



RESEARCH ARTICLE

Fruiting phenology, seed and seedling morphology of *Bentinckia condapanna* Berry ex Roxb., an altitude specific endemic palm species of the southern Western Ghats

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Abstract

Bentinckia condapanna is an endemic palm of the southern Western Ghats, which holds crucial ecological impact since it is a food source for many endemic frugivorous fauna. Patchy populations confined amongst cliffy niches is a cozy sight concerning consistent demographic loss. Seeds are the sole reproductive propagules of the vulnerable species; nevertheless, few data are available regarding fruiting phenology and seed biology. The present study monitored the fruiting phenology, seed and seedling morphology of *B. condapanna*, which is a pre-requisite for the conservation strategies. The fruit maturation in the palm is a supra-annual process. It exhibited year-round flowering and fruiting; however, mast spadix exposure was found during the dry season and the peak fruit maturation overlapped the period between May to August. The sinuate ridged seed lodges a top-shaped embryo in the cavity beneath the operculum, proximal to the endocarpic stalk-like ridge above the hilum. The moisture content of the mature seed indicates its recalcitrant nature. The seed germination was found to be adjacent and displayed a slow erratic pattern with low germination and a prolonged dormancy period. The cotyledonary petiole emerges from the seed as a button-like structure, which later subtends the primary root and the plumular axis. Eophyll emerges from the plumular axis subsequently after the emission of a single ligule and two cataphylls. The suspected recalcitrance with dormancy nature might be the contributing factor for its low regeneration in the habitat.

Keywords: adjacent germination; *Bentinckia condapanna*; dormancy; fruiting phenology; recalcitrant seed

Introduction

Bentinckia condapanna Berry ex Roxb. (Arecaceae), commonly known as Bentinck's palm, Condapanna and Kanthakamuk, is an altitude-specific endemic palm species which exhibits a highly restricted distribution pattern (1). The genus *Bentinckia*, which displays disjunct geographical distribution, consists of only two species - *B. condapanna* Berry ex Roxb. and *B. nicobarica* (Kurz) Becc. Both being endemic to India, the former is confined to the high altitude (1200-1800 MSL) rocky cliffs along the southern Western Ghats, while the latter is native to the lowland rainforest of the Nicobar archipelago in the Bay of Bengal. The occurrence of Condapanna either in homogenous breaks or interspersed with the evergreen forests along the inaccessible high-altitude rocky cliffs of Kerala and Tamil Nadu (2) provides validation of a historical wider spread in the tail end of the southern Western Ghats. The restricted allocation, niche specificity and limited population of the palm have led to its classification as a vulnerable species on the IUCN Red List since 1998, highlighting the need for conservation and restoration efforts.

Among all the Indian palms, the tall, slender, solitary-stemmed *B. condapanna* (Fig. 1A) occupies the second highest elevation (3) after *Trachycarpus takil* Becc. of the Himalaya mountain slopes of Kumaon. 'Condapanna' is fog resilient, strong sunlight demander and its' niche is closely associated with first or second order streams which maintain the soil moisture regime. Even though IUCN categorised the palm as vulnerable, it has been reported (4) as endangered due to its' much-reduced number in the highly scattered niches. The narrowly endemic palm range is indicative of significant habitat fragmentation, likely driven by critical challenges such as deforestation for tea plantation (5), felling for apical tender shoots, inner core and tender foliage by elephants and humans (3), habitat destruction by the gradual invasion of *Ochlandra* reed brakes (6) and low regeneration in the natural habitat (7). The native Kani tribes consume the edible terminal buds and juvenile foliage (8), harvest the inflorescence for religious ceremonies and use various palm parts for treating various ailments (9) like the use of fruits for the treatment of asthma (10). The pericarp of the fruits is eaten by frugivorous birds like Great Malabar Hornbill, Malabar Grey Hornbill, Malabar Barbet, White-cheeked Barbet

and Grey-fronted Green Pigeon and mammals like Brown Palm Civet, Bonnet Macques, elephant and bats. Although the predation by frugivores reduce the likelihood of fruit maturation and seed set, they may play a crucial role in seed dispersal. Moreover, the palm, in turn, ensures the food supply for the endemic fauna of the habitat. Many attempted to raise the palm outside the natural habitat due to its' elegant feather like foliage and brightly coloured infructescence, but the chance of survival is least (7). This accounts for the relevance of *in situ* conservation and restoration of the palm in its natural habitat.

To conserve and restore the last sentinels of the vulnerable species, a better understanding of the seed biology of *B. condapanna* is crucial, as the seeds serve as the sole reproductive propagules. In the palm, flowering and fruiting cycles, floral components, fruiting stages, germination pattern and morphological structures of seed and seedling are not explored. A better understanding of the elements regarding seed is of prime concern as an initial step towards designing the restoration protocols (11) of the vulnerable species. The present study aims to characterize the fruiting phenology, seed germination and seedling morphology of *B. condapanna* and to respond to the following questions: (i) Identify the type of seed germination. (ii) Is there any relationship between flowering and major seasons of the niche? (iii) What might be the factors affecting regeneration in the habitat? (iv) What are the adaptive features, if any, in the flowering and fruiting cycle, fruit, seed and seedling?

Materials and Methods

Study area and sample collection

B. condapanna samples were collected from the southern Western Ghats region at the Peppara Wildlife Sanctuary (8°40' 46.0"N and 77° 11' 35.9" E, altitude 1334 m) with a moderately hot and humid climate and mean annual rainfall of 2800 mm. The area experiences diurnal temperature shift with an average of 35 °C during the daytime and 16 °C during the night. Twenty different palms were randomly selected collectively from the natural palm population for the sample collection. The flowers and fruits from the spadix of selected development stages such as 3, 5, 9 and 13 months after anthesis (MAA) were collected from the palms for the study.

Phenology of flowering and fruiting

Phenological data of flowering and fruiting of *B. condapanna* and seed development was done during January 2019 to October 2023. Spadix from the selected palms were tagged at its exposure after the abscission of leaf and was tracked up to maturation. Open flowers and fruits of selected development stages (3, 5, 9 and 13 MAA) were collected and analyzed for their phenological changes, especially in the pericarp, endosperm and embryo.

