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Alleviation of seed dormancy in *Butia odorata* palm tree using drying and moist-warm stratification

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Summary

Pindo palm (*Butia odorata*) is a native, endangered palm species from southern Brazil. Seed dormancy limits its use and conservation. The aim of this study was to evaluate the interactive effects of incubation temperature, drying and storage of diaspores of *Butia odorata* on seed germination. In a first trial, diaspores were submitted to the 15 possible combinations of five temperature regimes and three drying conditions. In a second trial, the germination from diaspores that underwent the drying treatments and had been stored for 90 days was compared with that from non-stored diaspores. The greatest rate of seedling emergence was obtained when diaspores were pre-heated at 40°C for 21 days in moist sand, and then kept at a constant temperature of 30°C. Continuous temperatures of 30 and 40°C did not favour emergence. Drying periods of 24 and 48 hours reduced the initial moisture content of the diaspores and increased the speed of emergence index from 1.5 to 3.1 and 2.6, respectively. Storage did not affect germination but changed the response to the seed-drying conditions. We suggest that a dry and warm stratification requirement for the alleviation of seed dormancy could be acting in order to ensure germination and seedling establishment of *B. odorata* after the summer.

Introduction

Pindo palm [*Butia odorata* (Barb. Rodr.) Noblick and Lorenzi] belonging to the Arecaceae family, is native to southern Brazil (Mattos, 1977), with significant ornamental and economic value. It produces fruits that can be eaten fresh or processed into liqueur, juice or pulp (Rossato, 2007; Tonietto *et al*., 2009). The increased use of this species has generated a great demand for seedlings, whose production is restricted by seed dormancy, a feature that can delay their germination by more than two years (Broschat, 1998). As a consequence, seedlings are being removed from their natural environment, causing a strong negative pressure on this species, which is today included in the list of endangered species for the State of Rio Grande do Sul. Thus, the development of an adequate seed

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propagation procedure is of paramount importance, both from the economic and ecological perspectives.

Seed dormancy in the Arecaceae family is commonly related to structures that enclose the embryo. In the case of *B. odorata*, the diaspore is characterised by the presence of a stony endocarp, which encloses one to three seeds (Mattos, 1977). It has been suggested that the endocarp, combined with other structures of the fruit, could physically constrain germination. This would require a scarification procedure in order to overcome dormancy, as reported for another palm species, *Hyphaene thebaica* (L.) Mart. (Moussa, 1998). However, according to Pérez (2009), the inability of the embryo in growing and breaking through the surrounding tissues is related to the combined processes of physiological and morphological dormancy. This is why many studies in this family have indicated that procedures other than scarification can reduce seed dormancy. Some have shown that it can be either overcome by removal of the embryo from the seed (Carpenter, 1988a) or by removal of parts of the operculum (Hussey, 1958; Pérez, 2009; Ribeiro *et al.*, 2011). Germination of intact seeds was also shown to be promoted by high temperatures (Hussey, 1958; Rees, 1962; Broschat and Donselman, 1986; Carpenter, 1988a,b; Carpenter and Ostmark, 1993), with moisture content of the seeds significantly interacting with temperature regime (Hussey, 1958; Rees, 1962). However, much of the studies involving the dormancy of palm seeds have not considered or evaluated the interaction of these factors (Broschat and Donselman, 1986; Carpenter, 1988a; Carpenter and Ostmark, 1993; Broschat, 1998).

The few studies on the germination of Pindo palm were conducted on specimens growing outside the natural geographical range of the species (Carpenter, 1988a; Broschat, 1998) and generated contrasting results. Carpenter (1988a) concluded that the seeds of *B. odorata* will accelerate their germination when passing through a warm stratification (40°C) for a period of 21 days. In contrast, Broschat (1998) tested this same procedure, but did not obtain positive results, and suggested that germination would be favoured by endocarp removal, thus relating seed dormancy to a physical restraint. Part of this disagreement could be attributed to the punctual nature of the evaluations plus the lack of control of seed moisture content, seed-source, and storage conditions and duration.

