

Article

Morphological Characterization of Diaspores, Seed Germination and Estimation of Reproductive Phenology of *Cereus fernambucensis* (Cactaceae)

João Henrique Constantino Sales Silva ^{1,*}, Aline das Graças Souza ¹ and Edna Ursulino Alves ^{1,2}¹ Postgraduate Program in Agronomy, Federal University of Paraíba, University Campus II, Areia 58397-000, PB, Brazil; alinedasgracas@yahoo.com.br (A.d.G.S.); ursulinoalves@hotmail.com (E.U.A.)² Department of Plant Science and Environmental Sciences, Center for Agrarian Sciences, Federal University of Paraíba, University Campus II, Areia 58397-000, PB, Brazil

* Correspondence: joaohenriqueconst@gmail.com

Abstract

In this study the objective was to morphologically characterize fruits, seeds and seedlings of *Cereus fernambucensis* Lem., as well as evaluate the seed germination and phenological dynamics of these columnar cacti, native to Brazil, which occur in restinga ecosystems. Biometric and morphological determinations were performed using 100 fruits, describing seed morphology in external and internal aspects and considering five stages of development for the characterization of seedlings. In the study of seed germination, two light conditions (12 h photoperiod and complete darkness) were tested under 25 °C, in a completely randomized design with four replicates of 50 seeds each. In the estimation of reproductive phenology, information was collected from herbarium specimens on the SpeciesLink online platform, and the exsiccatae were analyzed for the notes on their labels to evaluate reproductive aspects. Fruits showed an average mass of 21.11 g, length of 44.76 mm, diameter of 28.77 mm and about 336 seeds per fruit. Seeds behave as positive photoblastic, with a high percentage of germination under controlled conditions (94%). Germination is epigeal and phanerocotylar, with slow growth and, at 30 days after sowing, the seedling measures approximately 2 cm, which makes it possible to visualize the appearance of the epicotyl and the first spines. The species blooms and bears fruit throughout the year, with peaks of flowering and fruiting in January and March, respectively. The various characteristics make *C. fernambucensis* a key species for maintaining the biodiversity of restingas.

Keywords: beach mandacaru; biometrics; coastal forest; exsiccata; herbarium records

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1. Introduction

The morphophysiological characterization of fruits, seeds and seedlings of Cactaceae is essential for understanding the forms of reproduction and dispersal of these plants, in addition to evaluating their quality and potential for the production of seeds and seedlings, as well as developing conservation strategies for these species [1,2]. However, there is a lack of information in the literature on the germination and morphological characterization of diaspores, especially in relation to Brazilian native species [3]. Research in this area is considered recent, since few species have been studied to date [4], although these data are essential for the taxonomy of Cactaceae [5,6].

Cactus propagation can occur sexually or asexually, the former being less frequent due to the scarcity of information, although sexual propagation results in seedlings with

genetic variations and morphological characteristics valued in the ornamental market [3]. Studying seeds and germination is essential to preserve biodiversity, propagate species and differentiate those of the same genus [2]. This type of research also contributes to the rehabilitation of degraded areas, allowing the reintroduction of species into the wild, since the natural reproduction of some cacti occurs exclusively by seeds and often requires an initial phase of propagation in a controlled environment [7]. In addition, the possibility of cultivating plants through sexual propagation could reduce the pressure on natural populations in their habitats [8].

The conservation of many cactus species would benefit from a clear understanding of the biotic and abiotic factors that influence population dynamics [9]. Understanding the factors that affect cactus seed germination is essential in the propagation of wild species for conservation purposes and to understand the ecology of this process [10]. Light is one of the main environmental factors that regulate seed germination, and can both stimulate and inhibit this process, depending on the specific characteristics of each species [11,12].

In recent years, some tropical Cactaceae have been recognized as economically relevant to the horticultural industry, especially due to their tolerance to environmental stresses, which makes them potential candidates for cultivation [13]. An example is *Cereus fernambucensis* Lem., locally known as “mandacaru-da-praia” (beach mandacaru), a columnar cactus endemic to Brazil found in the Atlantic Forest, especially in restingas and rocky outcrops [14]. This species is a promising crop that is still little explored, both as an ornamental and as a fruit-bearing plant [15]. Historical, geomorphological and climatic events have led to unique evolutionary changes in *C. fernambucensis*, allowing its distribution and adaptation to the xeric habitats of the Atlantic Forest over time [16]. This cactus can be found singly or in groups, forming large populations in sandy and exposed soils, playing an important role in the colonization of areas with scarce vegetation in the restinga [17,18].

In the reproductive biology of Cactaceae, another aspect to be considered is reproductive phenophases, since phenology studies investigate the seasonal cycles of biological events in plants, such as flowering and fruiting, which are influenced by environmental factors [19]. These data are essential for predicting how cactus species will respond to climate change, since seasons define reproductive periods linked to variations in temperature and precipitation [20,21]. Herbarium collections are valuable in these studies because they provide information on reproductive cycles and temporal variations, helping to understand the impacts of climate change and to develop strategies for the conservation and management of plant resources [22,23].

Due to the intense extractivism, it is essential to conduct studies on the morphology and propagation of *C. fernambucensis* to support conservation initiatives for this cactus and other species with potential for tropical cultivation. The reproduction of the beach mandacaru cactus can occur both sexually and vegetatively, but seed propagation (sexual) is crucial for ensuring the genetic diversity of the species. Thus, in this study the objective was to morphologically characterize the fruits, seeds and seedlings of *C. fernambucensis*, as well as evaluate the seed germination and phenological dynamics of these columnar cacti, native to Brazil, which occur naturally in restingas.

