



## Seed structure and germination in buriti (*Mauritia flexuosa*), the Swamp palm



Renata Santana Silva<sup>a</sup>, Leonardo Monteiro Ribeiro<sup>a,\*</sup>, Maria Olívia Mercadante-Simões<sup>a</sup>, Yule Roberta Ferreira Nunes<sup>a</sup>, Paulo Sérgio Nascimento Lopes<sup>b</sup>

<sup>a</sup> Departamento de Biologia Geral, Universidade Estadual de Montes Claros, Campus Prof. Darcy Ribeiro, Montes Claros, MG 39401-089, Brazil

<sup>b</sup> Instituto de Ciências Agrárias, Universidade Federal de Minas Gerais, Avenida Universitária, 1.000, Montes Claros, MG 39404-006, Brazil

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### ABSTRACT

Associations of recalcitrance and dormancy are rare, and little information is available concerning the structure of seeds demonstrating this type of behavior or their ecological implications. *Mauritia flexuosa* is a palm tree associated with swampy environments in the Amazon rainforest and areas of Cerrado (neotropical savanna), the latter biome having marked climatic seasonality. We describe the structures and physiological aspects of the seeds and seedlings of this species to examine its adaptations to swampy environments and its germination control mechanisms, as well as the relationship between recalcitrance and dormancy in terms of reproductive success. Morphoanatomy and histochemistry of the seeds and seedlings were evaluated using standard methodologies, and the effects of temperature and operculum removal on germination were investigated. Differentiated tracheal elements in the embryo are associated with recalcitrance, and presence of numerous stomata on the embryo and the abundance of secondary metabolite compounds in the seedling indicate their adaptations to swampy environments. The inability of the embryo to overcome the resistance of the adjacent tissues determines dormancy of the physiological type, thus the removal of the operculum is an efficient method for promoting propagation. Cellular elongation in the cotyledon promotes seedling protrusion. Mobilization of endosperm reserves is achieved by symplastic flux and is associated with overcoming of dormancy by weakening the tissues adjacent to the embryo. The association between recalcitrance, which favors adaptation to swampy environments, and dormancy, which favors dispersal, is crucial for the reproductive success of this species and its broad geographical distribution.

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### Introduction

*Mauritia flexuosa* L.f. (Arecaceae), the “buriti” palm, has wide distribution throughout South America (Bernal et al., 2011; Dransfield et al., 2008; Endress et al., 2013; Horn et al., 2012) and is the most abundant palm tree in Brazil (Lorenzi et al., 2010). This species is restricted to swampy environments with hydromorphic soils having high organic material contents (Endress et al., 2013; Kahn, 1991). It produces many fruits that are important food resources for birds and mammals (Cymerys et al., 2005). *Mauritia flexuosa* is also of social and economic importance to humans, and is widely utilized by indigenous communities (Endress et al., 2013; Gilmore et al., 2013; Horn et al., 2012) and other traditional populations

(Manzi and Coomes, 2009; Martins et al., 2012; Sampaio et al., 2008). This species demonstrates significant potential for commercial use in terms of food resources (Bernal et al., 2011; Martins et al., 2012), and in the production of cosmetics (Koolen et al., 2013; Zanatta et al., 2010), medicines (Koolen et al., 2012) and bio-fuels (Luz Jr et al., 2011). However, commercial plantations and the conservation of natural populations have encountered difficulties due to rapid losses of seed viability and low germinability (Orozco-Segovia et al., 2003; Spera et al., 2001).

In contrast to the ecological and economic importance of Arecaceae, our knowledge of the biology of palms seeds is still very limited (Baskin and Baskin, 2013; Orozco-Segovia et al., 2003). Palm seeds produced in humid environments are usually recalcitrant due to their intolerance of dehydration and low temperatures—which cause the loss of viability during storage (Hong et al., 1997; Orozco-Segovia et al., 2003). Recalcitrance is associated with particular structural and physiological characteristics related to the lack of quiescence (Farnsworth, 2000). There is very little information

\* Corresponding author. Tel.: +55 38 3229 8154; fax: +55 38 3229 8180.

E-mail addresses: [leomrib@hotmail.com](mailto:leomrib@hotmail.com), [leonardo.ribeiro@unimontes.br](mailto:leonardo.ribeiro@unimontes.br) (L.M. Ribeiro).

available concerning these ecophysiological aspects of the Arecaceae as detailed descriptions of their seeds and seedling structures have generally been restricted to orthodox seeds (Panza et al., 2004), and there have been no detailed studies of the germinative processes of recalcitrant seeds.

Diaspores of various palm species demonstrate dormancy, which is an intrinsic limitation of germination under conditions in which non-dormant seeds would otherwise germinate (Baskin and Baskin, 2004; Finch-Savage and Leubner-Metzger, 2006). Dormancy among the Arecaceae is frequently attributed to the structure of their diaspores, which can have a hard endocarp, corneous endosperm or germinative pores obstructed by fibers (Neves et al., 2013; Orozco-Segovia et al., 2003; Ribeiro et al., 2011). On the other hand, morphological and morphophysiological dormancy are widespread in the family, and are related to presence of an underdeveloped embryo (Baskin and Baskin, 1998, 2013; Orozco-Segovia et al., 2003). However, recent studies on Brazilian palms (Magalhães et al., 2012; Neves et al., 2013; Oliveira et al., 2013; Ribeiro et al., 2011, 2012) indicated that the diaspores have non-deep physiological dormancy caused by the difficulties encountered by the embryos in overcoming restrictions imposed by adjacent tissues (Finch-Savage and Leubner-Metzger, 2006). The causes and classification of the pronounced dormancy observed in *M. flexuosa* have not yet been determined (Spera et al., 2001), and no efficient methods of overcoming their dormancy have been described.

