



Temperature as the main factor affecting the reproductive phenology of the dioecious palm *Mauritiella armata* (Arecaceae)

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Received: April 04, 2021

Accepted: November 9, 2021

ABSTRACT

Our research focused on the reproductive phenology of *Mauritiella armata*, a key *veredas* species in southeastern Brazil, and aspects of its floral and fruit morphology and sexual system. We observed the reproductive phenological patterns of *M. armata* for 36 months, and examined the relationships between phenophases and environmental variables to describe its phenological patterns in relation to environmental filters, as well as its floral and fruit morphologies, sexual system (to evaluate dioecy), and the biometry of its reproductive parts. Flowering was observed in the dry season and at the beginning of the rainy season, with fruiting occurring during the rainy season. The reproductive phenophases responded to environmental seasonality, principally temperature in the period immediately preceding the expression of the phenophase, as well as to environmental variations that had occurred up to six months earlier. The dioecious sexual system of *M. armata* was confirmed, with flowering synchronization between the sexes. The population studied did not exhibit apomixis, having xenogamy as its reproductive system. The staminate inflorescences were larger than the pistillate inflorescences and had greater numbers of flowers, although the pistillate flowers were larger. Wind pollen dispersal was not observed, thereby indicating that this species requires biotic pollination for fruit production.

Keywords: reproductive pattern, floral biology, palm tree, Cerrado, *vereda*, swamp ecosystem.

Introduction

Palm trees (Arecaceae) are widely distributed throughout tropical regions, and have significant ecological (Henderson *et al.* 2000; Eiserhardt *et al.* 2011), economic, and social importance (Henderson *et al.* 1995). Palms provide important

resources for pollinator and frugivore communities (Barfod *et al.* 2011) and are considered key species in several tropical ecosystems (Henderson 2002; Eiserhardt *et al.* 2011). Most palm tree species show preferences for humid climates (Eiserhardt *et al.* 2011), although the Brazilian Cerrado (neotropical savanna), with a seasonal climate (Silva *et al.* 2008), is rich in species (Mendonça *et al.* 2008). The

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Cerrado biome is composed of savanna formations, but also includes vegetation associated with marshy water courses known as *veredas*, with the characteristic occurrence of *Mauritia flexuosa* L.f. (buriti or aguaje) (Ribeiro & Walter 2008). *Veredas* (palm wetlands) are complex systems and, depending on their evolutionary stage, may be associated with hygrophilous forest formations (Nunes et al. 2015).

Another palm tree, *Mauritiella armata* (*buritirana* or *xiriri*, a sister species to *M. flexuosa*) can occur in dense populations in some *veredas* (Nunes et al. 2015). That species likewise has significant ecological and social importance – mainly in relation to its fruits, which are used by the local fauna as well as traditional human populations (Martins et al. 2014), and shows potential for bioprospecting (Royo et al. 2019; Souza et al. 2020a; 2020b, 2021). *Mauritiella armata* is widely distributed in Brazil (Lorenzi et al. 2010) and is considered a key species where it occurs. The genus *Mauritiella* is part of the subtribe Mauritiinae, a small monophyletic group with only three genera: *Lepidocaryum* (with only one species, *L. tenue* (Lorenzi et al. 2010)); *Mauritia* L.f. (with two species, *M. flexuosa* and *M. carana* (Henderson et al. 1995)); and *Mauritiella* (with two species that occur in Brazil, *M. aculeata* and *M. armata* (Lorenzi et al. 2010)). All Mauritiinae species share characteristics such as fruits covered by scales, occurrence mostly in swampy environments (Reis et al. 2017), and dioecy as sexual system (Henderson et al. 1995; Listabarth 1999; Lorenzi et al. 2010; Khorsand Rosa & Koptur 2013). With the exception of *M. armata*, all species of the subtribe Mauritiinae have already been described in the literature as dioecious. Dioecious species have xenogamy as their reproduction system, requiring cross-pollination (Storti 1993), so that synchrony among staminate and pistillate individuals and pollinating agents (biotic or abiotic) are required for fruit production.

Phenological monitoring allows the evaluation of plant population strategies, including the degree of synchronization of their vegetative and reproductive phenophases (Fenner 1998) and flowering synchrony between individuals of both sexes (Listabarth 1999). Climatic variables (including precipitation, temperature, and relative humidity) are the main factors controlling and regulating both the vegetative and reproductive phenologies of most plant species (Azevedo et al. 2014). The peak flowering of *M. flexuosa*, the other key palm species found in *veredas*, occurs during the wet season/dry season interface, while peak fruiting occurs during the rainy season (Khorsand Rosa et al. 2013). The influences of climatic variables on flowering and fruiting phenologies in palms have been reported in various studies (Listabarth 1999; Henderson et al. 2000; Khorsand Rosa et al. 2013; Silva & Scariot 2013; Mendes et al. 2017; Chagas et al. 2019), as well as the floral morphologies and sexual systems of species of the subtribe Mauritiinae (Henderson et al. 1995; Listabarth 1999; Lorenzi et al. 2010; Khorsand Rosa & Koptur 2013), although similar studies for *M. armata* are still missing.

There are large gaps in our knowledge concerning the biology of *M. armata*, which represent serious barriers to its conservation. Detailed information concerning aspects of its reproductive biology and the biometric parameters of its reproductive structures will be fundamental to develop management strategies for the species. The objective of the present study was, therefore, to describe the reproductive phenology of *M. armata* and to correlate these features with environmental variables (including precipitation, temperature, day length, soils and air humidity) in the *veredas* of southern Brazil. We also characterized its sexual and reproductive systems, the biometric variations of its inflorescences and floral morphologies, and the biometric parameters of its fruits and seeds, which can be used to estimate fruit production and quantify its reproductive effectiveness. We expected the phenological pattern of *M. armata* to be similar to that of *M. flexuosa* in response of the same environmental filters, to confirm the dioecious sexual system pattern of the Mauritiinae subtribe, and to obtain additional information concerning the biology of the species to guide conservation strategies.