2. Materials and Methods

2.1. Location of the Fruit Collection Area

The seeds used in the experiment were obtained from ripe fruits harvested from at least 20 individuals of *Cereus fernambucensis* in a natural population in the municipality of Pitimbu, Paraíba, Brazil (7°31'41" S, 34°49'18.3" W) (Figure 1a,b). This sample represents a significant genetic base, reflecting the natural variability of the population studied. The municipality of Pitimbu is within the geoenvironmental unit of the Coastal Tablelands,

on the southern coast of the state of Paraíba, at a distance of 68 km from the capital João Pessoa. The climate of the region is Aw according to the Köppen–Geiger classification, with annual precipitation and average temperature of 1165 mm and 25.9 °C, respectively [24].

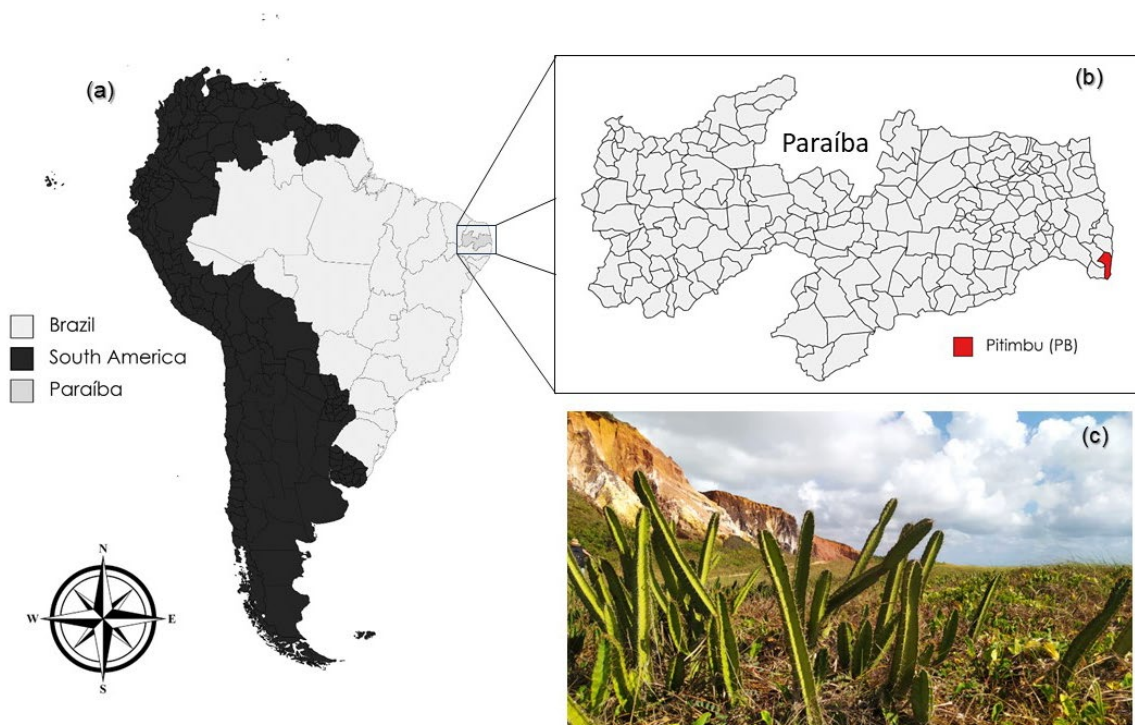


Figure 1. Map of South America highlighting the geopolitical division of Brazil (a) and the State of Paraíba highlighting the municipality of Pitimbu (b). Location of the area used to collect *Cereus fernambucensis* Lem. (Cactaceae) fruits in restinga areas (c).

The vegetation which contains the population of *C. fernambucensis* is typical of restinga areas (Figure 1c) and is found along beaches and coastal plains, since its plants are able to withstand high temperatures, salinity and desiccation and survive with little nutrient availability. The climate of the restinga, characterized by the influence of the sea and humidity, makes it a fragile ecosystem, as its physical conditions being greatly transformed by human activities [25].

2.2. Floristic Identification of the Species

The morphological identification and taxonomic confirmation of the species was performed by consulting databases such as Flora e Funga do Brasil [14] and Plants of the World Online [26]. To prepare the exsiccatae, which served as voucher material for this research, three samples of vegetative and fertile branches were collected and herbariumized using the succulent herbariumization techniques suggested by Fidalgo and Bononi [27]. These samples are currently being processed and will later receive an identification number for registration in the collection. They will be deposited in the botanical-scientific collections of the Jayme Coelho de Moraes Herbarium (EAN) at the Center for Agricultural Sciences (CCA/UFPB).

2.3. Physical and Morphological Characterization of Diaspores

After collection, the fruits were packed in plastic bags and transported to the Seed Analysis Laboratory (UFPB), where biometric determinations were carried out using a digital caliper (precision of 0.01 mm), and morphological determinations were performed using 100 fruits, measuring their length, diameter, mass and number of seeds per fruit.

Length was considered as the distance between the base and the apex, while diameter was measured in the intermediate part of the fruits. In the description of fruit morphology, external aspects were considered, such as type, shape, epicarp color, and number of seeds. Fruit fresh mass was obtained on a precision analytical scale (0.001 g) and, to determine the number of seeds per fruit, the seeds were extracted by opening the fruits and removing the pulp through maceration with the aid of a sieve, followed by washing under running water. Then, the seeds were placed to dry in the shade on the laboratory bench ($T = 25 \pm 2^\circ\text{C}$; $\text{RH} = 70\%$) for four days.