The flowers and fruits of the spadix were morphologically examined and the stereo images were taken with stereomicroscope (Leica EZ4 E; Leica Microsystems, Wetzlar, Germany). Scanning electron microscopic images of the endocarp of mature pyrene were captured with Carl Zeiss

EVO 18 Research, Jena, Germany. Randomly selected three replicates of fifty fruits of 3, 5, 9 and 13 MAA were collected to determine the morphometric parameters. The moisture content of whole fruit of 3 and 5 MAA, as well as whole fruit, pericarp, pyrene and embryo of 9 and 13 MAA, were determined by the low constant temperature oven method (12). Fresh weight of the chopped 5 g sample was weighed in a pre-weighed petri-plate and was then air dried in oven at 103 °C for 24 hr. The dry weight was recorded to determine the moisture content by

Moisture content % (MC%)

$$\frac{\text{Fresh weight} - \text{Dry weight}}{\text{Fresh weight}} \times 100 \quad (\text{Eqn. 1})$$

Seed viability was assessed using the tetrazolium test following the standard protocol (12). Three replicates of randomly selected 25 water imbibed 13 MAA pyrenes were cut longitudinally and incubated overnight in 0.1 % (w/v) 2,3,5-triphenyl tetrazolium chloride solution at room temperature in the dark. After incubation, the seed viability was evaluated under a stereomicroscope (Leica EZ4 E; Leica Microsystems, Wetzlar, Germany) based on red formazan formation. Seeds exhibiting red staining were classified as viable, whereas unstained seeds as non-viable. The viability percentage was calculated by

Viability % =

$$\frac{\text{Number of viable seeds}}{\text{Total number of tested seeds}} \times 100 \quad (\text{Eqn. 2})$$

Seed germination and seedling morphology

The collected fruits were manually depulped and disinfected with 2 % sodium hypochlorite solution for 5 minutes, followed by repeated rinses in sterilized distilled water. Three replicates of fifty pyrenes were rolled in a previously humidified acid free germination paper and wrapped with a plastic film to reduce dehydration. The acid free germination paper was rehydrated regularly. The germination assessment was carried out daily and the observations were recorded. The criterion for germination was the emergence of the cotyledonary petiole (13, 14). Germination percentage was calculated.

To describe the morphology of developing seedlings, evaluation of the germination process was tracked during the germination study. The seedling morphological characterizations were done (15-17).

Statistical analysis

All the investigated parameters were analyzed using analysis of variance (ANOVA) in SPSS software, with significance determined at $p < 0.05$. The means were compared using Duncan's Multiple Range Test (DMRT) and variability in the data was expressed as mean \pm standard error.

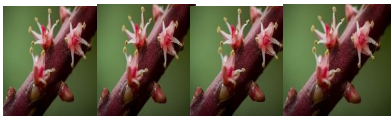
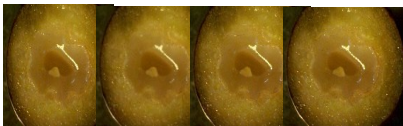

Results

Phenology of flowering and fruiting

Floral phenology and morphology: In *B. condapanna*, flowering occurred throughout the year with mast spadix exposure recorded during mid-January to April (Table 1) and mast anthesis during April to July. The inflorescence is an infrapolar spadix which is borne on the axil of the fallen leaves on the crownshaft (Fig. 1B). The crownshaft is characterised by a dark maroon colouration with a grey powdery coating, transitioning to a dark, brown-tinged maroon while retaining the grey powdery surface prior to leaf abscission. The spadix,

initially covered by an ensheathing spathe, got exposed after the abscission of subtending leaves. It took around 5 weeks to break open the ensheathing spathe and a further 1.5 to 2 months for anthesis. The scarlet-red coloured spadix bear minute unisexual flowers sunken in spirally arranged pits on the branched rachis. Bracts formed a two lipped vertical mouth to each sunken pit of the rachis. Each pit has one or two unisexual flowers. The terminal pits of the rachis have single male flower while the majority of the pits of the rachis bears 2 unisexual flowers - the male flower being arranged above the female flower in the pit. The male flower has six

Table 1. Phenology of peak flowering and fruiting in *B. condapanna*

Events	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Spadix exposure												
Anthesis												
3 MAA												
5 MAA												
9 MAA												
13 MAA												

Flowering and fruiting occur throughout the season in *B. condapanna*, but the peak flowering and fruiting follows the above-mentioned pattern.



Fig. 1. *Bentinckia condapanna* in its natural habitat (A) and the crownshaft bearing brightly coloured spadix (B).

stamens arranged in two whorls of three around a conical, scarlet-red coloured pistillode with 3 stigmas. It has bilobed anther per stamen. The female flower is hypogynous with a whitish yellow ovary. The female flower is tricarpellate but pseudomonomerous gynoecia, i.e., the drupe develops from a single carpel while the other two aborts eventually.

Fruiting phenology and morphology: *B. condapanna* takes approximately 13 months after anthesis to complete physiological maturation of the seeds and 4 distinct morphometric stages (3, 5, 9 and 13 MAA) with significant ($p < 0.05$) difference were obtained during the fruit maturation period (Table 2 and 3). In the mature seed stage, the spadices are 2 feet long and 3 feet wide. In the 3 MAA stage, the yellowish white ovary (Fig. 2B) of the female flower develops into dark scarlet-red coloured subspherical drupe. The fruit has persistent perianth and remnant of trilobed stigma (Fig. 2D). The whole fruits of 3, 5, 9 and 13 MAA have 88.5 %, 84.19 %, 77.11 % and 68.29 % whole fruit moisture content (Table 3). The 3 MAA and 5 MAA fruits were devoid of distinct pyrenes. The pericarp of 3 MAA and 5 MAA has a thin epicarp, fleshy edible mesocarp and the endocarp and seed coat development is visibly demarcated (Fig. 2E and F). The pericarp envelopes the free nuclear-liquid endosperm in the central portion of the 3 MAA fruit (Fig. 2E). Towards the 5 MAA stage, centripetally cellularized gel-like endosperm fills the central cavity (Fig. 2F). The 9 MAA fruit (Fig. 2G) have visually observable differentiated seed but the seed cannot be separated intact from the fruit as the seed coat and endocarp are not rigid. The cellular white coloured endosperm completely fills the pyrene except at the cavity which lodges a single conspicuous embryo. The 13 MAA fruit possesses physiological mature seed (Fig. 2H and J). As the endocarp and seed coat development were completed, it has distinct pyrenes that can be separated from the fruit. The pyrenes of the 9 MAA and 13 MAA fruits were found to have 48.06 % and 30.10 % each moisture content whereas the pericarp has 80.94 % and 74.13 % moisture content (Table 3). The 9 MAA and 13 MAA pyrenes exhibited radical dry matter accumulation and a conspicuous embryo. The moisture content of the embryo reduced from 72.58 % in 9 MAA to 69.72 % in 13 MAA stage (Table 3). All the 13 MAA pyrenes in three replicates during the tetrazolium test developed red coloured formazan in the embryonic region as well as in the endospermic region (Fig. 2L), yielding hundred percentage viability. From the 9 MAA to 13 MAA stage, the deep scarlet-red coloured epicarp turns to brownish black colour and the fleshy mesocarp becomes more fibrous in nature with the pyrenes get squeezed out of the subspherical fruit with gentle pressure. The prominent fibre strands of the mesocarp run along the groove on the endocarp.