Materials and methods

Study area and species

We studied four populations of *Mauritia armata* Mart., distant from 4 to 14 km from each other, in *veredas* of the Pandeiros River Environmental Protection Area (EPA). The *veredas* are near Bonito de Minas, in northern Minas Gerais State, Brazil (44°55'00 W and 15°13'29 S), and are part of the same hydrographic basin (the Pandeiros River Basin) (Fig. 1). The *vereda* soils in the region are water-saturated and composed of plant residues in different stages of decomposition (Ávila et al. 2016). The *veredas* examined show the same phytophysiognomic characteristics, with the presence of some human impacts, but all are considered conserved (Ávila et al. 2021). There were no variations in climatic parameters or in the phenological strategies of the individuals evaluated in the *veredas* studied, and we therefore chose to disregard any differences among them.

The regional climate in the study area is Aw according to the Köppen classification system, with well-defined dry winters and rainy summer seasons (Alvares et al. 2014). The rainy season extends from November to January, and the dry season from May to September (Azevedo et al. 2014). The mean annual rainfall is approximately 920 mm and the mean annual temperature is 26.8° C. During the study period, highest monthly temperature was 25.5° C (October/2016) and the lowest was 18.9° C (July/2017). The highest monthly rainfall (249 mm) occurred in February/2018, and there was no rainfall between June and August/2017 (Fig. 2).

Mauritiella armata is widely distributed in South America (Bolivia, Colombia, Ecuador, Guyana, Peru, Suriname, and



Venezuela) (Leitman *et al.* 2015). In Brazil, it is found in the Amazon (tropical rain forest), Cerrado, and Caatinga (scrub dry forest) vegetation domains associated with humid soils, and can form dense, clumped stands (Leitman *et al.* 2015). *Mauritiella armata* is a canopy palm, with multiple stipes, up to 20 m tall, branched interfoliate inflorescences, and produces globular fruits approximately 3 cm long that are covered with reddish-brown scales (Borchsenius *et al.* 1998).

Reproductive phenology

We selected a total of 100 adult *M. armata* individuals, 25 per population (later identified as 59 pistillate and 41 staminate plants), in good condition (without apparent diseases or parasitic infestations) for the phenological studies. The palm clumps were growing at minimum distances of 10 m between each other. Due to the difficulty of defining a single individual due to their agglomerations of stems, only one stipe was marked and monitored. In selecting the stipes, the presence of reproductive structures and their ease visualization for phenology observations were prioritized. Phenological evaluations were done monthly for 36 months (November/2015 to October/2018). The phenophases of flowering (appearance of buds and flowers)

and fruiting (mature and immature fruits) were recorded (Fig. 3).

We used an activity index (frequency of the phenophases in the population, Bencke & Morelato 2002) to evaluate their reproductive phenology; only data from female individuals were used for the fruiting phenophase. To estimate the occurrence and intensity of seasonality of phenophase distributions throughout the year, we used the Rayleigh (z) test to determine their circular distributions (Zar 2010). To that end, the months of the year were converted into angles (0° = January, and successively until 330° = December, in intervals of 30°), and the average angle, the angular standard deviation vector length r , and angle significance were calculated (Zar 2010). Phenophases that showed significant mean angles ($p \leq 0.05$) were converted into mean dates. These analyses were performed using Oriana 4.0 software (Kovach 1994).

To assess the synchrony between the occurrence of flowers, we used the Augspurger index (Augspurger 1983) applied to individuals of each group (pistillate and staminate) and to the general population, without differentiation. The Augspurger index produces a value ranging from 0 to 1, so that the closer to 1, the more synchronous is the event among individuals in the population (Augspurger 1983).

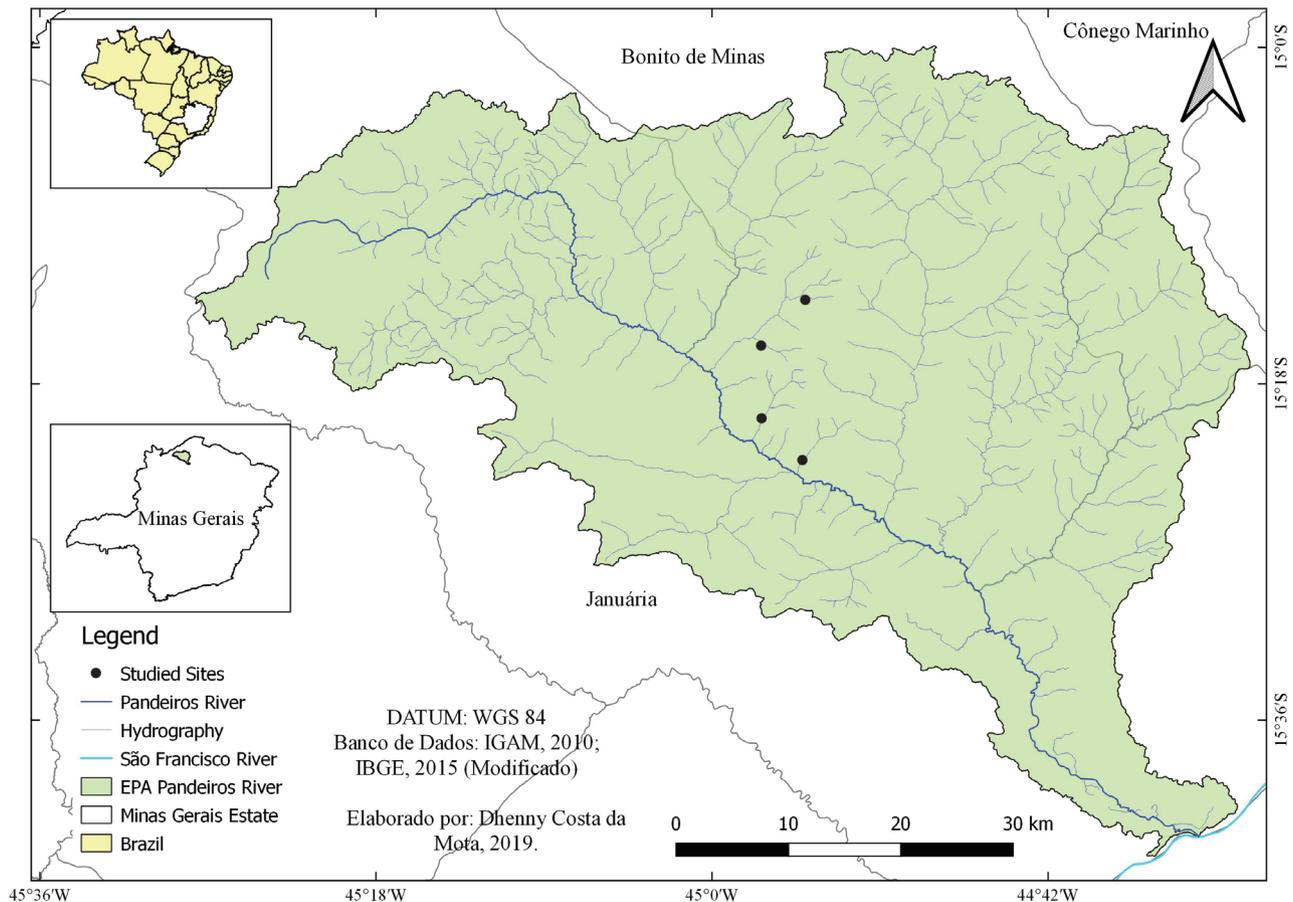


Figure 1. Location of the Pandeiros River Environmental Protection Area in Minas Gerais State (southeastern Brazil), indicating the *veredas* (black dots) where the study individuals were marked.