Subsequently, water content and thousand-seed mass were determined following the methodology described in the Standards for Seed Analysis [28]. In the description of seed morphology, external and internal aspects were considered. For internal morphological observations, the seeds were previously immersed in distilled water for 24 h, to achieve the softening and hydration of the tissues. After this period, longitudinal sections were made with a metal blade and then observed under a ZEISS Stereo Discovery V20 optical stereomicroscope. In the characterization of seedlings, the most vigorous ones were selected, and the following parts were described according to the specialized literature: root system, collar, epicotyl and hypocotyl. The germination and seedling growth process was evaluated over a period of 150 days, and five stages of development were characterized based on the morphological differences observed.

2.4. Germination Test

In the germination study, the seeds were placed in Biological Oxygen Demand (B.O.D) germinators at a constant temperature of $25 \pm 1^\circ\text{C}$ and under two light conditions (a 12-h photoperiod and complete darkness) with four replicates of 50 seeds each. The choice of a 12 h photoperiod was based on the intention to simulate conditions similar to those observed in the natural environment of the species' population. The seeds were placed to germinate on paper substrate (on blotter papers), previously sterilized and moistened with distilled water in a volume (mL) equivalent to 2.5 times their dry weight inside acrylic boxes (Gerbox) [28]. The Gerbox boxes with the seeds were kept in continuous darkness, covered with aluminum foil and black polyethylene plastic bag, to avoid any incidence of light on the seeds, which remained under this condition until the end of the test, when only the final percentage of germination was evaluated.

The counts were daily until the 21st day after sowing to obtain the following variables: germination percentage [$G = (N_g \times 100)/N_t$, where N_g is the number of germinated seeds and N_t is the total number of seeds]; mean germination time [$\text{MGT} = \sum n_i \cdot t_i / \sum n_i$, where t_i is the period from the beginning of the experiment to the first observation (days) and n_i is the number of seeds germinated at time i (number corresponding to the umpteenth observation)]; mean germination rate ($\text{MGR} = 1/\text{MGT}$, where MGT is the mean germination time) and synchrony ($Z = \sum C_{ni,2} / N$; where $C_{ni,2} = n_i(n_i - 1)/2$ and $N = \sum n_i(\sum n_i - 1)/2$; where $C_{ni,2}$ is the combination of seeds germinated at time i , two together, and n_i is the number of seeds germinated at time i) [29], considering as germinated the seeds that originated seedlings with a primary root length ≥ 1 mm.

2.5. Estimation of Reproductive Phenology

In the collection of phenological data, a comprehensive survey of herbarium specimens was carried out using the online platform SpeciesLink (<http://splink.cria.org.br/>) (accessed on 10 November 2024), a system that provides free access to collection data of various groups of organisms. The search was carried using the scientific name of the species (*Cereus fernambucensis*), covering the obsolete classification of the two subspecies (*C. fernambucensis* subsp. *fernambucensis* and *C. fernambucensis* subsp. *sericifer*), identifying and examining

as many exsiccatae that contained information about their reproductive phenophases (flowering and fruiting) as possible. The presence of flower buds was considered along with the flowering observations. The selection of herbarium specimens was based on their careful examination and criteria such as (1) identifications by cactus specialists; (2) presence of buds, flowers or fruits on the herbarium labels; (3) examination of additional notes on exsiccatae; (4) collection location; (5) herbarium in which they were deposited; (6) date of collection; and (7) exclusion of all duplicates or exsiccatae containing only vegetative material or those without any information on reproductive aspects.

The search on SpeciesLink filtered 460 exsiccatae of *C. fernambucensis*, distributed in 50 herbaria. Useful collections were available in 35 herbaria (ALCB, ASE, CAP, CESJ, CVRD, EAN, GCPP, HBRA, HRCB, HST, HUEN, HUENF, HURB, HVASF, IPA, JPB, MAC, MBM, MBML, NIT, PEUFR, RBR, RFA, RFFP, RN, SAMES, SP, SPSF, UB, UEC, UFMT, UFP, UPCB, VIC and VIES—acronyms according to the Index Herbariorum). Of the total number of exsiccatae, 21 were recorded for the obsolete subspecies *C. fernambucensis* subsp. *sericifer* (= *Cereus sericifer* (F. Ritter) P. J. Braun) and were excluded. In terms of *C. fernambucensis* (387 records) and *C. fernambucensis* subsp. *fernambucensis* (52 records), we identified 170 exsiccatae that contained legible reproductive data (120 with buds/flowers and 83 with fruits) for the period from 1965 to 2024, totaling a period of 59 years of records (Table S1-Supplementary Materials), while 259 exsiccatae did not contain information on their respective reproductive phenophases. In addition, 10 duplicates were identified, all of which were excluded during filtering.

This methodology is valid and has been frequently used in the literature to estimate the reproductive phenology of tropical plants [30–32], especially those that occur in hostile environments, such as most cacti, as movement and access become a limitation for phenological studies.

2.6. Statistical Analysis

Seed germination and vigor data were calculated using GerminaQuant® 1.0 software [33], while quantitative data on fruit biometrics were analyzed using descriptive statistics. Next, Spearman's correlation (r_s) was performed for all combinations between the variables, and the significance of the r_s values was determined by the t -test ($p \leq 0.05$). The adjectives adopted to describe the magnitude of the correlations were defined according to the methodology of Davis [34]: $r_s = 0.01$ to 0.09 are insignificant correlations, $r_s = 0.10$ to 0.29 are low correlations, $r_s = 0.30$ to 0.49 are moderate correlations, $r_s = 0.50$ to 0.69 are substantial correlations, $r_s = 0.70$ to 0.99 are very high correlations and $r_s = 1.0$ is the perfect correlation.