The natural distribution of *B. odorata* ranges from southern Brazil to northeastern Uruguay (Mattos, 1977). In southern Brazil, it grows on the sandy soils and rocky outcrops of the coastal plains, sometimes composing a savanna-like vegetation (Waetcher, 1985). The climate in these environments is subtropical, with no marked seasonal variations of water availability (Moreno, 1960), although events of drought, combined with very high temperatures, are frequently recorded during the summer (Mota *et al.*, 1970). These more extreme conditions could act on diaspores which are buried in the soil, breaking their dormancy, and thus resulting in seed germination after the end of the summer, when conditions for seedling establishment are more favourable. We then hypothesised that seed drying, followed by the permanence of the seeds in a warm and moist soil (warm stratification), may act on releasing the seeds of *B. odorata* from dormancy. To test this hypothesis, we conducted a factorial experiment under laboratory conditions, where diaspores of this species were submitted to different combinations of seed drying, temperature and storage conditions.

Materials and methods

Diaspores were collected in March 2007 from a single individual of *Butia odorata* growing on a savanna-like formation, made up by sparse palm trees, at the west side of the Patos Lagoon (30°54'22"S, 51°30'01"W), Arambaré city, RS, Brazil. Fruit mesocarp (pulp) was removed upon collection, and the remaining endocarps (diaspores) were stored in a humid chamber (relative humidity of ~ 90% and temperature of 8 ± 1°C) for 30 days, until the onset of the experiments. Diaspores were, on average, 11.3 mm wide and 11.4 mm long, and contained 1-3 seeds.

In the first experiment, we tested the effects of seed moisture and temperature on seed germination. A completely randomised design was used, with three drying treatments and five temperature regimes. Diaspores were dried in a forced-air oven at 30°C for 0, 24 or 48 hours (‘control’, ‘dry 24 h’ and ‘dry 48 h’, respectively). They were then sown in sterilised sand at a depth of 0.5 cm in 12 × 12 × 3.5 cm (L × W × D) germination boxes and incubated under light (approximately 10 µmol m^{-2} s^{-1}) for 70 days at one of the following temperature regimes: constant 30°C, constant 40°C, 40°C for seven days followed by 30°C (‘40°C 7d-30°C’), 40°C for 21 days followed by 30°C (‘40°C 21d-30°C’), or alternating 30°C 16 hours / 40°C 8 hours (‘30/40°C’). Twenty seeds were sown per box with four replicates per drying treatment × temperature regime.

In the second experiment, we tested the effects of seed moisture and storage. A batch of seeds from each drying treatment (‘control’, ‘dry 24 h’ and ‘dry 48 h’) was stored for 90 days in germination boxes placed in a growth chamber at 20°C and 70% relative humidity. After storage, diaspores were sown in the same germination boxes previously described, using four boxes (20 diaspores in each one) for each drying treatment. The germination boxes were incubated for 70 days under the ‘40°C 21d-30°C’ temperature regime. Seedlings growing under these conditions were compared with those under the same drying and temperature conditions from the previous experiment, which were not stored.

In both experiments, the moisture content of the diaspores was measured after the drying treatments and after storage, in three replicates of five diaspores each, following ISTA (2008). Briefly, after breaking the endocarps, they were weighed, dried in an oven at 105 ± °C for 24 hours and reweighed. Percentage moisture content is expressed on fresh weight basis.

Shoot emergence was used as the criterion for germination. Because more than one seedling can emerge from a given diaspore, the emergence results were expressed in two different ways: as the percentage of diaspores that resulted in emergence (E%) and as the number of emerged seedlings per endocarp. We also computed the speed of emergence index (SEI) by adding the ratios between the number of emerged seedlings and the number of days elapsed from sowing for all successive evaluations (Maguire, 1962), and the mean emergence time (MET) obtained by multiplying the number of emerged seedlings by the number of days elapsed and then dividing by the final number of emerged seedlings (Labouriau, 1983).