Seed morphology: Depulping the 13 MAA fruit, pyrenes are obtained which have thin-papyraceous rigid endocarp. The hard endocarp is found closely placed with the testa and encloses the entire seed forming the pyrene. When the pyrene is desiccated, the endocarp gets detached from the testa and forms a brittle papyraceous-stony pit enveloping the seed. The brownish black coloured endocarp could then be removed by applying gentle force. The pyrene has an oblong shape and is sinuately ridged (Fig. 2J). In the largely water impermeable endocarp and testa, a prominent groove runs

Table 2. Morphometric parameters of the fruit and pyrene of selected developmental stages of *B. condapanna*

Development Stage	Fruit Length (mm \pm SE)	Fruit Width (mm \pm SE)	Fruit Least Width (mm \pm SE)	Fruit Weight (g \pm SE)	Pyrene Length (mm \pm SE)	Pyrene Width (mm \pm SE)	Pyrene Least Width (mm \pm SE)	Pyrene Weight (g \pm SE)	Embryo Weight (g \pm SE)	Embryo Length (mm \pm SE)	Embryo Width (mm \pm SE)	Embryo Least Width (mm \pm SE)	Embryo Weight (g \pm SE)
3 MAA	12.56 \pm 0.09 ^d	10.75 \pm 0.04 ^d	10.29 \pm 0.03 ^d	0.76 \pm 0.01 ^d	-	-	-	-	-	-	-	-	-
5 MAA	14.18 \pm 0.04 ^c	12.63 \pm 0.04 ^c	12.27 \pm 0.04 ^c	1.24 \pm 0.02 ^c	-	-	-	-	-	-	-	-	-
9 MAA	14.79 \pm 0.05 ^b	14.44 \pm 0.05 ^b	14.05 \pm 0.05 ^b	1.59 \pm 0.05 ^b	9.63 \pm 0.11 ^b	7.55 \pm 0.09 ^b	6.61 \pm 0.06 ^b	0.26 \pm 0.01 ^b	2.21 \pm 0.06 ^b	1.14 \pm 0.01 ^b	1.14 \pm 0.01 ^b	1.14 \pm 0.01 ^b	0.0009 \pm 0.00 ^b
13 MAA	16.38 \pm 0.07 ^a	15.93 \pm 0.07 ^a	15.55 \pm 0.07 ^a	2.52 \pm 0.06 ^a	9.84 \pm 0.06 ^a	8.35 \pm 0.14 ^a	6.80 \pm 0.06 ^a	0.36 \pm 0.00 ^a	2.32 \pm 0.02 ^a	1.22 \pm 0.01 ^a	1.22 \pm 0.01 ^a	1.22 \pm 0.01 ^a	0.0011 \pm 0.00 ^a
Df (n-1) = 3	639.36***	1782.03***	2000.43***	339.91***	7714.53***	3163.74***	8842.38***	2600.95***	1671.26***	8118.30***	6603.83***	6603.83***	1224.00***
F value													

Values are expressed as mean \pm standard error. Mean within a column followed by the same letters are not significantly ($p < 0.05$) different as determined by Duncan's Multiple Range Test. Morphometric parameters of pyrene and embryo were evaluated only when the distinct visible structure is observed in the selected development stages. Width and least width of embryo corresponds to the measurement of the same of the cotyledonary petiolar base of embryo. *MAA - months after anthesis, mm - millimeter, SE - standard error, g - gram, Df - degrees of freedom, n - number of variables and F - frequency.

Table 3. Moisture content of whole fruit, pericarp, pyrene and embryo of the selected development stages of *B. condapanna*

Development stage	Whole fruit (% \pm SE)	Pericarp (% \pm SE)	Pyrene (% \pm SE)	Embryo (% \pm SE)
3 MAA	88.50 \pm 0.37 ^a	-	-	-
5 MAA	84.19 \pm 0.24 ^b	-	-	-
9 MAA	77.11 \pm 0.42 ^c	80.94 \pm 0.77 ^a	48.06 \pm 0.23 ^a	72.58 \pm 0.30 ^a
13 MAA	68.29 \pm 0.16 ^d	74.13 \pm 0.17 ^b	30.10 \pm 0.34 ^b	69.72 \pm 0.43 ^b
Df (n-1) = 3 F value	797.62***	13054.48***	22339.35***	34291.89***

Values are expressed as mean \pm standard error. Mean within a column followed by the same letters are not significantly ($p < 0.05$) different as determined by Duncan's Multiple Range Test. Moisture content of pericarp, pyrene and embryo were evaluated only in 9 MAA and 13 MAA stages when the distinct pyrene and embryo structures are discretely observed in the selected development stages. *MAA - months after anthesis, % - percentage, SE - standard error, Df - degrees of freedom, n - number of variables and F - frequency.