The reproductive period was evaluated by circular analysis of data from the collection records of exsiccatae with flowering or fruiting. For each phenophase, the mean angle (μ) and the mean vector length (r) were calculated and the Rayleigh test (z and p) was performed. Peak dates were based on the frequency of exsiccatae with flowering or fruiting records in each month, calculated using Oriana 4.0 software [35]. The mean date corresponding to the mean angle (μ) for each phenophase was determined by converting the mean angular directions to the corresponding mean dates, with r values < 0.5 indicating low seasonality. The Rayleigh test was used to determine the significance of the mean angle, verifying whether the data were evenly distributed throughout the year [36]; if the test is significant (rejection of the null hypothesis), the pattern is considered seasonal [37].

3. Results

3.1. Physical and Morphological Characterization

Cereus fernambucensis is a succulent, shrubby and spiny plant, forming clusters of cladodes (branches with ± 5 cm in diameter and 3 to 5 ribs) of dark green, yellowish-green or bluish color when young, which rarely exceed 1 m in height (Figure 2a). The flowers showed a lilac-white perianth and nocturnal anthesis (Figure 2b). The shoots arise from the areolas, from which the spines and flower buds also emerge (Figure 2c). The epicarp of *C. fernambucensis* is greenish in color during its maturation (Figure 2d) and magenta after reaching physiological maturity (Figure 2e). The fruits are berry-type, polyspermic, dehiscent, fleshy, with a thick, smooth, slightly shiny and juicy pericarp. The endocarp is white, fleshy and edible, with hundreds of very small seeds, and it must be pointed out that the dehiscence of some very ripe fruits, exposing the pulp and seeds, has been observed in nature (Figure 2f).

C. fernambucensis seeds are orthodox, dark, campylotropous, reniform and bitegumentary, their testa is rough, and the hilum has a micropylar depression (Figure 2g–h). The embryo is cylindrical and large, white in color, occupying almost all the space of the seed, and is easily observed when the seed is hydrated. Its reserve tissue is cotyledonary, white in color and with firm consistency (Figure 2i); seed germination begins between 4 and 6 days after imbibition and lasts for a week. The seeds were considered to be germinated when the hypocotyl–root axis protrudes from the hilum rupture, the testa breaks in their dorsal portion, and the operculum opens completely, with protrusion of the main root, with yellowish-white color, which curves towards a positive geotropism (Figure 2j).

After 24 h, a dense piliferous zone appears on the main root, forming a dense ring of hairs, accompanied by hypocotyl elongation (Figure 2k). In the post-seminal development of *C. fernambucensis*, cotyledons expand from seed coats through the elongation of the hypocotyl in an epigeal-phanerocotylar germination. Between 10 and 15 days after sowing, the greenish seedling develops, and the testa detaches and exposes the cotyledons (Figure 2l), which are rudimentary and photosynthetic. At 30 days, it is possible to clearly visualize the epicotyl and the appearance of the first spines (Figure 2m), a phase in which the root system is well developed and has numerous absorbent hairs. The seedlings assume a columnar shape and are about 6.5 cm tall, around the 150th day, when the epicotyl becomes very well developed (Figure 2n).

Table 1 shows the data of the descriptive statistics regarding the biometrics of *C. fernambucensis* fruits, with an average length of 44.76 mm, diameter of 28.77 mm, mass of around 21.11 g and about 336 seeds per fruit. The highest relative dispersion was found in the number of seeds per fruit and fruit length, in that order, as denoted by their coefficients of variation. The average thousand-seed mass was 1.58 g, which makes it possible to infer that one gram of *C. fernambucensis* contains approximately 633 seeds.

Table 1. Descriptive analysis of the physical data of fruits and seeds of *Cereus fernambucensis* Lem. (Cactaceae).

Biometric Characteristics	Minimum	Maximum	Mean	Standard Deviation	CV (%)
Length (mm)	23.05	78.20	44.76	11.68	62.38
Diameter (mm)	20.31	44.82	28.77	5.65	26.10
Fruit mass (g)	5.28	76.69	21.11	13.17	19.63
Number of seeds	82	1221	336	233.30	69.48
Thousand-seed mass (g)	1.11	2.16	1.58	0.22	13.92

Legend: coefficient of variation (CV).