The index was obtained using the SI2 of the flower package (Wang 2015). In addition, we obtained the value of the Pearson correlation between the activities of the two groups, considering their reproductive activities during the months.

Data concerning environmental variables were obtained from a meteorological station installed in the study area (Davis Vantage Pro2 Plus weather station); day length measurements were obtained from the Solar Top site (<http://www.solartopo.com/duracao-do-dia.htm>). We used cross-correlation time series analysis to study the effects of the environmental variables of temperature (maximum, mean, and minimum), total precipitation (mm), air humidity (%),

and day length on the flowering and fruiting of *M. armata*, correlating six months before the major manifestation (peak) of the phenophases (January to October 2018). We also correlated the monthly values of the activity peaks with the different climatic variables using the PAST program (Hammer et al. 2001). Considering the natural relationship between the environmental variables, we evaluated the existence of collinearities among them using the Pearson correlation (Fig. S1). However, as most of the correlations were not high (lower than 0.6), we decided to maintain all variables to assess all possible correlations among environmental and phenological variables.

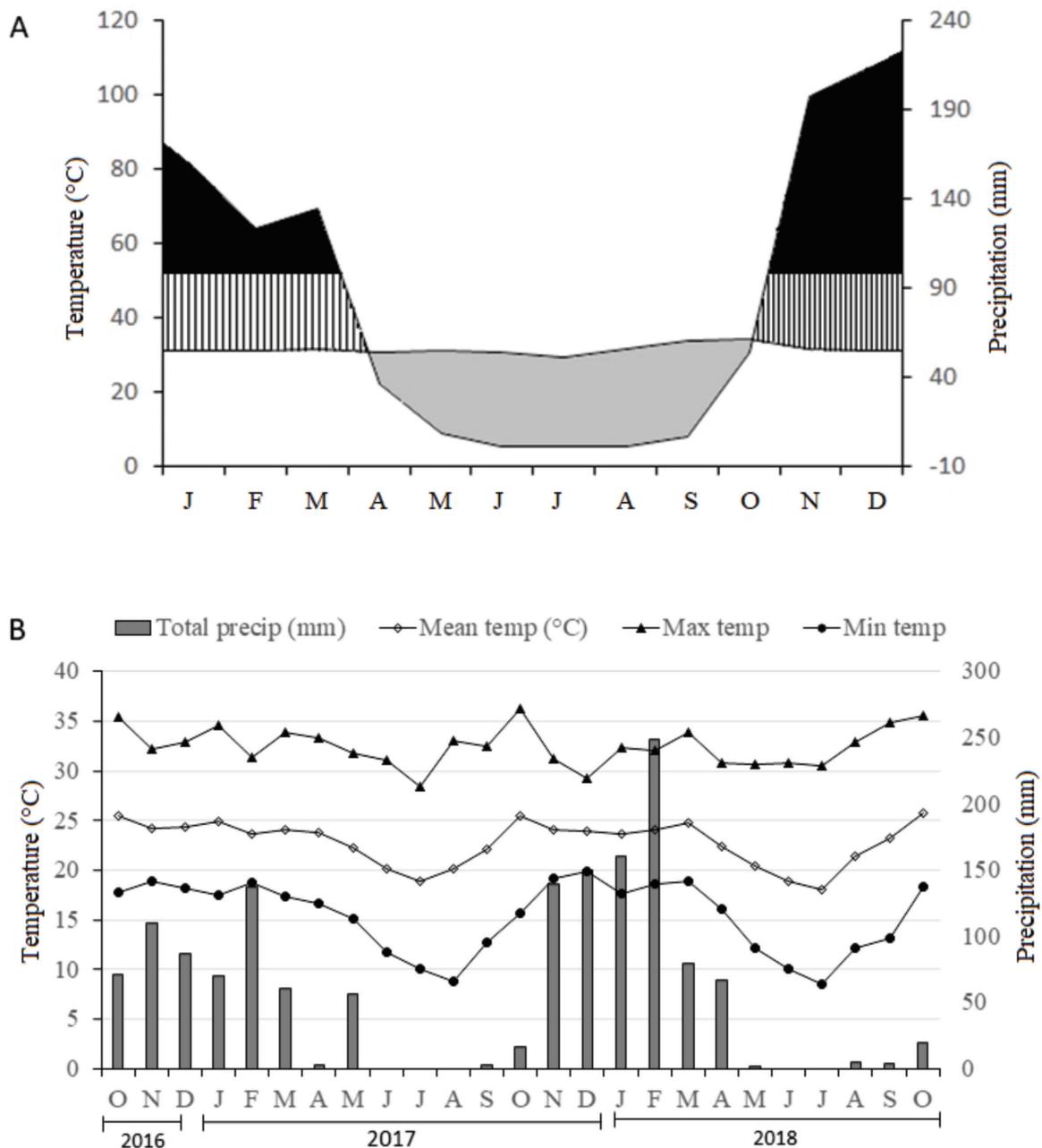


Figure 2. (A) Climate diagram from the Januária Weather Station (Davis Vantage Pro2 Plus) in the study area, for the years 1988-2018; and (B) monthly precipitation data (bars) and monthly mean, minimum, and maximum temperatures (lines) for the period between October/2016 and October/2018.