In order to assess the effectiveness of the drying treatments in reducing seed moisture, we compared the three drying conditions of the first experiment (control, ‘dry 24 h, and ‘dry 48 h’) by means of a single-factor ANOVA. In the second experiment, two-way ANOVA was carried out to look at the effects of drying and storage on seed moisture. Finally, in both experiments, seedling parameters were submitted to two-way ANOVA, with drying and temperature as the two factors in the first experiment, and drying and storage as the two factors in the second experiment. In case of significance of the ANOVA ($\alpha = 0.05$), individual means were compared using the LSD mean separation procedure. The square roots of moisture content, E% and number of seedlings per diaspore were arcsine-transformed prior to ANOVA. Statistical analyses were performed using the statistical package Sigmastat, version 2.0 (SPSS Inc.).

Results

The drying treatments imposed in the first experiment resulted in significant differences in seed moisture between the ‘dry 24 h’ (mean 8.6 ± SE 0.2%) and ‘dry 48 h’ (7.5 ± 0.04%) treatments, and between these and the control group (17.0 ± 1.3%).

Seed drying and temperature regimes significantly affected E%, MET and SEI. There was also a significant or marginally significant ($P = 0.08$ in the case of SEI) interaction effect. Seed drying caused significant increases in E% as well as in SEI, but this effect was clearly expressed only on those temperature regimes that caused a significant amount of seedling emergence: ‘40°C 21d-30°C’, in particular, and ‘30/40°C’, to a lesser extent. Within that first treatment, diaspores that were dried for 24 hours had the highest E%, followed by the drying treatment ‘dry 48 h’ and the control (table 1). The ‘dry 24 h’ treatment nearly doubled the number of seedlings per endocarp (from 0.6 to 1.2), as well as SEI (from 1.5 to 3.1), when compared with the control (figure 1).

Incubation at temperatures of 30 or 40°C or with a brief (seven days) pre-heating of 40°C yielded the lowest number of emerged seedlings per diaspore after 70 days, which resulted in lower SEI and E% (figure 1, table 1). In all three drying treatments, the ‘40°C 21d-30°C’ temperature regime resulted in the highest number of seedlings per diaspore and SEI at the end of the evaluation period (figure 1). This temperature regime also resulted in the highest E% for the ‘dry 24 h’ and ‘dry 48 h’ treatments. The two temperature regimes which included pre-heating at 40°C resulted in lower MET (table 1).

Table 1. Effects of seed drying (24 or 48 hours) and temperature regime on percentage of diaspores with emergence (E%) and mean emergence time (MET) of *Butia odorata*. Mean followed by different small letters within columns and different capital letters in the rows are significantly different ($P \leq 0.05$).

Temperature	E%			MET (days)		
	Control	Dry 24 h	Dry 48 h	Control	Dry 24 h	Dry 48 h
30°C	0 Ab	0 Ac	1.3 Ad	-	-	61 a
40°C	0 Ab	0 Ac	0 Ad	-	-	-
40/30°C	27.5 Ba	42.5 Ab	38.8 ABb	60 Aa	59 Aa	58 Ab
40°C 7d-30°C	6.2 Ab	5.0 Ac	17.5 Ac	39 Ac	40 Ab	36 Bd
40°C 21d-30°C	40.0 Ca	70.0 Aa	56.2 Ba	42 Ab	39 Bb	41 Abc