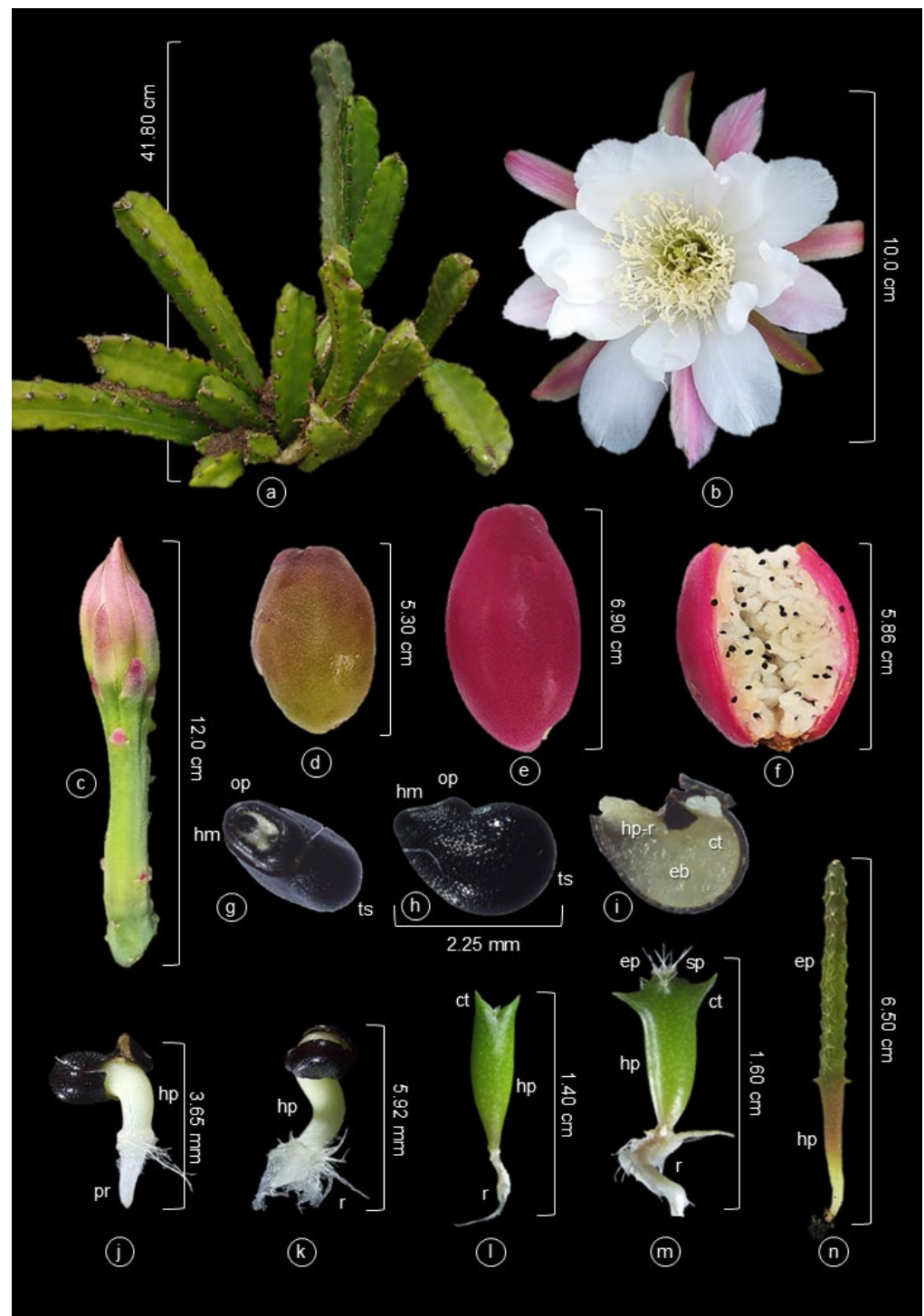


Figure 2. Morphological characterization of the reproductive and vegetative structures of *Cereus fernambucensis* Lem. (Cactaceae). (a) Adult individual; (b) flower in anthesis; (c) flower bud; (d) un-ripe fruit; (e) ripe fruit; (f) internal aspects of the ripe fruit; (g,h) external aspects of the seed; (i) internal aspects of the seed; (j–n) root protrusion and different stages of seedling growth at (j) 5 days, (k) 6 days, (l) 12 days, (m) 30 days and (n) 150 days after sowing. Legend: *eb*—embryo, *hm*—hilum-micropyle region, *op*—operculum, *ts*—testa, *hp-r*—hypocotyl-radicle axis, *ct*—cotyledons, *hp*—hypocotyl, *ep*—epicotyl, *pr*—primordial root, *r*—root, *sp*—spines.

For amplitude (maximum and minimum values) of the biometric characteristics of *C. fernambucensis* fruits, a considerable variation was observed (Table 1). In relation to length and diameter, there was a variation from 23.05 to 78.20 mm and from 20.31 to 44.28 mm for

minimum and maximum values observed, respectively. For fruit mass, the maximum value observed was 76.69 g and the minimum value was 5.28 g, and there were 82 to 1221 seeds per fruit, which points to the presence of phenotypic variation among the individuals of this population. The thousand-seed mass was the trait that had the lowest coefficient of variation (14%), and its minimum and maximum values varied between 1.11 and 2.16 g.

The values obtained through Spearman's correlation (Figure 3) for the physical characteristics of *C. fernambucensis* fruits and seeds evaluated indicated that there was a significant ($p < 0.05$) and positive association between fruit mass (FM), fruit length (FL), fruit diameter (FD), number of seeds per fruit (NS) and thousand-seed mass (TSM). The correlations between fruit mass, length and diameter and the number of seeds per fruit are considered to be of "very high" magnitude, while the correlations observed between thousand-seed mass and the other characteristics are considered "moderate" (Figure 3). These correlations were expected, as longer fruits have a greater number of seeds and are heavier, just as wider fruits are heavier.

