et al.*, 1998). However, this is not the case. Robertson and Small (1977) showed that the hard, thick pericarp of *Jubaeopsis caffra* was permeable to water (and oxygen), and Perez *et al.* (2008) demonstrated that imbibition of seeds inside fruits of *Pritchardia remota* was not blocked. The water content of isolated seeds of *Acrocomia aculeata* did not differ significantly from that of intact fruits with a thick, stony endocarp (21.7 and 22.9%, respectively) after 60 d on a moist substrate (Ribeiro *et al.*, 2011). After 45 d of imbibition, the percentage moisture content (MC) of isolated seeds, seeds in intact fruits and seeds inside scarified fruits of *Attalea vitriovir* was nearly identical; seed MC increased from c. 6–7% to c. 22–23% (Neves *et al.*, 2013).

We consider the embryo in palm seeds to be underdeveloped. The proximal end of the embryo, i.e. the cotyledonary petiole, is adjacent to the operculum, and germination of palm seeds is often defined as dislodgment of the operculum resulting from elongation of the cotyledonary petiole (Fong, 1978; Perez *et al.*, 2008; Fior *et al.*, 2011; Ribeiro *et al.*, 2011; Neves *et al.*, 2013). Further, the cotyledonary blade (haustorium) expands to fill most of the seed, albeit after the cotyledonary petiole emerges from the seed (germination), i.e. expansion of the cotyledon/haustorium occurs and tissue development continues following germination (DeMason, 1984, 1985, 1988b). In which case, germination occurs before emergence of the radicle and shoot from the cotyledonary petiole/sheath and after the latter has protruded through the opening left by displacement of the operculum. Thus, the embryo requires further development outside the seed before germination in the strict sense of the word (i.e. radicle emergence) is complete. In fact, de Queiroz (1986) defined the germination in seeds of *Euterpe edulis* as occurring in two distinct stages: (1) protrusion of the cotyledonary petiole, and (2) growth (emergence) of the radicle and shoot from the cotyledonary petiole, which he described as 'the germination itself'. He found that the second stage was completed about 6 weeks after the first stage. The whole-seed germination process in palms, as described by Pinheiro (2001) for *Schippia concolor*, in which germination is a variation of the two remote types described below, begins with protrusion of the cotyledonary petiole and ends with emergence of the plumule through the base of the cotyledonary sheath. In *S. concolor*, the cotyledonary petiole emerges from the (isolated) seed 8–9 d after planting, and the

root and plumule from the cotyledonary petiole about 30 and 80–90 d, respectively, after planting. In the mangrove species *Nypa fruticans*, germination is 'incipiently viviparous' (Tomlinson, 1986).

In a review of information on time to germination in palms [unit(s) of germination not specified, i.e. whole fruit, seed + endocarp ('nut') or seed ('kernel')] that included 1281 published records on 457 species, seeds in about 10% of the observations germinated within 30 d, and for the other 90% time to germination ranged from between 31 and 40 to 1941 d. Seeds in about 53% of the 1241 observations germinated between days 31 and 40 to 121–130 (Orozco-Segovia *et al.*, 2003). The facts that seeds (diaspores) of most palms take longer than 30 d (usually much longer) to germinate and have underdeveloped embryos indicate that morphophysiological dormancy (MPD) is the major dormancy class in the family. The 10% of the diaspores that germinated in ≤ 30 d would have morphological dormancy (MD) (Baskin and Baskin, 2004).

All palms have hypogeal germination since the seed is not raised above the soil; in monocots with epigeal germination, the seed is raised above the soil surface by elongation of the cotyledon (Tillich, 2007). Three morphological types of seedlings (germination) are commonly recognized in palms: remote-tubular, remote-ligular and adjacent-ligular (Fig. 1c). In the latter two types, the cotyledonary petiole bears a ligule, a distal projection of the leaf sheath. In remote-tubular (e.g. *Phoenix*) and remote-ligular (e.g. *Sabal*, *Washingtonia*) types of germination, the embryonic axis (inside the cotyledonary tube/sheath) is pushed into the soil to varying depths by downward extension (positive geotropism) of the cotyledonary petiole with an enlarged basal sheath from which the seedling develops at varying distances from the seed. The persistent radicle (primary root) breaks through the base of the cotyledonary sheath, and the plumule emerges from the cleft in the cotyledonary sheath in the remote-tubular type and from the mouth of the cotyledonary sheath (ligular extension) in the remote-ligular type. Thus, in these two types of germination the seedling is moved some distance from the seed, hence 'remote'. In the adjacent-ligular type (e.g. *Archontophoenix*), the cotyledonary tube elongates very little at germination, forming a 'button' or mass of tissue just outside the seed, from which the radicle and shoot emerge next to the seed, hence 'adjacent' (Tomlinson, 1960, 1990; Corner, 1966; Jordan, 1970; Moore and Uhl, 1973; Brown, 1976; Fong, 1978; Uhl and Dransfield, 1987; Henderson, 2006; Tahir *et al.*, 2007). Henderson (2006) has pointed out that these three germination types are not completely satisfactory because of the great variation in length attained by the petiole in developed seedlings. Some modifications of these three basic germination types have been described by Tomlinson (1960, 1990) and Pinheiro (2001).

The germination type is related to the internal structure of the embryo. In remote-tubular germination, the plumular-radicular axis is straight with respect to the cotyledon axis, the embryo is straight, the cotyledon elongates and the radicle is persistent. The plumular-radicular axis is oblique with respect to the cotyledon axis in the remote-ligular type, the embryo is straight, the cotyledon elongates and the radicle is persistent. In the adjacent-ligular type, the plumular-radicular axis is at an obtuse angle with respect to the cotyledon axis, the embryo is curved, the cotyledon does not elongate and the radicle is not persistent; soon after germination, the radicle is replaced by adventitious roots (Tomlinson, 1960; Henderson, 2006).