We measured soil moisture monthly by taking soil samples (20 cm depth) within a 30 cm radius of each marked individual. That characterization was carried out during a period of 14 months (August/2016 to September/2017). The samples were transported to the laboratory in sealed plastic containers, where they were weighed to determine their fresh masses (MF), and subsequently dried at 70° C (until reaching a constant mass), and again weighed to determine their dry masses (DM). Soil moisture contents were calculated using the formula: $Usol (\%) = [(MF-MS) / MF] \times 100$, where: MF = fresh soil mass, and DM = dry soil mass (adapted from Blake 1996).

Mixed Generalized Linear Model (GLMM) procedures were employed using the package lme4 (Bates *et al.* 2015) for the R program v. 4.0.1 (R Development Core Team 2020) to analyze relationships between flowering and fruiting with soil moisture, assuming individuals and areas as random factors to control the temporal dependence of the observations and the existence of sub-replications. When we observed the presence of overdispersion using the Poisson family, negative binomial was used as the residual distribution family. The spatial correlation of residuals was tested using the Moran correlogram. We obtained $p > 0.05$ in all possibilities, with absence of spatial autocorrelation in the models used.

Biometry, reproductive morphology, and sexual system

We collected a total of 37 staminate inflorescences and 31 pistillate inflorescences from different individuals,

measured the total lengths of their inflorescences (including the petiole and main rachis), and counted the numbers of branches. We selected three branches from the base, middle, and apex of each inflorescence for measuring and determining the numbers of rachis on each branch and flowers on each rachilla. The measures of the different parts of the inflorescence indicate whether flower production was uniform on the inflorescence. Inflorescences from the previous season were used for that characterization as they are rigid and maintain their characteristics as well as the scars of flowers and/or fruits. The average number of flowers per inflorescence was also calculated by quantifying the scars of flowers on the inflorescences.

We determined the biometry of the flowers using fresh material, measuring the lengths of 50 staminate flowers and 50 pistillate flowers from 10 different individuals (using a digital caliper). The GLMM was used to verify differences among inflorescence variables and between male and female flowers, followed by LsMeans tests in the R program v. 4.0.1 (R Development Core Team 2020), verifying normality of residuals, the absence of overdispersion, and homoscedasticity. We used adequate residual distributions for each variable, in which continuous variables were worked in the gaussian family and count variables were worked in the Poisson family (numbers of branches and numbers of flowers in the rachilla), or negative binomial family when overdispersion was detected (numbers of rachilla). We made biometric measurements of the fruits and seeds based on 800 fruits collected from 10 different individuals. The



Figure 3. Individual of *Mauritiella armata* showing the stipes. In detail, the development of the staminate inflorescences and flowers (on the left), and the pistillate inflorescences, flowers, infructescences and fruits (on the right).



pulps of the fruits were removed to measure each seed. The lengths, widths, and weights of each fruit/seed were measured to determine their maximum, median, and minimum sizes, thicknesses, and weights.

In order to obtain information concerning floral morphology and the sexual systems of *M. armata*, we collected flowers from 10 different individuals (both pistillate and staminate), and fixed them in 70 % ethanol to examine their morphological structures. The presence and locations of floral odor-producing regions in fresh staminate flowers were determined by separating the different floral parts and then agitating them in Eppendorf flasks to stimulate and activate the release of any odors. It was not possible to evaluate the pistillate flowers using this technique due to the absence of reproductive material during data collection. To verify the locations of the odor-producing regions, we submerged fresh flowers in neutral red (Vogel 1983) and then washed them in running water; any stained areas were observed under a stereomicroscope.

To test pollen viability, we collected five pre-anthesis buds from 10 staminate individuals and stored them in 70 % ethanol. We subsequently removed the anthers and macerated them on slides with three drops of 2 % acetic carmine (Radford *et al.* 1974) for five minutes. Five slides were mounted for each individual and 300 grains were analyzed per slide. Pollen grains were classified as viable if they had intact exines, and were considered non-viable when not stained, or when visibly abnormal in size, or stained only a light color (Radford *et al.* 1974).

We tested for apomixis by bagging the pistillate flowers. This test was performed on only two individuals, due to the difficulty of assessing the inflorescences because of their height and presence of spines. We bagged 20 rachillae with pre-anthesis buds on each individual. Twenty rachillae were marked on the same inflorescence as controls. The rachillae were then monitored for three months to follow fruit formation.

We evaluated wind transport of pollen using 15 Petri dishes coated with petroleum jelly (adapted from Khorsand Rosa & Koptur 2013) that were distributed on five individuals. The plates were fixed in horizontal and vertical positions near the pistillate inflorescences. After 24 hours, the Petri dishes were removed and observed for trapped pollen under a stereoscopic microscope.

Results

Reproductive Phenology

The flowering of *Mauritia armata* occurred during the dry season and early rainy season, with fruiting occurring during the rainy season (Fig. 4). During the first year of evaluation, flowering was seasonal, occurring from April/2016 to October/2016, with a peak in September (average date

= 20/09/16; $r = 0.645$; $Z = 27.451$; $p < 0.001$). During the second phenological year (2016/2017) flowering was aseasonal ($r = 0.392$; $Z = 13.226$; $p < 0.001$), with continuous flowering throughout the period. During the third year, flowering peaked in October/2018 (average date = 18/10/18; $r = 0.759$; $Z = 56.407$; $p < 0.001$), with a seasonal pattern. Fruiting was observed at the beginning of phenological monitoring, with a peak in December/2015 (mean date = 13/12/2015; $r = 0.801$; $Z = 50.012$; $p < 0.001$). Fruiting was irregular and aseasonal during the second year ($r = 0.238$; $Z = 6.961$; $p < 0.001$) and at a low frequency in the population evaluated; in the third year, fruiting was concentrated in December/2017 and January/2018, although it was also aseasonal ($r = 0.414$; $Z = 13.215$; $p < 0.001$), due to a previous flowering.

There was a general synchrony of the flowering periods between the two sexes (Fig. 5), with a slight asynchrony in July/2017, accompanied by a slight increase in the production of pistillate flowers and a decrease in the production of staminate flowers. Both staminate and pistillate individuals showed greater expressions of flowering in October/2018. The synchrony by Augspurgers' index was 0.857 among pistillate individuals, 0.783 among staminate individuals, and 0.797 for the total population. The Pearson's correlation coefficient of phenological activity between staminate and pistillate individuals was 0.603. These analyses showed high synchrony within and between sexes.