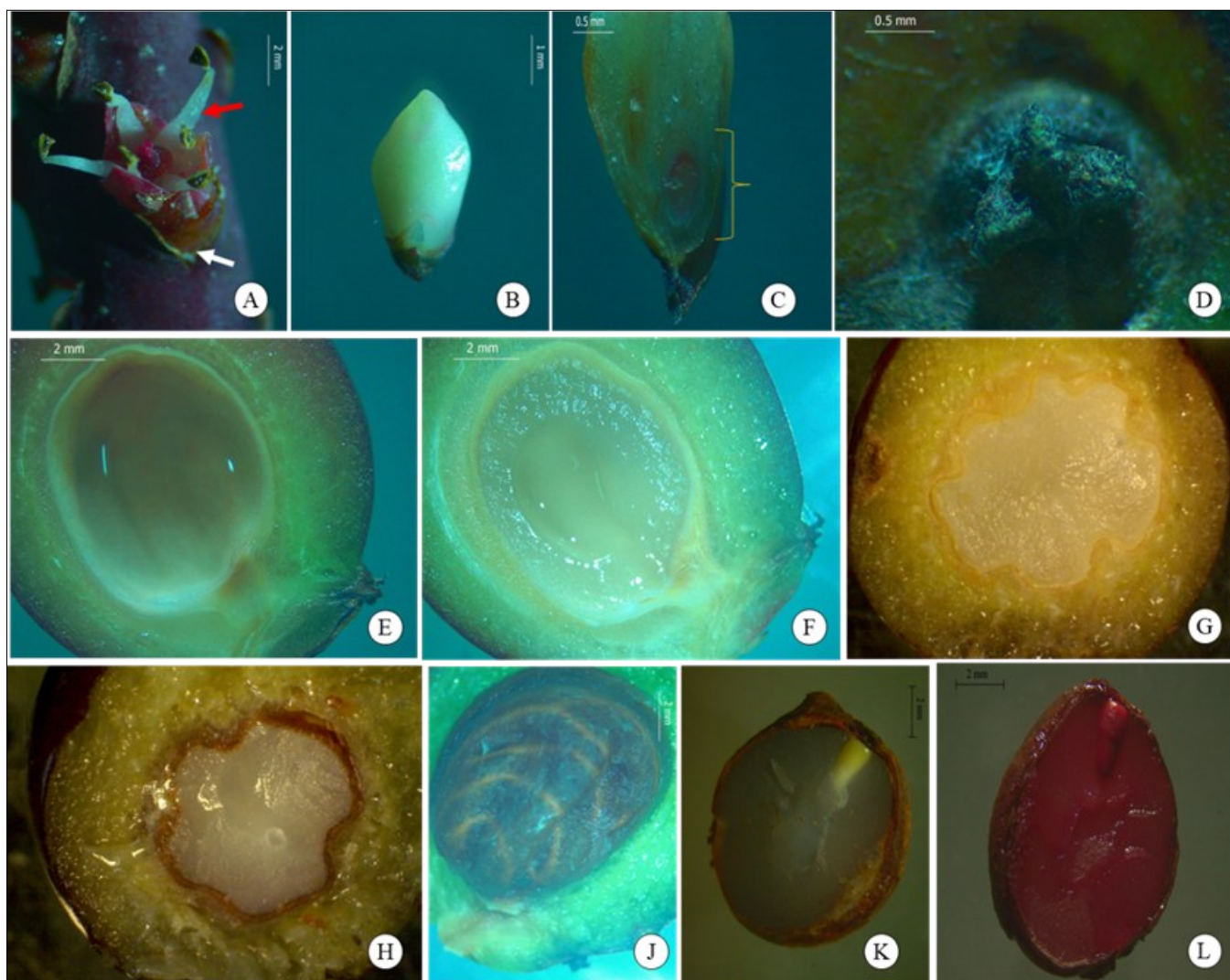


Fig. 2. *B. condapanna* floral and fruit components: (A) The pattern of arrangement of male flower (upper red arrow) above the female flower (lower white arrow) in the spadix groove. (B) The pistil of the female flower, (C) L.S. of the pistil exhibiting the ovule (curly bracket) and (D) the persistent trilobed stigma on the mature fruit. L.S. of selected stages of fruit maturation (E-H). (E) 3 MAA fruit with liquid endosperm and visibly demarcated endocarp and seed coat, (F) fruit before 5 MAA with centripetally cellularising endosperm, (G) 9 MAA fruit with pyrene and (H) 13 MAA fruit with pyrene and fibrous mesocarp. (I) The matured pyrene exhibiting the sinuately ridged endocarp in 13 MAA fruit and (K) L.S. of 13 MAA pyrene with embryo lodged near the operculum in the endosperm. (L) Represents the tetrazolium treated pyrene in which the embryo and the endosperm exhibits formazan formation.

from one side of the endocarpic stalk-like ridge above the hilum to the other side along the dorsiventral margin. These ridges and grooves of the endocarp have rough silica-like texture (Fig. 3A). The scanning electron microscopic image of the endocarp of the pyrene shows microscopic concave grooves on the endocarpic surface (Fig. 3C). Adjacent to the endocarpic stalk-like ridge above the hilum, tip cap can be seen with visible demarcation for the circular opercular abscission zone (Fig. 3B). The testa is dark brown coloured.

The endosperm is non-ruminate and entire with a basal cavity for lodging the yellowish-pale green embryo (Fig. 2K). Embryo is top shaped and is located beneath the operculum with the root pole oriented towards the testa. The embryo consists of proximal white-coloured haustorium and distal pale yellowish green cotyledonary petiole. The cotyledon at its distal base is circular in outline and tapers to a point in the center.

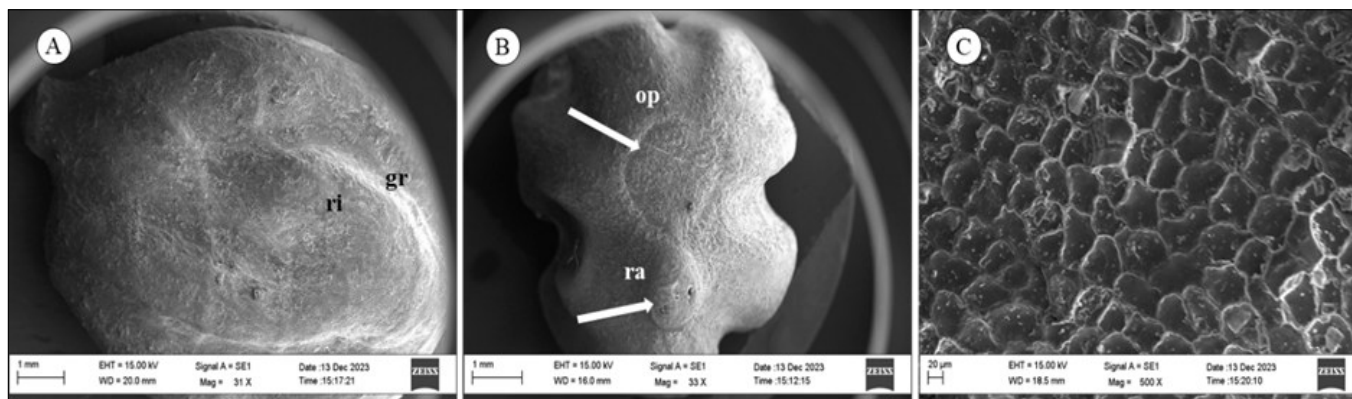


Fig. 3. The scanning electron microscopic image of the endocarp of *B. condapanna* pyrene (A-C). (A) The ridges and groove patterns on the rough textured endocarp. (B) The circular opercular abscission zone and endocarpic stalk-like ridge above the hilum found on the endocarp. (C) The concave-shaped endocarp surface provides a rough silica-like texture to the endocarp. gr: groove on the endocarp; ri: ridge on the endocarp; op: operculum; ra: endocarpic stalk-like ridge above the hilum.