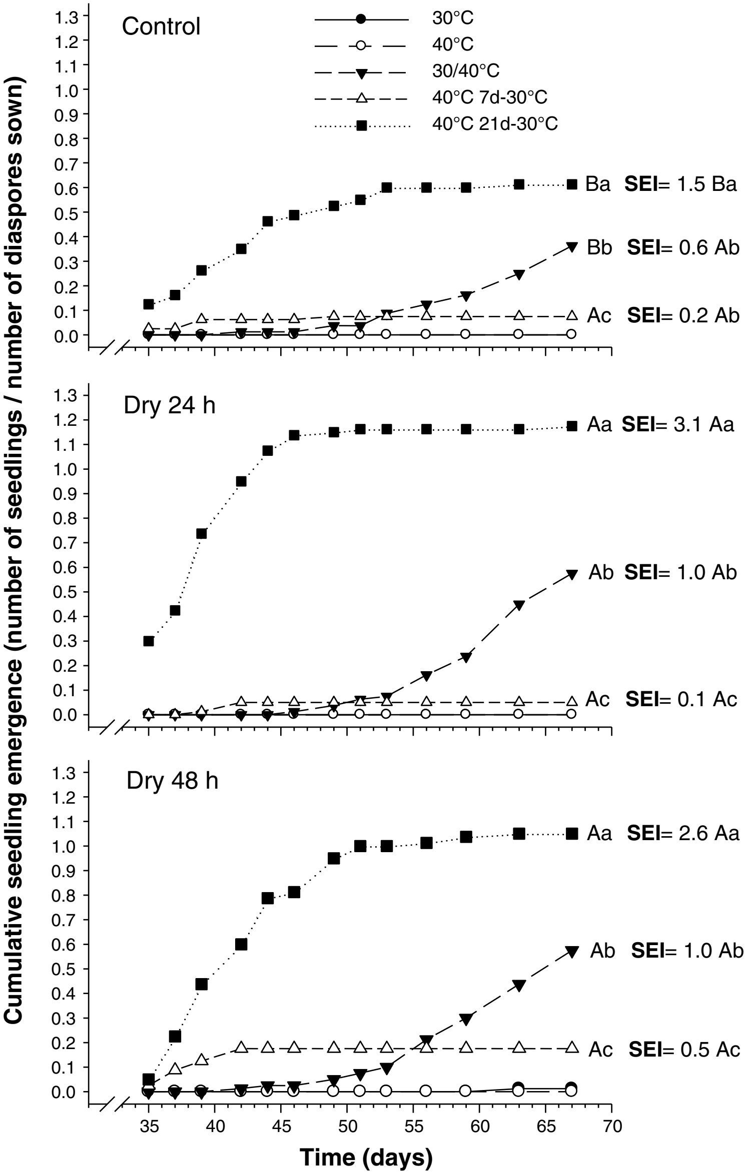

Figure 1. Cumulative seedling emergence from diaspores of *Butia odorata* following different seed drying treatments: control, 'dry 24 h' and 'dry 48 h'. Different curves in each graph represent the five temperature regimes under which emergence took place (see legend in top graph). Speed of emergence index (SEI) is indicated on the right of each curve. Different capital letters indicate significant differences in SEI and in the final number of emerged seedlings between drying treatments for a given temperature regime; different small letters indicate significant differences between temperature regimes for a given drying condition ($P \leq 0.05$). The emergence data of seedlings at a temperature of 30°C (closed circles) are hidden by points corresponding to the 40°C temperature data (open circles).

Seed exposure to alternating temperatures (‘30/40°C’) generated intermediate values of most parameters.

In the second experiment, storage and seed drying affected the moisture content of the diaspores. The interaction between these two factors was also significant and resulted in seed drying treatments only affecting seed moisture content of the diaspores when these were not stored. In response to storage, diaspores which had been submitted to the ‘dry 24 h’ and ‘dry 48 h’ treatments exhibited a slight increase in seed moisture, while the controls had their moisture content decreased. As a result, they all converged to a moisture content of ~10% after the 90-day storage period (10.0 ± 0.01%, 9.8 ± 0.06% and 9.7 ± 0.15% for the control, ‘dry 24 h’ and ‘dry 48 h’, respectively). There was a significant effect of seed drying but no effect of storage on E%, MET and SEI. For MET and SEI, a significant or marginally significant ($P = 0.09$, in the case of SEI) interaction between these two factors was also present. When diaspores were stored, differences in E% between the two drying treatments were no longer detected. In contrast to the non-storage condition, the effect of seed drying in reducing MET was detected for both the 24- and 48-hour period when diaspores were stored (table 2). Finally, the promoting effect of seed drying on SEI reported under the non-storage condition in the first experiment was restricted to the ‘dry 48 h’ treatment when diaspores were stored (figure 2).