Flowering showed a positive correlation only with the maximum temperature, and negative correlations with the minimum and mean temperatures, humidity, and day length. Maximum temperatures exerted a positive influence on flowering in the month previous to the flowering peak ($r = 0.680$; $p = 0.021$). Minimum and mean temperatures exerted negative influences, three ($r = -0.728$; $p = 0.026$ and $r = -0.717$; $p = 0.007$ respectively), four ($r = -0.856$; $p = 0.007$; and $r = -0.856$; $p = 0.007$ respectively), and five ($r = -0.945$; $p = 0.001$ and $r = -0.956$; $p = 0.001$ respectively) months earlier of the flowering peak. Humidity negatively influenced the flowering peak in the month of greatest flowering ($r = -0.584$; $p = 0.046$) and in the previous one to four months (1st mo. $r = -0.609$; $p = 0.047$; 2nd mo. $r = -0.737$; $p = 0.015$; 3rd mo. $r = -0.854$; $p = 0.003$; 4th mo. $r = -0.767$; $p = 0.026$), indicating that flowering is influenced by the dry season. Day length also negatively affected flowering five ($r = -0.793$; $p = 0.033$) and six ($r = -0.943$; $p = 0.004$) months before of its peak.

Fruiting showed positive correlations with almost all of the climatic variables tested, the minimum and mean temperatures, precipitation, humidity, and day length. The minimum temperature influenced fruiting during its peak ($r = 0.688$; $p = 0.013$), as well as one ($r = 0.891$; $p < 0.001$), two ($r = 0.778$; $p = 0.008$), and three ($r = 0.671$; $p = 0.048$) months before the fruiting peak. The mean temperature affected fruit production one ($r = 0.743$; $p = 0.009$) and two ($r = 0.714$; $p = 0.020$) months before the



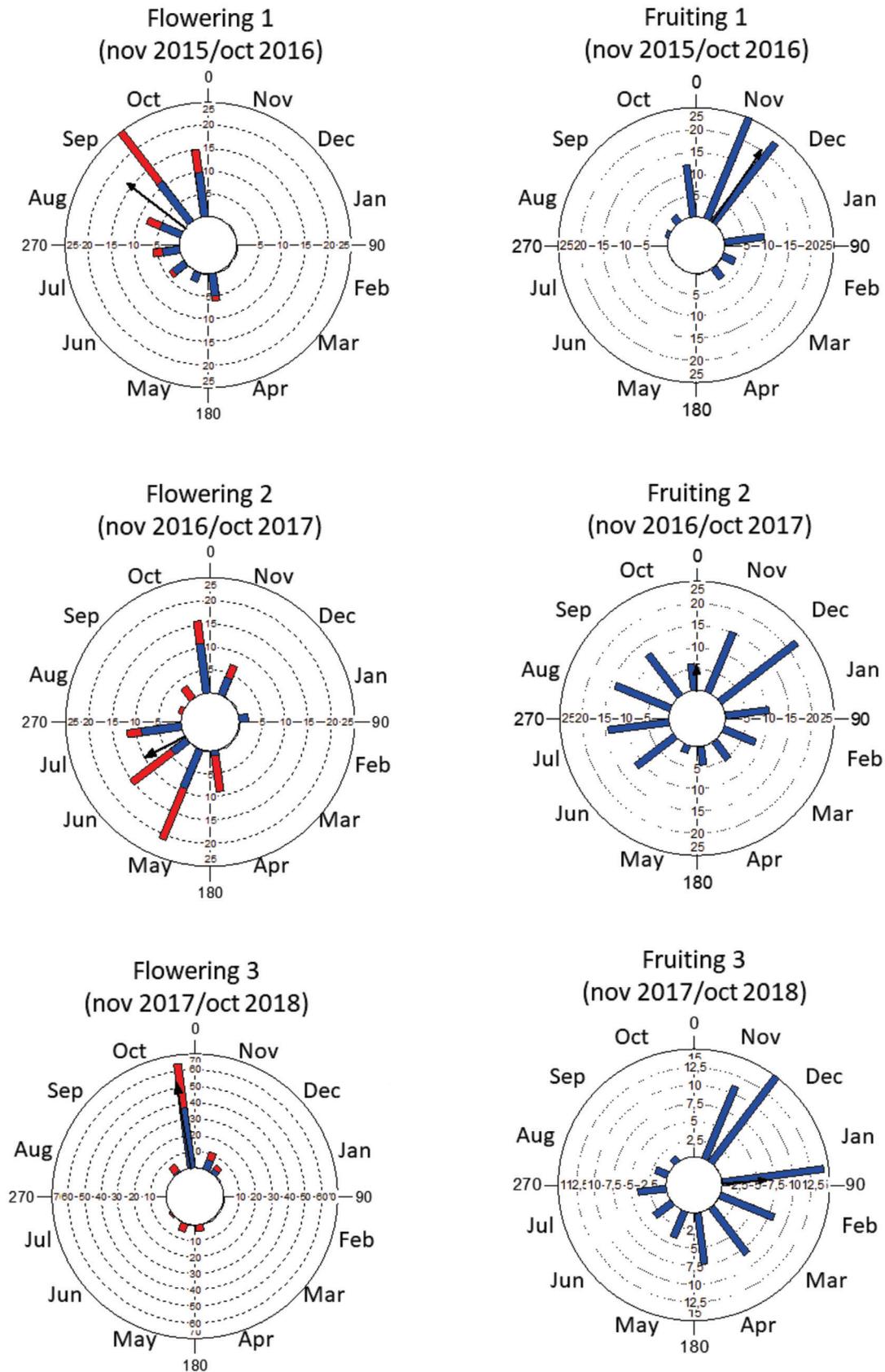


Figure 4. Circular histograms (in chronological order) of the peak frequencies of flowering (pistillate in blue and staminate in red) and fruiting of *Mauritiella armata* during three years of observations (November/2015 to October/2018). Black arrows indicate the average angle, while the lengths of the arrows correspond to the means of the vector values (r), or the degrees of seasonality.