Seed germination and seedling morphology

In *B. condapanna*, the seeds are the only propagating medium and the seed germination is adjacent-ligular (Fig. 4 A-D) and hypogeal type. They exhibit erratic delayed germination pattern with 20 % germination and a dormancy period spanning from 54 days to 8 months. In germinating seeds, during the initiation of germination, i.e., in the imbibition phase, the cotyledonary petiole gradually swells and elongates causing it to fill the entire seminal cavity. Concomitantly, the haustorium begins to expand. The enlargement of the embryo forces out the testa and the endocarp covering the distal portion as a disc-like operculum along the demarcated circular abscission zone. A button-like cotyledonary petiole emerges out through the operculum (Fig. 4A). The button-like structure then subtends radicular and plumular axis (Fig. 4B). The radicular axis yields a primary root with well-established conspicuous root cap. Eophyll emerges from the plumular axis after subtending a ligule and two cataphylls (Fig. 4D). At this point, the haustorium engages in remarkable development by transforming it into a highly porous spongy structure within the endosperm. The adjacent endosperm correspondingly converted its solid texture to spongy porous. The primary roots generated are ephemerals, which are later replaced by shoot-borne adventitious roots (Fig. 4C) which protrude through the cotyledonary sheath at the plumular base.

The ad motive germinating seed remains neither above nor below the symmetric plumular-radicular axis (Fig. 4D). Germination being adjacent, the hyperphyll is inconspicuously negligible. The seedling is ligulate and has two prominent cataphylls. The proximal cataphyll splitting apically towards the seed while the distal one splits apically away from the seed. Eophyll is entire, broad, oblanceolate with acute apex. The venation is parallel and the mid vein is not distinct from the other longitudinal veins. The veins of the lamina converge at the apex. Slightly sinuous plication with proximal and distal marginal induplicate fold.

Discussion

In *B. condapanna*, flowering and fruiting occurs all the year-round with mast spadix exposure spread broadly over mid-January to April and peak fruiting during mid-May to August.

The aseasonal, all the year-round flowering in *B. condapanna* could be well endorsed with Corner's (18) briefing on palm. In palms, a direct association could be drawn between inflorescence bud and leafing (19). At the time of leaf emergence, a single axillary bud inflorescence is initiated at each leaf node. Flowering starts as the preformed bud undergoes enlargement and expansion. In *B. condapanna*, continuous leafing phenology ensures potential aseasonal reproductive activity throughout the year. The phenological events are regarded as a physiological response to a wide range of environmental variables, both abiotic and biotic factors (20). The pattern of mast flowering and fruiting could be correlated to (21) phenological data for tropical plants which claims that abiotic factors tend to mostly regulate the phenological patterns. Solar radiation has been reported (21, 22) as the most significant variable due to its influence on light and temperature, which in turn affect primary production in plants. The increase in the flowering frequency correlates with the period of greatest luminosity in *B. condapanna*. A similar pattern is observed in palm species like *Orbignia phalerata* Mart. and *Socratea exorrhiza* (Mart.) (23). The solar radiation and plant size influence the fruit production, which reinforces the importance of sunlight in the stimulation of the flowering phenophases has been reported (24).

The cue for peak spadix initiation might have begun well before leaf abscission, i.e., occurred during the monsoon or thereafter. Seasonal rainfall can impact the phenological events (21, 25). Even though most of the *B. condapanna* habitats maintain moderate soil moisture content throughout the year and have water streams within its range, rainfall significantly play a major role in sustaining the ground water level which in turn ensure sufficient supply of water for the production of reproductive structures. The swamp palm species, *Mauritia flexuosa*, which flowers throughout the year, exemplifies how mast flowering and seed set are significantly influenced by abiotic factors such as soil moisture content and flooding during the wet season (26). One of the principal determinants of flowering in tropical trees is the rainfall levels (27). This accounts for the fact that flowering represents a delayed response to rainfall. In *B. condapanna*, the maintained soil moisture regime and soil nutrient could account for the continuous flowering in the year but the mast flowering may be the delayed response to the monsoon cues.