Thus, it might be expected that the embryo does not fit the standard definition of an underdeveloped embryo, i.e. the embryo must grow inside the seed before the radicle emerges (Baskin and Baskin, 2004). However, Perez *et al.* (2008) showed that the length of the embryo of *P. remota* must increase 1.6-fold to displace the operculum, i.e. for the seed to germinate. Furthermore, radicle emergence, a standard definition for germination, does not occur in palms until after the embryo has definitely grown. Of the seven genera and nine species of palms included in their compilation of the kinds of seed dormancy in seed plants, Nikolaeva *et al.* (1985) listed them as having either morphological dormancy (6), a combination of morphological dormancy and chemical dormancy (A₁-6), a combination of morphological dormancy and mechanical dormancy (A₂-6) or a combination of morphological dormancy, mechanical dormancy and non-deep physiological dormancy (A₂-6-B₁). Nikolaeva (1999) stated that palms '... exhibit the morphological type of dormancy'.

The rejection of palm seeds as having MD (or MPD) by some investigators (e.g. Ribeiro *et al.*, 2012a; Megalhães *et al.*, 2013; Nazario *et al.*, 2013) is based on the fact that seeds will germinate before the hypocotyl-radicle is fully differentiated or that the embryo is fully differentiated histologically. Ribeiro *et al.* (2012a) stated that seeds of *A. aculeata* did not have morphological dormancy '... because the intermediary degree of differentiation [of the meristematic tissues] of the embryo does not restrict its germination...'. Nazario *et al.* (2013) concluded that the seeds of *Bactris gasipaes* do not have morphological dormancy because the embryo is fully differentiated histologically. Corner (1966) thought that palm seeds '... have little power of dormancy...', since tissue development continues in the anatomically immature embryo of mature seeds while germination is arrested. This way of thinking about MD (and MPD) differs from the traditional meaning of that (these) class(es) of seed dormancy (see above).

Thus, in the second edition of *Seeds: ecology, biogeography, and evolution of dormancy and germination* (Baskin and Baskin, in press) we have assigned seeds of all palms included in our survey of kinds of dormancy

in the various vegetation zones on Earth to either MD or MPD. A caveat here is that decisions about assignment to either MD or MPD may be based on results of the responses of isolated seeds rather than on those of seeds within the natural germination unit, i.e. in some cases a drupe with a hard endocarp. In the literature on palm germination, the word 'seed' is often used for seed + endocarp (Corner, 1966; Tomlinson, 1990). Thus, since the drupe endocarp has been shown to inhibit germination of seeds inside them, some of our assignments to MD may be a case of diaspore (fruit) MPD. In other words, the seed freed from the fruit may exhibit MD and the natural germination unit MPD. An example of this is found in *P. remota*, in which the isolated seeds germinated much faster than the drupes (Perez *et al.*, 2008). We agree with Perez (2009) who concluded that most palm diaspores have MPD.

It should be pointed out, however, that isolated seeds of some palm species may exhibit MPD, i.e. those isolated from fruits with a thick stony endocarp (Hussey, 1958; Broschat, 1998; Wood and Pritchard, 2003; Ribeiro *et al.*, 2011; Neves *et al.*, 2013) or from those with a thin membranous endocarp (Carpenter, 1987, 1988). In addition, the operculum has been shown to inhibit germination of isolated palm seeds, and thus its removal promoted germination (Carpenter *et al.*, 1993; Perez *et al.*, 2008; Fior *et al.*, 2011; Ribeiro *et al.*, 2011). In *A. aculeata*, the micropylar endosperm (endosperm cap) part of the operculum (i.e. seed coat portion of operculum removed) was inhibitory to germination (Ribeiro *et al.*, 2011).

Isolated embryos of palms have been reported to be non-dormant (Hussey, 1958; Ribeiro *et al.*, 2011, 2012a). However, since removal of the endocarp, operculum or endocarp and operculum (see references above) and gibberellic acid (GA₃) treatment (Nagao and Sakai, 1979; Nagao *et al.*, 1980; Roberto and Habermann, 2010; Ribeiro *et al.*, 2011; Neves *et al.*, 2013) promote germination, it seems likely that the embryo is not completely non-dormant, i.e. it has low growth potential and thus some degree of physiological dormancy. GA₃ would be expected to promote germination in palm seeds by increasing the growth potential of the embryo and also by weakening the resistance of the (living) micropylar endosperm covering the proximal end of the cotyledonary petiole. Abscisic acid (ABA) also would be expected to play a role in palm diaspore dormancy by inhibiting the growth potential of the embryo and by weakening of the endosperm cap (da Silva *et al.*, 2004; Finch-Savage and Leubner-Metzger, 2006). With regard to germination of oil palm seeds, Hussey (1958) stated that '... rupture of the operculum appears to be dependent upon intercellular breakdown in the abscission layer [of the micropylar endosperm] as well as on growth pressure of the embryo'. Jiménez *et al.* (2008) found that a sharp reduction in concentration of ABA in the

embryo of oil palm was correlated with dormancy break (heat treatment). However, changes in concentration of GAs and other plant growth regulators could not be related to release of dormancy. Much remains to be learned about germination of palm diaspores, both at the whole-seed and biochemical–molecular levels.

Conflict of interest

None.

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