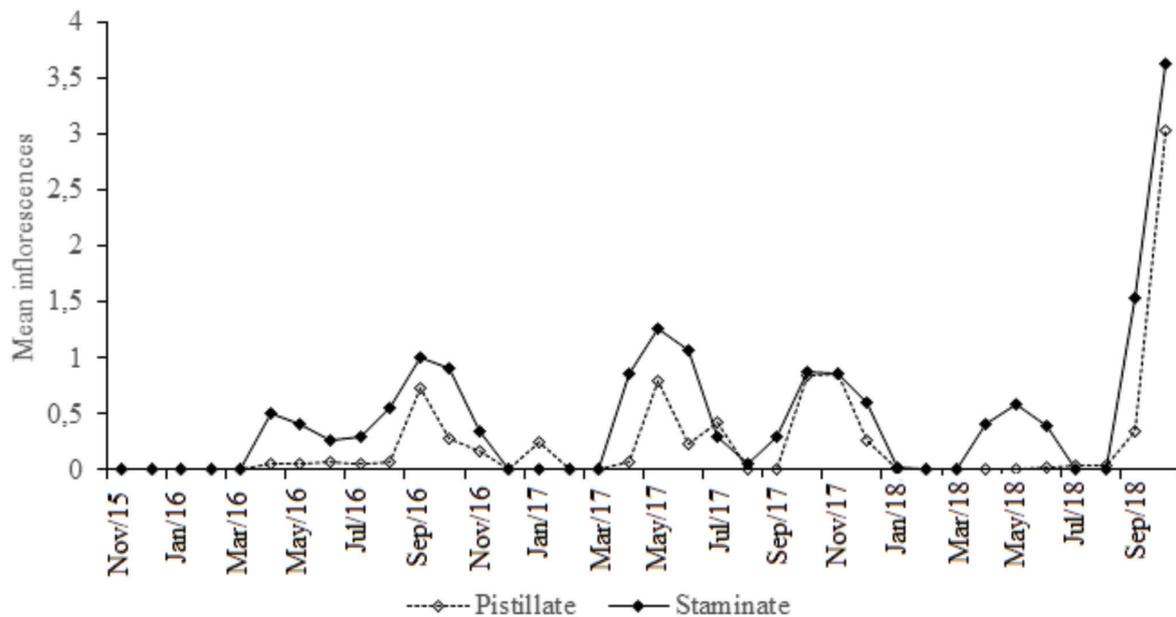


Figure 5. Mean numbers of staminate and pistillate inflorescences per individual of *Mauritiella armata* during a three-year period (November/2015 to October/2018).

fruiting peak. Precipitation positively influenced fruiting during the peak ($r = 0.853$; $p < 0.001$), and one ($r = 0.870$; $p < 0.001$) and two ($r = 0.811$; $p = 0.005$) months prior to the fruiting peak. The humidity likewise positively affected the period of peak fruit production in the month of greatest expression ($r = 0.842$; $p < 0.001$) and one ($r = 0.680$; $p = 0.021$) month before. Day length also positively influenced the fruiting peak in the month of its greatest expression ($r = 0.577$; $p = 0.049$) and one to four months before (1st mo. $r = 0.879$; $p < 0.001$; 2nd mo. $r = 0.929$; $p < 0.001$; 3rd mo. $r = 0.851$; $p = 0.004$; 4th mo. $r = 0.725$; $p = 0.042$). Flowering ($p < 0.05$) and fruiting ($p < 0.05$) peaks were negatively affected by soil moisture in terms of individuals, with the highest flowering and fruiting intensities occurring among individuals growing in lower humidity sites (Tab. S1).

Floral morphology and biometry of reproductive structures

The flowers of *M. armata* have three sepals and three light-yellow coriaceous petals. Pistillate flowers have a trilobate stigma and six staminodes, while staminate flowers have six stamens and a central trilobate pistilodium. All parts of the staminate flowers exhale a strong and slightly sweet odor. The neutral red test showed the stamens staining completely from the base of the filaments to the anthers, suggesting concentrated osmophores. Estimated pollen viability was high in all of the individuals analyzed, with a mean of 94%. The tests indicated that autonomous apomixis did not result in fruit formation. Wind transport of pollen was not demonstrated, as pollen grains of *M. armata* were not found in Petri dishes placed near pistillate inflorescences.

The inflorescences of *M. armata* are interleaved with the main rachis and are large structures, with several first-order ramifications from the base to the apex of the rachis. Short and numerous rachillae that emit flowers are inserted in the ramifications. Branches and rachillae are arranged alternately in the inflorescences. The inflorescences of the two sexes showed differences in all biometric parameters (Tab. 1). The staminate inflorescences were larger (75-215 cm), with larger numbers of branches (13-47), rachillae (5-95) and flowers per rachis (2-56), and an average of 31,641 staminate flowers per inflorescence, all of small size (4.91-6.37 mm). The pistillate flowers were larger (8.78-12.7 mm), while the pistillate inflorescences (43-160 cm), the number of branches (14-34), rachilla (3-65), and pistillate flowers per rachilla (1-9) were smaller, with approximately 3,956 flowers per inflorescence. Each inflorescence produced an estimated 550 fruits. Pistillate individuals produce from one to seven inflorescences (average of four per individual), so that an individual will produce an estimated 15,824 flowers.

When assessing the ramifications of the two sexes, according to their positions on the main rachis (the apex, middle, or base), we found differences in relation to their sizes, lengths, and the numbers of flowers (Tab. 2). The branches at the apex were smaller than those at the base or mid-region; the numbers of rachillae and flowers followed the same pattern, with smaller numbers at the apex. The rachillae at the base were larger than those in the middle, and smaller at the base as compared to the other parts. The fruits varied in length from 1.64 to 4.12 cm (3.04 ± 0.37 cm), in thickness from 1.50 to 2.97 cm (mean 2.07 ± 0.17 cm), and in weight from 1.14 to 13.95 g (7.38 ± 1.74 g). The seeds varied in length from 1.31 to 3.20 cm (2.36 ± 0.29 cm), in



Table 1. Biometric variables (means and standard deviation values) of the reproductive structures of the staminate and pistillate inflorescences of *Mauritiella armata*. Means followed by the same letter in the columns are not significantly different according to the LsMeans test (t) at a significance level of 0.05 (df = degrees of freedom; and p = probability).