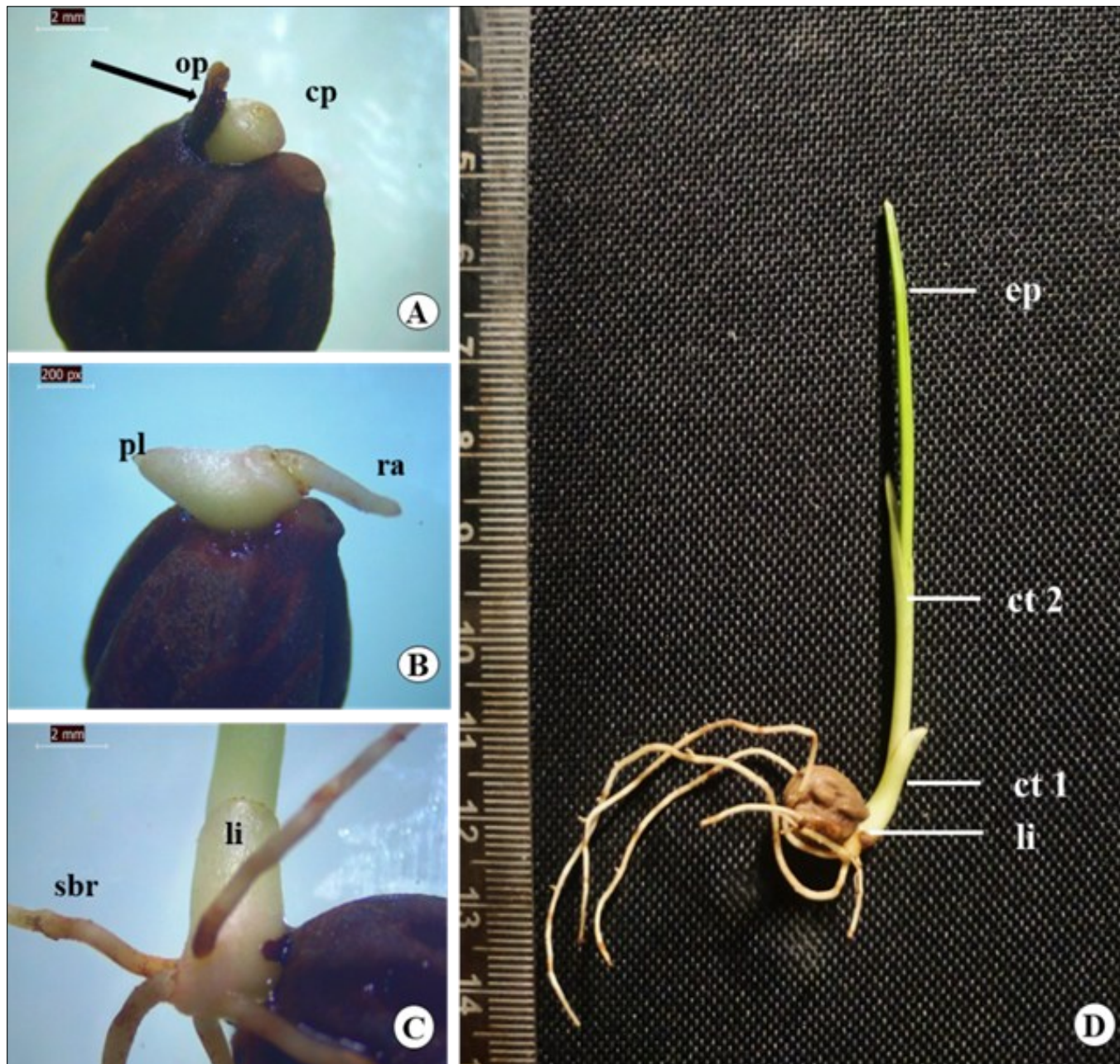


Fig. 4. Seed germination and seedling morphological characteristics. (A) Emergence of the cotyledonary petiole as a button-like structure. (B) Plumular and radicular axis emerging from the cotyledonary petiole. (C) Shoot borne roots emerge through the ligule. (D) Seedling with an entire eophyll subtended through two basal cataphylls. Proximal to the seed, ligular remnants and abundant shoot-borne roots are seen. *cp: cotyledonary petiole; ct: cataphyll; ep: eophyll; li: ligule; op: operculum; pl: plumular axis; ra: radicular axis; sbr: shoot borne roots.

Other tropical palms which exhibit flowering during less rainy season includes *Butia purpurascens* Glassman (28), *Cocos nucifera* L. (29) and *Oenocarpus bataua* Mart. (30). Another reason for the peak flowering in summer is the greater number of pollinators during the more favourable dry season, which could account for the higher pollination success (21, 31). However, this might not be the case with *B. condapanna*. Successful initiation of fruiting could be seen in spadix corresponding to anthesis at any season throughout the year, which indicates that in the palm, the pollination and fertilization success is irrespective of the season.

The peak fruit maturation correlated with the past monsoon season pattern which might have ensured humid moist condition in the former times to retain the viability of the suspected recalcitrant seed with dormancy. However, the recent drastic shift in increased rainfall events during monsoon to August could have adversely affected the seed

viability after its' maturation in the natural habitat. Multiple reproductive episodes within a year lead to the occurrence of more than one phenophase at a given time in a single individual. This has a great ecological significance which is not yet explained. The presence of multiple phenophase at the same time on a palm which takes more than one year to mature ensures enough food supply to the red listed frugivores in the selected habitat like palm civet, Nilgiri Langur, Malabar gaint squirrel and Nilgiri Malabar Hornbill throughout the year. In the high-altitude niche, *B. condapanna* is the only phytospecies which could supply enough fruit source to the frugivorous species throughout the year. This points to the fact that the urgent call for the conservation and restoration of the palm in the southern Western Ghats stretch is a pre-requisite for the conservation of the endemic frugivorous fauna.

The bright coloured and large sized spadix inflorescence, bright coloured-lustrous drupe, the fleshy edible mesocarp until 9 MAA and the deep-coloured leaf sheath, all these factors attract frugivorous birds and mammals which in turn help in seed dispersal. The fruit maturation is a supra-annual process which ensures the visit of frugivore throughout the season. Pollination might be predominantly anemophilous due to the presence of minute flowers, hairy stigma, comparable length of the filaments and the pattern of arrangement of the flowers. The cellularization of the free nuclear endosperm proceed centripetally from the inner integument to the seed center as seen in flowering plants (32). *Condapanna* fruits exhibits persistent perianth like most other palms *Cocos nucifera* L., *Phoenix dactylifera* L., *Acrocomia aculeate* (Jacq.) Sweet and *Attalea microcarpa* Mart. *B. condapanna* exhibits pseudomonomerous pistillate flowers like *Acrocomia aculeate* (Jacq.) Sweet (33), *Dypsis* palms (34) and *Ptychosperma* palms (35), which are a key taxonomic character of Indo-Pacific palms (36). The palm seed possesses basal trilobed stigmatic remains. The position of stigmatic remains tends to be conserved within some Arecaceae clades, hence it is considered a key fruit character in the taxonomy of Arecaceae (37, 38).

During fruit maturation, the whole fruit moisture content declined from 88.50 % (3 MAA) to 68.29 % (13 MAA), whereas in the fruit pulp from 80.94 % (9 MAA) to 74.13 % (13 MAA) and in the seeds from 48.06 % (9 MAA) to 30.10 % (13 MAA). In the embryo, the moisture content reduced from 72.58 % in 9 MAA to 69.72 % in 13 MAA stage. The reduction in moisture content occurs by the radical dry matter accumulation rather than rapid desiccation. The comparatively higher moisture content of the mature *B. condapanna* seeds indicates its' recalcitrant behaviour (39-42). This defended the fact that the seeds in natural habitat would lose their viability soon, if humid-moist conditions is not available throughout the dormancy period. The rough silica-like texture on the endocarp could help in briefly retaining water molecules, thereby assisting in maintaining viability even for a short while. The germination percentage was found to be 20 %, a pattern in most of the palm species (43). The low germination of the 100 % viable seed might be accounted for the hard testa and endocarp, which needs to be evaluated. *B. condapanna* seeds exhibit adjacent-ligular germination pattern as described (15, 44-46) *Cocos nucifera*, *Butia capitata* and *Syagrus romanzoffiana* are other palms which show adjacent germination (47). The adjacent-ligular germination is displayed by palms belonging to phylogenetically younger genera (15, 48).