Discussion

Our results have shown that seed germination of intact diaspores of *B. odorata* is favoured by a moist-warming treatment, regardless of whether these diaspores were previously dried or not, and that a prior reduction of their moisture content enhances germination, provided that the moist-warming treatment is also imposed. On the other hand, seed germination responses were not altered by a period of storage of the diaspores.

Carpenter (1988a) also reported an increased rate of seedling emergence of Pindo palm after 3 to 10 weeks pre-heating of intact diaspores at 40°C, followed by a constant temperature of 30°C. However, in contrast to our results, a constant germination temperature of 40°C also favoured germination of seeds. Brochat (1998) repeated and challenged the method of pre-warming proposed by Carpenter (1998), and concluded that the removal of the endocarp, coupled with the permanence of the diaspores in a constant temperature of 40°C, would act as the key factor in overcoming the dormancy of Pindo palm. What those two studies and the present one have in common is the increased germination resulting from seed exposure to a temperature of 40°C. However, our results have shown that such high temperature is beneficial only when used as a short-term, pre-treatment. The efficiency of pre-heating as a seed germination promoter was also reported for the African oil palm (*Elaeis guineensis* Jacq.) in the pioneer studies of Hussey (1958) and Rees (1961, 1962), and, more recently, by Fondon *et al*. (2010).

The 7- and 21-day pre-heating treatments reduced MET compared with the ‘30/40°C’ alternating-temperature treatment. This suggests that seven days of pre-heating is enough to initiate germination in a small fraction of the incubated seeds, keeping the MET similar to the period of 21 days. In the ‘30/40°C’ treatment, dormancy was released more slowly,

Table 2. Effects of seed drying (24 or 48 hours) and dry storage on percentage of diaspores with emergence (E%) and mean emergence time (MET) of *Butia odorata*. Plants were grown under a temperature of 40°C for 21 days, followed by constant temperature of 30°C. Mean followed by different small letters within columns and different capital letters in the rows are significantly different ($P \leq 0.05$).

Storage (days)	E%			MET (days)		
	Control	Dry 24 h	Dry 48 h	Control	Dry 24 h	Dry 48 h
0	40.0 Ba	70.0 Aa	56.2 ABa	42 Aa	39 Ba	41 ABa
90	52.0 Aa	58.3 Aa	67.8 Aa	44 Aa	39 Ba	36 Bb