Variable	Staminate	Pistillate	df	t	p
Inflorescence length (cm)	125.7 ± 6.9 a	91.4 ± 6.4 b	64	4.45	< 0.001
Number of branches	31.9 ± 1.3 a	24.6 ± 1.1 b	64	4.46	< 0.001
Branch lengths (cm)	37.3 ± 1.8 a	23.0 ± 1.7 b	64	4.46	< 0.001
Number of rachillae	43.1 ± 1.4 a	30.6 ± 0.9 b	610	12.88	< 0.001
Number of flowers in rachilla	15.7 ± 0.6 a	4.0 ± 0.2 b	6206	154.81	< 0.001
Flower length (cm)	5.6 ± 0.2 b	11.1 ± 0.1 a	98	-46.87	< 0.001

Table 2. Biometric variables (means and standard error values) of the reproductive structures of *Mauritiella armata* in different positions on the inflorescences (apex, middle, and base). Means followed by the same letter in the columns are not significantly different according to LsMeans test (t) at a significance level of 0.05 (df = degrees of freedom; and p = probability).

Variable	Apex	Middle	Base	df
Branch length (cm)	23.9 ± 7.1 b	32.1 ± 7.1 a	34.1 ± 7.1 a	609
Rachilla length (cm)	7.5 ± 0.3 c	8.3 ± 0.4 b	8.8 ± 0.4 a	6205
Number of rachillae	31.8 ± 0.9 b	39.8 ± 1.1 a	38.5 ± 1.1 a	609
Number of flowers in rachilla	9.0 ± 0.9 b	11.3 ± 0.9 a	10.5 ± 0.9 a	6205

Pair test	Apex - Base		Apex - Middle		Base - Middle	
	t	p	t	p	t	p
Branch length (cm)	-8,40	< 0.0001	-6.71	< 0.0001	1.71	0.201
Rachilla length (cm)	-15,56	< 0.0001	-9.68	< 0.0001	5.88	< 0.001
Number of rachillae	-8,58	< 0.0001	-6.89	< 0.0001	1.84	0.150
Number of flowers in rachilla	-6,63	< 0.0001	-4.82	< 0.0001	1.81	0.167

thickness from 0.58 to 2.86 cm (1.58 ± 0.17 cm), and in weight from 1.04 to 9.51 g (3.82 ± 1.04 g).

Discussion

The reproductive strategy of *Mauritiella armata* showed synchronization of flowering between the two sexes, responses to climatic seasonality, and positive relationships among phenophases and certain climatic variables. Dioecy was confirmed in the sexual system of *M. armata*, with individuals producing only pistillate or staminate flowers. Female flowers required biotic pollination for fruit production. The male and female inflorescences and flowers had differential biometric reproductive parameters, with greater numbers of smaller male flowers in larger inflorescences, and smaller numbers of larger female flowers in smaller inflorescences. These results are discussed in detail below.

Reproductive phenology

The phenological pattern of flowering of *M. armata* was annual with an extended duration, while fruiting was continuous. Both were irregular (*sensu* Newstrom *et al.* 1994) throughout the three year study. The phenological cycles of tropical plants can be complex with irregular patterns that are difficult to recognize, especially in short-term studies (Bencke & Morellato 2002). Because there are intrinsic relationships between environmental factors (such as climate) and reproductive success (pollination and

dispersion) and phenology, annual variations in flowering and fruiting times are common (Bencke & Morellato 2002). There have been few phenological studies focusing specifically on palm trees, and those have mainly considered their reproduction (Castro *et al.* 2007). The phenological patterns of palm trees are not always seasonal (Henderson *et al.* 2000; Sampaio & Scariot 2008), as they tend to bloom in a specific climatic season, although with little synchrony, but have long fruiting periods (Henderson *et al.* 2000) – making them key species, as their fruits are generally available even in times of scarcity (Eiserhardt *et al.* 2011). Flower production by *M. armata* begins at the end of the dry season, then decreasing during the transition into the rainy season. Fruiting tends to occur at the beginning of the rainy season (although with great irregularity among individuals).

The reproductive phenology of *M. armata* was associated with environmental variations during the three study years. Although peak flowering occurred at the transition between the dry and rainy seasons, with fruiting in the rainy season, their environmental triggers were related to earlier events, such as the influence of previous temperatures (Khorsand Rosa *et al.* 2013; Morellato *et al.* 2016) on the emission of reproductive structures. Fruiting was also influenced by temperature. Temperature has been found to be one of the most important environmental factors related to plant reproduction, as it affects their photosynthetic processes and carbon/nitrogen balances during the ideal period for initiating flowering (Kramer & Kozlowski 1979). Precipitation and day length are also determinant



environmental factors of reproductive phenology (Morellato *et al.* 2000; McLaren & McDonald 2005; Begnini *et al.* 2013, Khorsand Rosa *et al.* 2013). The influence of rainfall on the flowering of palms varies according to the species and local edaphoclimatic conditions (Begnini *et al.* 2013; Pires *et al.* 2016). In *M. flexuosa*, for example, flowering occurs in the transition period from the wet to the dry season (from August to November), with precipitation exerting a negative influence (Khorsand Rosa & Koptur 2013). One of the main triggers of flowering in that species, however, is the occurrence of rainfall three months earlier (Khorsand Rosa & Koptur 2013). Similarly, both the inflorescences and the infructescences of the *Syagrus romanzoffiana* palm were observed to have both positive and negative correlations with photoperiod, precipitation, and temperature (Begnini *et al.* 2013). Reproduction in *M. armata* is likewise determined by variations in temperature and precipitation, both in the month of their greatest manifestation, as well as in previous months, evidencing them as environmental triggers that determine the occurrence of flowering and fruiting peaks. Borchert *et al.* (2004) noted that seasonal variations in rainfall and soil water availability appear to be not only the immediate causes – but also the ultimate causes of flowering periodicity in tropical dry forests.

In addition to the influence of climatic variables on the reproductive phenology of *M. armata* populations, individuals showed differential flowering and fruiting responses in relation to soil moisture levels. The greatest reproductive activity was observed in individuals growing on drier soils. Although the species preferentially inhabits soggy and humid soils, decreases in moisture appear to serve as environmental triggers that induce increased flower and fruit production. Greater reproduction in drier soils may represent a plant response to an unfavorable growing condition driving resource allocation to reproduction instead (Kozłowski & Pallardy 2002). But the resulting phenological pattern is similar to the observed for woody Cerrado plants, which chiefly flowers at the transition between the dry and rainy season (Batalha & Martins 2004).