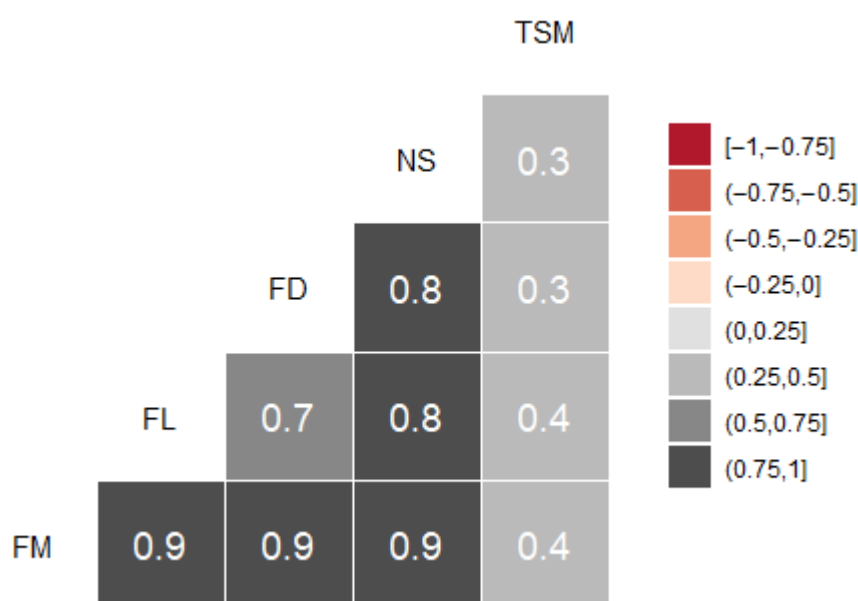


Figure 3. Spearman's correlation between the means of the physical characteristics of the fruits and seeds of *Cereus fernambucensis* Lem. (Cactaceae). Legend: fruit mass (FM), fruit length (FL), fruit diameter (FD), number of seeds per fruit (NS), thousand-seed mass (TSM).

3.2. Seed Germination

C. fernambucensis seeds did not germinate in continuous darkness, proving that the species is positive photoblastic. On the other hand, seed germination under light began 4 days after sowing, and a high percentage of germination, around 94%, was observed at the end of the experiment (Figure 4), indicating that light is a necessary condition for the germination of seeds of this species.

According to the data of mean germination time (MGT), mean germination rate (MGR) and seed germination synchronization index (Z) (Table 2), the values observed were around 7 days for MGT, around 0.14 days⁻¹ for MGR and 0.34 for Z, indicating that under controlled conditions, the germination of the seeds of this species is fast and relatively uniform.

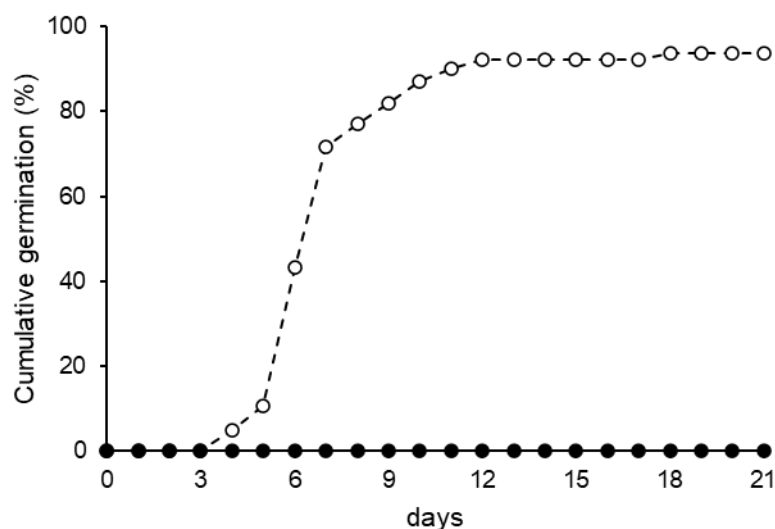


Figure 4. Germination (%) of *Cereus fernambucensis* Lem. (Cactaceae) seeds subjected to different light treatments. (○) White light; (●) continuous darkness.

Table 2. Mean germination time (MGT-days), mean germination rate (MGR-days^{−1}) and synchrony (Z) of germination of *Cereus fernambucensis* Lem. (Cactaceae) seeds subjected to different light treatments. “–” without seed germination.

Light Treatments	MGT (days)	MGR (days ^{−1})	Synchrony (Z)
White light	7.17 ± 1.58	0.14 ± 0.02	0.34 ± 0.05
Continuous darkness	–	–	–

3.3. Reproductive Phenology

Analysis of the data derived from the exsiccatæ showed low seasonality of the flowering and fruiting phases of *Cereus fernambucensis*, with flower and fruit production occurring virtually all year round in the restinga regions of the Brazilian coast, with a notable peak of flowering in January and its highest fruiting in March (Table 3).

Table 3. Results of the circular statistical analysis of the occurrence of seasonality in the reproductive phenology of *Cereus fernambucensis* Lem. (Cactaceae) based on herbarium data. Number of observations (N), mean date, mean vector angle (MVA), mean vector length (MVL), Rayleigh test (z) and (p).

Phenophase	N	Mean Date	MVA (μ)	MVL (r)	Rayleigh (z)	Rayleigh (p)
Flowering	120	January 1st	1.071°	0.265	8.414	2.22 × 10 ^{−4}
Fruiting	83	March 2nd	60.512°	0.164	2.231	0.107

Values of $r < 0.5$ indicate low seasonality.

Circular statistical analysis indicated that the first day of January represented the peak of flower production, while a high proportion of individuals formed fruits on the second day of March (Table 3, Figure 5). The peaks of flowering and fruiting occur between January and March and coincide with the highest average summer temperatures on the Brazilian coast, including the collection area of the evaluated population in Pitimbu, PB (±26 °C).