Conclusion

The present study on *B. condapanna* reveals that the palm seeds are possibly the rare and peculiar 'recalcitrant with dormancy' type. The dormancy in the recalcitrant seed might have led to the viability loss during the germination process, amounting to its low germination. It exhibits the advanced adjacent-ligular germination pattern. The flowering in the palm is observed throughout the year and is a supra-annual process. The mast flowering may be a delayed response to monsoon cues, resulting in peak anthesis during the mid-dry season, while the peak fruit

maturation corresponds to the period between May to August in the successive year. The fruit maturation during the period of study corresponds to the monsoon season of the earlier season pattern, which during the period of study was delayed by around two months. The hard seed coat and endocarp of the pyrene might hinder the emergence of the cotyledonary petiole. The heavy predation during the prolonged fruit maturation affects the fruit and seed set, whereas it can aid in the seed dispersal in the specific niche. The major adaptations observed in the palm includes: (i) the colour of the spadix and the infructescence heavily attracts the seed dispersers in the cliff habitat, (ii) the temporal overlap of peak fruit maturation with the successive year's peak phenophase with free-nuclear endosperm could attract the seed dispersers for the sugary endosperm, (iii) the rough silica-like texture of the endocarp could briefly retain the humidity to initiate the imbibition and (iv) the presence of shoot-borne fibrous root could extend better anchorage in the shallow soil of the rocky cliff habitat. The findings from the study prioritise the future work in *B. condapanna*: to confirm the recalcitrance with the dormancy nature of the seed using biochemical and germination assessment, to determine factors causing dormancy in the seed and to identify the best pre-germination protocol for improving the germination and seedling establishment.

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Authors' contributions

RMD was responsible for the study design, sample collection, experiment execution, data analysis and manuscript preparation. PMR and CA critically revised the article for significant intellectual content, edited the manuscript and approved it. All authors reviewed and approved the final version of the manuscript.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no competing interests.