*Mauritia flexuosa* is restricted to humid environments and is extremely successful in relation to its reproduction (Endress et al., 2013; Kahn, 1991; Lorenzi et al., 2010). It occurs in swampy areas in both the Amazon region and the Cerrado (neotropical savanna) biome (Dransfield et al., 2008; Lorenzi et al., 2010), the latter having marked climatic seasonality, with a pronounced dry season. This species dominates the arboreal strata in Cerrado environments in sites locally known as “veredas” or palm swamp known for its great ecological importance. Studies focusing on the structure of the diaspores and the seedlings of this species would contribute to our understanding of their peculiar reproductive strategy and the currently little-understood association of dormancy and recalcitrance (Tweddle et al., 2003).

In addition to germination control, seedling development patterns, including structures adapted to environmental conditions and access to seed reserves, are determinants of plant reproductive success (Baskin and Baskin, 1998; Finch-Savage and Leubner-Metzger, 2006). The peculiar anatomy of palm embryos, with a microscopic embryonic axis enveloped by the cotyledonary petiole (DeMason, 1988a; DeMason and Thomson, 1981), and the wide structural diversity among the seedlings, will require extensive studies involving detailed anatomical evaluations to be fully understood (Henderson, 2006). Additionally, access to their endosperm reserves is complex and involves the development of the largest and most specialized haustorium in the plant kingdom (DeMason, 1984; DeMason and Thomson, 1981). Studies focusing on reserve mobilization in palms have been restricted to just a few species (DeMason, 1988a,b; DeMason et al., 1983, 1985; Oliveira et al., 2013) and it is quite possible that there are differences to be found in *M. flexuosa*, as its seeds are not oleaginous (Lorenzi et al., 2010), in contrast to the Arecaceae species studied in detail until now.

The present work therefore sought to characterize the structures of the diaspores and seedlings of *M. flexuosa* and its germinative process, and respond to the following questions: (i) what are the relationships between seed and seedling structure and their adaptations to the natural environment? (ii) what are the functions of the different seed structures in controlling germination? (iii) what are the developmental patterns of the seedlings, and how are seed reserves mobilized? (iv) what are the relationships between recalcitrance and dormancy, and how do they affect the reproductive success of this species?

## Materials and methods

### Collections and preliminary procedures

Fruits were collected from the ground after natural dispersal in a population of *Mauritia flexuosa* located in the Rio Pandeiros Environmental Protection Area in the municipality of Bonito de Minas, Minas Gerais State, Brazil (15°13'19"S; 44°55'21"W). Collections were made in September, October and December/2012, and in January/2013, always just before the initiation of the experiments described here; only fruits with yellow abscission scars were collected (Fig. 1A) to guarantee the use of fresh fruits.

The pulp was manually removed from the fruits, and any seeds with signs of microbial deterioration or insect damage were discarded. The moisture content (MC) of the seeds and the isolated embryos was determined by weighing them when fresh and then again after drying at 105 °C for 24 h, using four replications of 10 seeds each (Brasil, 2009). Seeds to be incubated were maintained in Styrofoam boxes filled with water (changed daily) for one week and subsequently disinfected in a 2% solution of sodium hypochlorite for 15 min, followed by three rinses in running water and treatment with a fungicide solution (Derosal Plus® 50%); after drying in the shade, the seeds were held in plastic sacks (film thickness 500 µm) and stored at 20 °C until used.

### Fruit morphology

Ten fruits were sectioned longitudinally using a machete to examine their morphological characteristics, and photographed using a Samsung DV300F digital camera.

### Evaluation of germination

Six hundred seeds with their opercula removed (using a scalpel) (Neves et al., 2013), and an equal number of intact seeds, were sown into polyethylene containers (17 cm × 12 cm × 6 cm) containing sterilized vermiculite that had been moistened with distilled water to 80% retention capacity. Five replicates of 20 seeds each were incubated in germination chambers at 15, 20, 25, 30, 35 and 40 °C. After 60 days, the temperatures in all of the chambers were altered to 30 °C (the temperature at which the highest proportion of seeds germinate after 60 days) and the seeds were thus maintained for 49 more days. Germination was evaluated weekly, and the protrusion of the cotyledonary petiole was the criterion for germination (Ribeiro et al., 2011, 2012). Germination percentages were calculated at 60 days and also at the end of the experiment; the germination velocity index (GVI) was calculated up to day 60 (Maguire, 1962). Analysis of variance and the Tukey test were used to compare means at a 5% level of probability.

### Seedling morphology

One hundred seeds without opercula were sown as described above. They were observed daily for 30 days and the morphology of the most precocious seedlings was described, following Ribeiro et al. (2012). The material was photographically documented using a Samsung DV300F digital camera.

Biometric evaluations of the seeds and seedlings used 600 seeds (half of them without their opercula) that were incubated at 30 °C, as described above. Before sowing, and after 2, 5, 10, 15, 20 and 30 days of cultivation, 50 seeds from each treatment were removed and separated into germinated or non-germinated classes, and evaluated for petiole protrusion and root and leaf sheath emission. Embryo structures (haustorium and cotyledonary petiole) and seedling structures (haustorium, cotyledonary petiole, roots and leaf sheaths) were excised using a razor blade and subsequently

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