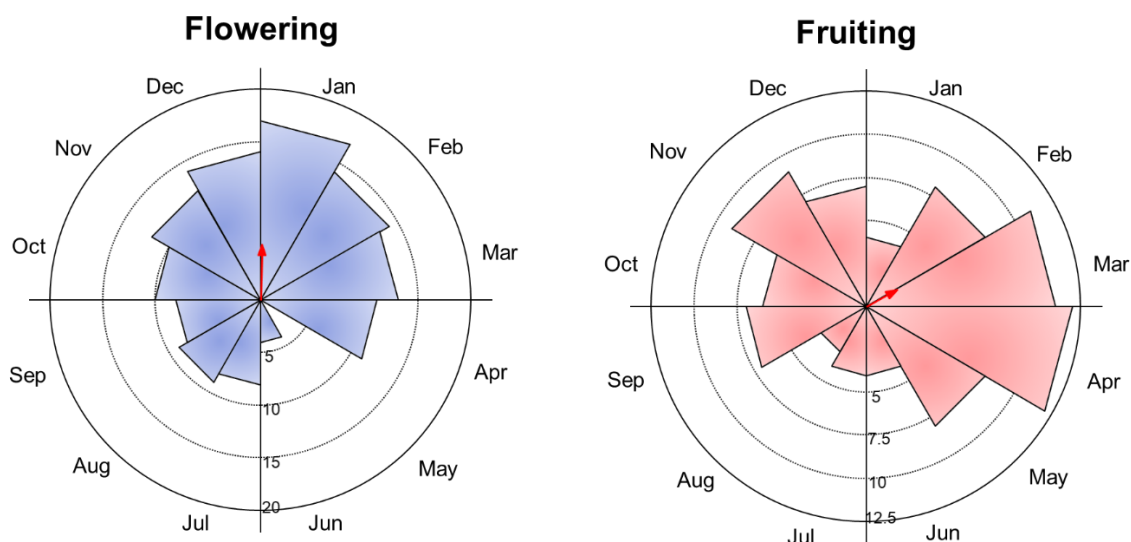


Figure 5. Circular diagram representing the reproductive period (flowering and fruiting) of *Cereus fernambucensis* Lem. (Cactaceae) in restinga based on data from virtual herbaria from 1965 to 2024.

4. Discussion

In this first study with data on morphological characterization and phenology based on herbaria of the species *Cereus fernambucensis*, crucial insights were found about its life cycles, flowering and fruiting. The results of the present research demonstrate that the species produces fruits of varying sizes, indicating genetic variability between individuals in the same population. Seed germination is high, and seedling growth is slow, with flowering and fruiting throughout the year, especially from January to March. These characteristics make the beach mandacaru a relevant species, from both a botanical and an ecological point of view, especially in its natural habitat in the restinga, as discussed below.

C. fernambucensis is a succulent plant that can reach considerable heights, with erect or decumbent branched stems, which are usually cylindrical and with well-defined ribs. Its flowers are white and have nocturnal anthesis, which begins around 11:00 pm and lasts until dawn the next day. Although this species is self-compatible, cross-pollination is more effective in fruit development, suggesting the action of hawk moths at night and bees during the day as pollinators [38]. The flowers of the beach mandacaru also serve as a shelter and food source for different insects, including coleopterans and their larvae, evidencing a broader ecological interaction beyond pollination [39].

C. fernambucensis fruits were characterized as berries, polyspermic and dehiscent, with a succulent pericarp of magenta color and a fleshy endocarp of white color, containing hundreds of seeds. In general, the structure and shape of *C. fernambucensis* fruits are similar to those of *Cereus jamacaru* DC. [40] and *Cereus hildmannianus* K. Schum [5]. These authors reported that *C. jamacaru* and *C. hildmannianus* fruits have characteristics very similar to those observed in *C. fernambucensis*, but with larger dimensions and a higher number of seeds (average of 1439 ± 189.78 in *C. jamacaru*; 787.7 ± 238.3 in *C. hildmannianus*; compared to 336 ± 45.73 in *C. fernambucensis*). Variation in fruit size and weight was observed both within the same individual and between different plants, suggesting high genetic variability in the population.

Due to the high nutritional value and significant antioxidant activity of *C. fernambucensis*, its consumption is encouraged [15]. The consumption of fresh cactus fruits in human food has also been reported for several other species of the Cactaceae family [41]. Although *C. fernambucensis* fruits are not yet commercially exploited, Souza et al. [15] highlighted that the stimulus to commercialization can cause negative environmental impacts, such as

increased movement of people in restingas and modification of their landscape. Therefore, it is essential to consider the sustainable exploitation and commercial cultivation of this endemic species to avoid negative environmental effects.

C. fernambucensis has small seeds (1.50×2.25 mm), which, compared to those of other cactus species, can be considered medium or large in size, according to the classification of Barthlott and Hunt [42]. These dimensions can facilitate the dispersal of large amounts of seeds by birds and lizards, as observed in *C. jamacaru* [43,44]. Several traits of *C. fernambucensis* favor the formation of seed banks in the soil and indicate an orthodox storage behavior for the species, according to the criteria of Thompson et al. [45]. These characteristics include low seed mass, low water content and positive photoblastism. Although no viviparous seeds were found in *C. fernambucensis* fruits, this phenomenon has been reported in other species of the genus [46,47]. The orthodox storage behavior in seeds of the Cactaceae family is well documented, as are positive photoblastism [48] and viviparity [49].