Ethical issues: None

References

- Nayar MP. Conservation of rare and endangered species of Indian flora: strategies for botanical gardens. *Conservation and Economic Evaluation of Biodiversity*. 1997;1:47-57.
- Abhilash ES, Sathian B. Status of the rare palm *Bentinckia condapanna* Berry in two habitats of Goodrich Reserve Forests; Western Ghats of India. *Asia Pacific Journal of Environment Ecology and Sustainable Development*. 2013;1(1):6-9. <https://doi.org/10.3126/apjeesd.v1i1.9503>
- Kulkarni AR, Mulani RM. Indigenous palms of India. *Current science*. 2004;86(12):1598-603.
- Gnanasekar S, Vidhya C, Sivarathinavel RA, Banu SS. Status and distribution of *Bentinckia condapanna* Berry ex Roxb (Arecaceae), an endemic endangered palm species of the Southern Western Ghats, Tamil Nadu. *Indian Forester*. 2021;147(12):1176-81. <https://doi.org/10.36808/if/2021/v147i12/166683>
- Nair NC. Endemism on the Western Ghats with special reference to *Impatiens* L. In: Karunakaran C, editor. *Proceedings of the Symposium on Rare, Endangered, Endemic Plants of Western Ghats*; 1991. p. 93-102.
- Sarkar MK. Management strategies for endemic and threatened medicinal plants in India: a geoinformatic approach. Dept. of Environment, Govt. of Tamil Nadu; 2012.
- Renuka C, Bhat KV, Basha SC. Palm resources of Kerala and their utilisation. Thrissur: KFRI; 1996.
- Mohanan M, Henry AN. Flora of Thiruvananthapuram Kerala. Coimbatore: Botanical survey of India; 1994.
- Ravikumar K, Ved DK. Illustrated field guide to 100 red listed medicinal plants of conservation concern in southern India. Bangalore: Foundation for Revitalisation of Local Health Traditions; 2000.
- Kamble MY, Benjamin JF, Poulouse VC. Taxonomic significance of seeds and seedling morphology in the threatened Indian endemic palm genus *Bentinckia* (Arecaceae). *Journal of Threatened Taxa*. 2024;16(10):26030-4. <https://doi.org/10.11609/jott.7944.16.10.26030-26034>
- Baskin CC, Baskin JM. Seeds: ecology, biogeography and evolution of dormancy and germination. San Diego: Academic press; 2000.
- ISTA. International Rules for Seed Testing. Switzerland: International Seed Testing Association; 2017.
- Ribeiro LM, Oliveira DM, Garcia QD. Structural evaluations of zygotic embryos and seedlings of the macaw palm (*Acrocomia aculeata*, Arecaceae) during *in vitro* germination. *Trees*. 2012;26:851-63. <https://doi.org/10.1007/s00468-011-0659-2>
- Silva RS, Ribeiro LM, Mercadante-Simões MO, Nunes YR, Lopes PS. Seed structure and germination in buriti (*Mauritia flexuosa*), the Swamp palm. *Flora - Morphology, Distribution, Functional Ecology of Plants*. 2014;209(11):674-85. <https://doi.org/10.1016/j.flora.2014.08.012>
- Henderson FM. Morphology and anatomy of palm seedlings. *The Botanical Review*. 2006;72(4):273-329. [https://doi.org/10.1663/0006-8101\(2006\)72\[273:MAOPS\]2.0.CO;2](https://doi.org/10.1663/0006-8101(2006)72[273:MAOPS]2.0.CO;2)
- Orozco-Segovia A, Batis AI, Rojas-Aréchiga M, Mendoza A. Seed biology of palms: a review. *Palms*. 2003;47(2):79-94.
- Lorenzi H, Noblick L, Kahn F, Ferreira EJ. *Flora Brasileira: Arecaceae (Palmeiras)*. Nova Odessa: Instituto Plantarum; 2010.
- Corner EJ. The natural history of palms. University of California Press; 1966.
- Steven DD, Windsor DM, Putz FE, de Leon B. Vegetative and reproductive phenologies of a palm assemblage in Panama. *Biotropica*. 1987;19(4):342-56.
- Fenner M. The phenology of growth and reproduction in plants. *Perspectives in Plant Ecology, Evolution and Systematics*. 1998;1(1):78-91.
- van Schaik CP, Terborgh JW, Wright SJ. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*. 1993;24(1):353-77.
- Wright SJ, van Schaik CP. Light and the phenology of tropical trees. *The American Naturalist*. 1994;143(1):192-9.
- Newstrom LE, Frankie GW, Baker HG. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica*. 1994;26(2):141-59.
- Cunningham SA. Pollen supply limits fruit initiation by a rain forest understory palm. *Journal of Ecology*. 1996;84(2):185-94.
- Reich PB, Borchert R. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology*. 1984;72(1):61-74. <https://doi.org/10.2307/2260006>
- Rosa RK, Barbosa RI, Koptur S. How do habitat and climate variation affect phenology of the Amazonian palm, *Mauritia flexuosa*? *Journal of Tropical Ecology*. 2013;29(3):255-9.
- McLaren KP, McDonald MA. Seasonal patterns of flowering and fruiting in a dry tropical forest in Jamaica 1. *Biotropica*. 2005;37(4):584-90.
- Guilherme FA, Vasconcelos EI, Coelho CP, Ressel K, Batista NT, Souza LF. Vegetative and reproductive phenology of *Butia purpurascens* Glassman (Arecaceae) under the effects of leaf harvesting. *Brazilian Journal of Biology*. 2015;75(1):77-85.
- Leite IR, Encarnação CR. Fenologia do coqueiro na zona costeira de Pernambuco. *Pesq. agropec. bras*. 2002;37(6):745-52.
- Ruiz RR, Alencar JD. Comportamento fenológico da palmeira pataú (*Oenocarpus bataua*) na reserva florestal Adolpho Ducke, Manaus, Amazonas, Brasil. *Acta Amazônica*. 2004;34(4):553-8. <https://doi.org/10.1590/S0044-59672004000400007>
- Bendix J, Homeier J, Cueva Ortiz E, Emck P, Breckle SW, Richter M, et al. Seasonality of weather and tree phenology in a tropical evergreen mountain rain forest. *International Journal of Biometeorology*. 2006;50:370-84.
- Olsen OA. Endosperm developments. *Plant Cell*. 1998;10:485-8. <https://doi.org/10.1105/tpc.10.4.485>
- Mazzottini-dos-Santos HC, Ribeiro LM, Mercadante-Simões MO, Sant'Anna-Santos BF. Ontogenesis of the pseudomonomerous fruits of *Acrocomia aculeata* (Arecaceae): a new approach to the development of pyrenarium fruits. *Trees*. 2015;29:199-214. <https://doi.org/10.1007/s00468-014-1104-0>
- Rudall PJ, Abranson K, Dransfield J, Baker W. Floral anatomy in *Dypsis* (Arecaceae-Arecaeae): a case of complex synorganization and stamen reduction. *Botanical Journal of the Linnean Society*. 2003;143(2):115-33. <https://doi.org/10.1046/j.1095-8339.2003.00207.x>
- Uhl NW. Developmental studies in *Ptychosperma* (Palmae). II. The staminate and pistillate flowers. *American Journal of Botany*. 1976;63(1):97-109. <https://doi.org/10.1002/j.1537-2197.1976.tb11789.x>
- Norup MV, Dransfield J, Chase MW, Barfod AS, Fernando ES, Baker WJ. Homoplasious character combinations and generic delimitation: a case study from the Indo-Pacific arecoid palms (Arecaceae: Arecaeae). *American Journal of Botany*. 2006;93(7):1065-80. <https://doi.org/10.3732/ajb.93.7.1065>
- Dransfield J, Uhl NW, Asmussen CB, Baker WJ, Harley MM, Lewis CE. *Genera palmarum-the evolution and classification of the palms*. Richmond (UK): Kew Publishing; 2008. <https://doi.org/10.34885/92>
- Matsunaga KK, Smith SY. Fossil palm reading: using fruits to reveal the deep roots of palm diversity. *American Journal of Botany*. 2021;108(3):472-94. <https://doi.org/10.1002/ajb2.1616>

39. Berjak P, Farrant JM, Pammenter NW. The basis of recalcitrant seed behaviour: cell biology of the homoiohydrous seed condition. In: Taylorson RB, editor. Recent advances in the development and germination of seeds. New York: NATO Scientific Affairs Division; 1989. p. 89-108. https://doi.org/10.1007/978-1-4613-0617-7_8
40. Chin HF, Krishnapillay B, Stanwood PC. Seed moisture: recalcitrant vs. orthodox seeds. In: Stanwood PC, McDonald MB, editors. Seed moisture. Vol. 14. Madison: Crop Society of America; 1989. p. 15-22.
41. Pammenter NW, Berjak P. A review of recalcitrant seed physiology in relation to desiccation-tolerance mechanisms. *Seed Science Research*. 1999;9(1):13-37. <https://doi.org/10.1017/S0960258599000033>
42. Barbedo CJ, Centeno DD, Ribeiro RD. Do recalcitrant seeds really exist? *Hoehnea*. 2013;40(4):583-93. <https://doi.org/10.1590/S2236-89062013000400001>
43. Broschat TK. Palm seed propagation. In: International Symposium on Ornamental Palms. Vol. 25. ISHS Acta Horticulturae 360; 1993. p. 141-8. <https://doi.org/10.17660/ActaHortic.1994.360.18>
44. Gatin CL. Recherches anatomiques et chimiques sur la germination des Palmiers: propositions données par la faculté. Doctoral dissertation, Masson et Cie., éditeurs. Ann. Sci. Nat., Bot. 1906;3:191-314.
45. Moore HE. Botany and classification of palms. *The American Horticultural Magazine*. 1960;40:17-26.
46. Tomlinson PB. Essays on the morphology of palms. *Principes*. 1960;5:46-53.
47. Robinson ML. Cultivated palm seed germination. Nevada. Univ Nevada Coop Ext SP-02-09; 2009. <https://extension.unr.edu/publication.aspx?PubID=3243>
48. Moore Jr HE, Uhl NW. Palms and the origin and evolution of monocotyledons. *The Quarterly Review of Biology*. 1973;48(3):414-36. <https://doi.org/10.1086/407702>

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