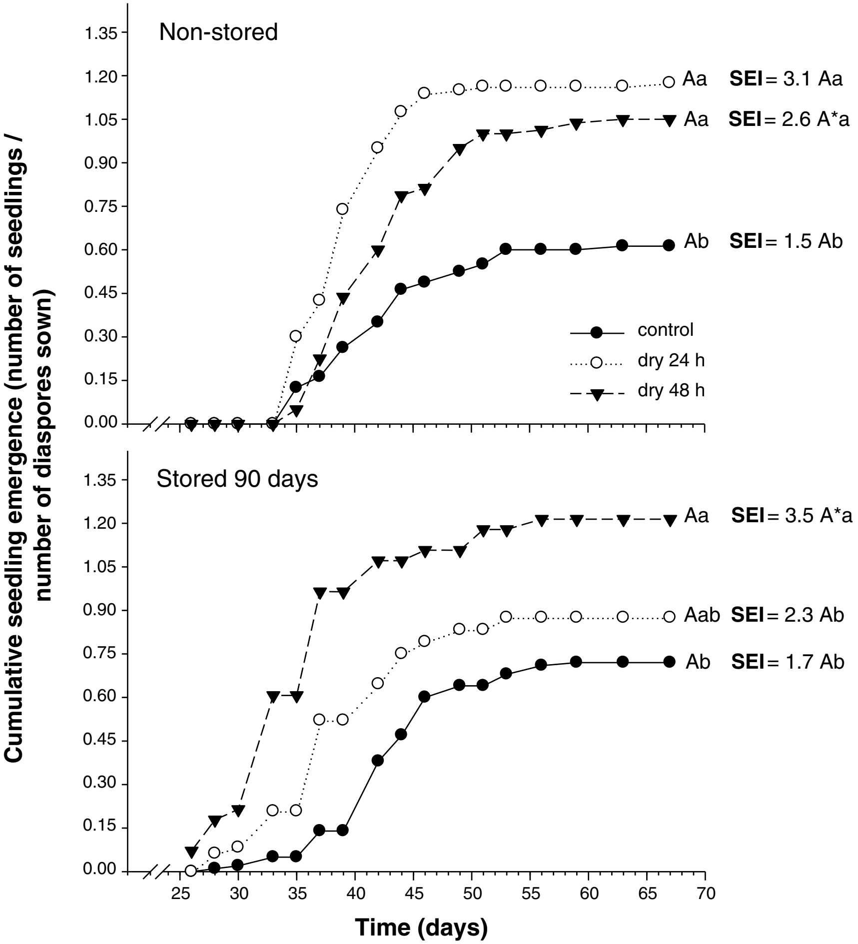

Figure 2. Cumulative seedling emergence from diaspores of *Butia odorata* which were not dry-stored or were dry-stored for 90 days. Different curves in each graph represent the three drying conditions (see legend in top graph). Speed of emergence index (SEI) is indicated on the right of each curve. Different capital letters indicate significant differences in SEI and in the final number of emerged seedlings between non-stored and 90-day storage for a given drying condition; different small letters indicate significant differences between drying treatments for a given storage level ($P \leq 0.05$). * Difference associated to $P \leq 0.1$.

but continuously, thus gradually increasing the proportion of seeds able to germinate. These responses indicate that 40°C has a regulatory role in the process of overcoming dormancy, even when endocarps remain intact.

The reduction of seed moisture prior to warm stratification also contributed to the alleviation of seed dormancy in *B. odorata*. Studies by Rees (1961, 1962) have also shown that the moisture content of the warm-stratified seeds of *E. guineensis* is a key factor in the process of dormancy release. Using procedures of seed soaking and seed drying, Rees (1962) was able to obtain four levels of seed moisture (between 14.2 and 24.2%) prior to the warm stratification period, and the best results in terms of dormancy alleviation were obtained when the diaspores entered this period with a moisture content of ~21%. In the present study, diaspores which entered the stratification period with a moisture content of around 8% gave higher emergence rates than those which initiated this period with 17%. Although these results suggest different responses to seed moisture between these two palm species, they should be compared with caution, because the range of diaspore moisture contents used for *E. guineensis* and *B. odorata* were not the same. Different warm stratification procedures also complicate such comparisons, because diaspores of *B. odorata* were stratified in moist sand, and their moisture content converged to 18 to 20%, regardless of the content they had before. In *E. guineensis*, diaspores were kept in plastic bags, and the moisture content of those diaspores with 21% moisture content decreased to ~18 % during the stratification period.