C. fernambucensis seeds were classified as orthodox, dark, campylotropous, reniform and bitegumentary, with the embryo occupying almost all their internal space. In summary, the morphological characteristics of seeds and seedlings, as well as the initial development of *C. fernambucensis*, are quite similar to those observed in *C. jamacaru* [40] and *C. hildmannianus* [5]. The water content of the seeds was 10.3%, a percentage that is within the standard for recently collected seeds of cactus of the genus *Cereus* [40,50]. Water content in seeds is a factor that directly influences their weight and may vary according to the conditions of collection, age and maturation [51].

C. fernambucensis germination did not occur in the total absence of light, indicating that the species is positive photoblastic, like other species of the subfamily Cactoideae [11,52]. Approximately 80% of cactus species produce positive photoblastic seeds, while some are indifferent to light or neutral photoblastic [48]. The high percentage of germination of *C. jamacaru* under different conditions of light intensity and light quality, except in constant darkness, was also reported by Meiado et al. [11]. The results obtained for the characteristics related to germination speed (Table 2) indicate a rapid and synchronized germination of *C. fernambucensis* seeds, similar to those of other species of the genus studied [5,40,53]. Considering that the fruits of *C. fernambucensis* were collected from several individuals, it is likely that the seeds exhibit broad genetic diversity. This variability may have influenced the results observed in the germination tests, increasing the representativeness of the data obtained for the natural population of the species.

Seed germination is a process that begins with imbibition and ends with the appearance of the radicle, which ruptures the seed coat [48]. Rapid germination is a crucial strategy in regions where water availability is often irregular, allowing species to take advantage of sporadic and unpredictable rainfall [54]. In addition, faster germination can offer ecological advantages, increasing the chances of colonization in “low competition” areas that arise after environmental disturbances, such as fires, which increases the chances of seedling survival [55]. Seeds that germinate very quickly and synchronously need small environmental windows for seedlings establishment, in contrast to those with slow and asynchronous germination [56].

According to the results, fruits and flowers are present during almost every month of the year, which is consistent with field observations. The low seasonality observed in the present study in the flowering and fruiting phases of *C. fernambucensis* are similar to results found in other studies within the Cactaceae family in the Caatinga with the genera *Xiquexique* [22] and *Melocactus* [23]. This is an interesting aspect, since the continuous availability of flowers and fruits throughout the year ensures a consistent source of food for pollinators and seed dispersers [57]. Peaks of flowering and fruiting of *C. fernambucensis*

occur between January and March, coinciding with the highest average summer temperatures on the Brazilian coast. In addition, precipitation, solar radiation and photoperiod are essential factors that influence plant phenology and the ecology of tropical organisms, so understanding these relationships is crucial to assessing the impact of climate change on biodiversity [58].

Data collection from herbarium records may have some limitations, so it is essential to approach these data with caution because the quality of samples and information may vary, requiring rigorous evaluations and validation methods to ensure the reliability of results in phenological research [22]. Herbaria represent a valuable asset for higher education institutions in Brazil, usually associated with departments that study biodiversity [23]. Therefore, the intensity of academic research in different centers can influence both the number of specimens and the size of the collections, resulting in concentrations of records in some regions and dispersion in others, which generates a spatial bias. In addition, the temporal distribution of collections, which tends to be concentrated in certain months, suggests a bias related to the reproductive season of the species [59].

Finally, the continuous flowering and fruiting patterns of the species *C. fernambucensis* provide resources for the fauna throughout the year and can help sustain pollinator and seed disperser populations, ensuring the reproductive success of this cactus. However, more studies on pollination and seed dispersal interactions are needed to confirm these conclusions, since the intense overlapping of these events can generate competitive or facilitating effects [57]. In the present study, it is worth noting that the results show that the propagation of *C. fernambucensis* by seeds is a viable and easy method to be employed in its conservation because, according to the IUCN [60], population decline has been observed in its habitat. Therefore, the conservation of coastal restinga forests becomes increasingly important as knowledge about this unique and fragile ecosystem increases, requiring attention to the protection of its biodiversity.

5. Conclusions

Cereus fernambucensis fruits have an average mass of 21.11 g, length of 44.76 mm, diameter of 28.77 mm and about 336 seeds per fruit. Its seeds behave as orthodox, positive photoblastic, with a high percentage of germination under controlled conditions. Germination is epigeal and phanerocotylar, with slow growth of seedlings, which measure less than 2 cm at 30 days after sowing, making it possible to visualize the appearance of the epicotyl and the first spines.

Virtual herbaria are becoming increasingly relevant tools in ecological research, but their effectiveness depends on more thorough documentation during collections.

The species *C. fernambucensis* relies primarily on animals for pollination and seed dispersal, as evidenced by the vibrant color pattern of its nocturnal flowers and fruits. Its reproductive period extends throughout the year, with a greater concentration of activities between January and March.

The conservation of *C. fernambucensis* is essential to ensure the sustainability and preservation of Brazilian coastal forests, as well as regional biodiversity.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/ijpb16030081/s1>, Table S1: Herbarium records with reproductive material of the species *Cereus fernambucensis* (Cactaceae).

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Abbreviations

The following abbreviations are used in this manuscript:

BOD	Biological oxygen demand
CCA	Centro de Ciências Agrárias
CV	Coefficient of variation
FD	Fruit diameter
FL	Fruit length
FM	Fruit mass
G	Germination percentage
IUCN	International Union of Conservation of Nature
MGR	Mean germination rate
MGT	Mean germination time
MVA	Mean vector angle
MVL	Mean vector length
NS	Number of seeds per fruit
RH	Relative humidity
T	Temperature
TSM	Thousand-seed mass
UFPB	Universidade Federal da Paraíba
Z	Synchrony index

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