Seed storage did not result in significant changes of the emergence parameters, but it did interact with the drying treatments: before storage, both drying treatments led to greater SEI but had no impact on MET; after storage the SEI of seeds from those diaspores which were dried for 48 hours became greater and the MET lower than those of the other two treatments. Carpenter (1988a) found that storage of the seeds for 90 days did enhance the effect of pre-heating on the alleviation of dormancy in *B. odorata*, and this enhancement effect was greater when storage temperature was higher. However, in this case, seeds were not previously dried before entering this storage period, such that the storage itself may have acted as the drying treatment and the major factor leading to dormancy alleviation. Martine *et al.* (2009), on the other hand, found that seeds from *E. guineensis* submitted to storage for three and six months gradually reduced the percentage of germination when compared to newly harvested seeds. Whether a period of storage prior to a moist-warm stratification treatment will enhance future seed germination might depend on the moisture content of the diaspores prior to the storage period, and on changes that take place in seed moisture content during storage.

Although seeds of some species are confined within rigid structures, this does not necessarily indicate that dormancy is associated with these structures. Dormancy breaking of the temperate, endocarp-containing *Sambucus* spp. (Hidayat *et al.*, 2000), *Symphoricarpos orbiculatus* Moench. (Hidayat *et al.*, 2001) and *Empetrum hermaphroditum* Hagerup. (Baskin *et al.*, 2002) was also shown to be broken by temperature treatments, such as cold-moist stratification. From an ecological perspective, this behaviour ensures germination and seedling establishment after the winter, thus increasing the chances of plant survival (Pritchard *et al.*, 1993; Tompsett and Pritchard, 1998; Baskin *et al.*, 2002). Likewise, a high-temperature requirement for dormancy release (moist-warm stratification) could be acting in order to ensure germination and seedling establishment of *B. odorata* after the summer, thus minimising the risks of mortality due to the high air temperatures and/or soil water deficits that typically occur in the sandy and rocky soils where the species grows.

The physiological equivalence between cold and warm stratifications was pointed very early by Rees (1961, 1962) and, more recently, by Baskin *et al.* (2002). According to Finch-Savage and Leubner-Metzger (2006), a warm stratification requirement for dormancy release is associated with a decline in the levels of ABA. A dry heat period and the addition of hydrogen cyanamide, a plant growth regulator successfully used to break dormancy in buds of temperate species, were found to reduce the ABA concentration in tissues of the embryo and endosperm of oil palm during dormancy release (Jiménez *et al.*, 2008). Carpenter (1988a) reported the immediate growth of isolated embryos of *B. odorata* in culture medium, and Fior *et al.* (2011) found the removal structures covering the embryo of this same species to speed embryo growth. Similar results were also reported for other palm species (Hussey, 1958; Pérez, 2009; Myint *et al.*, 2010; Ribeiro *et al.*, 2011), indicating that at least part of the dormancy of these palm species, including *B. odorata,* is associated to seed structures other than the embryo. Tissues that cover the embryo of *Pritchardia remote* (Kuntze) Becc. are not waterproof, and the inability of the embryo to grow and break its surroundings was attributed to a mechanical factor related to a physiological process of dormancy (Pérez, 2009). According to Baskin and Baskin (1998, 2004), mechanical strength is a non-deep physiological dormancy, regulated by temperature regimes, and related to metabolically active tissues of the endosperm, which can respond to temperature variations caused by seasonal changes. Seeds of some palms are characterised by the formation of an operculum in the micropylar endosperm (Hussey, 1958). Many studies have shown that enzymatic hydrolysis of these tissues facilitates the expansion of the embryo by mechanical relief (Leubner-Metzger, 2003; da Silva *et al.*, 2007; Taab and Andersson, 2008; Vandelook *et al.*, 2008). The involvement of ABA in preventing the synthesis of these enzymes may be a critical function of this hormone (Nambara *et al.*, 2010), and it is possible that dormancy alleviation of *B. odorata* by moist-warm stratification is the result of reduced levels of ABA and increased activity of enzymes that remove mechanical limitations to seed germination.

This study has shown that dormancy alleviation of *B. odorata* is mediated by a seed drying period, seed rehydration, and exposure to high temperatures. These results open new perspectives for future investigations of the underlying physiological mechanisms and the ecological implications of such responses as well as of the evolutionary relationships within the vast group of palm tree species.

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