Dioecy and floral aspects

The sexual expression of a species reveals its pollination system and, consequently, its reproductive system (Henderson 2002). *Mauritiella armata* is a dioecious species – a sexual system encountered in approximately 30% of all palm species – and which obliges cross-pollination (Nadot *et al.* 2016). The degree of sexual dimorphism observed in dioecious species is correlated with their modes of pollination and other ecological factors, as in the case of species that tend to produce flowers of the opposite sex under unfavorable environmental conditions (Freeman *et al.* 1997). With the complete separation of the sexes in different individuals within a population, cross-pollination by biotic or abiotic pollinator agents becomes mandatory, defining the reproductive system of *M. armata* as xenogamy

(as the possibility of apomixis was discarded). *Mauritiella armata* showed high flowering synchrony between pistillate and staminate individuals, a necessary strategy for cross-pollination and consequently reproductive success.

Dioecious species depend on cross-pollination (Henderson 2002), and various strategies facilitate the reproductive success of those plants, such as flowering synchrony between staminate and pistillate individuals (Listabarth 1999), high pollen grain viability (Oliveira *et al.* 2003; Ostrorog & Barbosa 2009), and floral biology traits that promote pollinator attraction (Storti 1993), such as those observed in *M. armata*. Studies have indicated that entomophily is the most frequent pollination syndrome in several groups of tropical palms, with pollination by beetles being observed in only some extremely specialized species (Henderson 1986; Scariot *et al.* 1991; Storti 1993; Henderson 2002; Barfod *et al.* 2011). There was no evidence of wind pollination in the present study. Odor production by the staminate flowers of *M. armata* and the absence of wind pollen dispersal indicated that biotic, and possibly entomophilous, pollination is required. In the sister dioecious palm *M. aculeata*, flowering is perfectly synchronized between sexes and it is pollinated by bees (Listabarth 1999). Wind seems to be important for the pollination of *M. flexuosa*, although beetles may also play an important role (Storti 1993; Khorsand Rosa & Koptur 2013).

The fruits of *M. armata*, as well as those of *M. flexuosa*, are ellipsoid-oblong, and they are covered with small reddish-brown scales. The mean fruit length observed here (approximately 3 cm) confirms data already published in the literature (2.5-3.5 cm) (Henderson *et al.* 1995). As *M. armata* does not produce abundant fruits, but is nonetheless exploited by local inhabitants, the morphometric characterization of the fruits could aid in the future selection of larger fruits and in the sustainable propagation and exploitation of that species. Sustainable management practices that favor the maintenance of harvested resources (Guedje *et al.* 2007) can avoid excessive collections that exceed recruitment capacities (Ticktin 2004). It is therefore fundamental to study the ecology of useful plants and evaluate harvesting impacts as sustainable management and conservation strategies (Hall & Bawa 1993).

The biometric variables of *M. armata* showed floral differences reflecting their positions on the inflorescences. Lower averages of all evaluated parameters were observed at the apex position. The greater abundances of structures (rachis and flowers) in the basal region may be related to the greater resource availability there, as differential access to nutritional resources can influence flower distribution, morphology, and functioning (Mazzottini-dos-Santos *et al.* 2015). The individuals evaluated had larger staminate inflorescences with larger numbers of flowers than pistillate inflorescences, although the pistillate flowers were larger. That same pattern was observed in *M. flexuosa* (Storti



1993), and is considered a characteristic of the family, with the larger female flower developing into large fruits (Tomlinson 1990). There are different patterns of resource allocation between the sexes (Willson 1979), and many of the dimorphic sexual characters in *M. armata* possibly reflect responses to reproduction costs (Barret & Hough 2013).

Biometric characterizations and quantifications of the reproductive structures of *M. armata* inflorescences generated information that can directly contribute to the sustainable management and harvesting of their economically and socially valuable fruit resources. Projecting from the estimate of 14% of natural fruit formation reported for *M. flexuosa* (Storti 1993), each pistillate inflorescence of *M. armata* could produce approximately 550 fruits and, with an average of four inflorescences per individual, 2,216 fruits could potentially be produced per individual. The average fruit production by *M. flexuosa* in the Amazon region was 479 fruits per bunch (Storti 1993), so that the estimated production of *M. armata* fruits would be even higher – although our results show wide variations in the sizes of its fruits and seeds. The morphometric characterization of the fruits, as reported here, could aid in the selection of larger fruits and in the propagation and sustainable exploitation of the species. Sustainable management practices that favor the maintenance of harvested resources (Guedje *et al.* 2007) can prevent collections that exceed recruitment capabilities (Ticktin 2004). Therefore, it is essential to study the ecology of useful plants and assess the impacts of harvesting to develop sound management and conservation strategies (Hall & Bawa 1993).

Concluding remarks

Veredas are important humid environments in the Cerrado that provide habitat for plant species with the ecological functions needed to maintain the water balance of those systems (Bijos *et al.* 2017; Ávila *et al.* 2021). *Mauritiella armata*, like *M. flexuosa*, is a key species in vereda ecosystems, and the species has high ecological and social importance. The lack of ecological information concerning *M. armata* (and its potential economic value) provides an incentive for further investigations – and elucidating its pollination system will be critical to guaranteeing its reproductive success and sustainable use.

Acknowledgments

This research was supported by the Long-term Ecological Research Network (PELD-VERE) of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 441440/2016-9; 441583/2020-2; 308877/2019-5), the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES 88887.136273/2017-00), the Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG APQ-04816-17; CRA-PPM-00539-18), and the Ministério

da Ciência, Tecnologia e Inovações. The authors thank FAPEMIG for the first author's doctoral scholarship and the field assistance of the Plant Ecology Laboratory (Unimontes) and Instituto Estadual de Florestas staffs.

References

- Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G. 2014. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* 22:711-728.
- Augsburger CK. 1983. Phenology, flowering synchrony, and fruit set of six neotropical shrubs. *Biotropica* 15:257-267.
- Ávila MA, Mota NM, Souza SR, Santos RM, Nunes YRF. 2021. Diversity and structure of natural regeneration in swamp forests in southeastern Brazil. *Floresta e Ambiente* 28: e20190110. doi: 10.1590/2179-8087-FLORAM-2019-0110.
- Ávila MA, Souza SR, Veloso MDM, Santos RM, Fernandes LA, Nunes YRF. 2016. Structure of natural regeneration in relation to soil properties and disturbance in two swamp forests. *Cerne* 22: 1-10.
- Azevedo IFP, Nunes YRF, Ávila MA, Silva D L, Fernandes GW, Veloso RB. 2014. Phenology of riparian tree species in a transitional region in southeastern Brazil. *Brazilian Journal of Botany* 37: 47-59.
- Barfod AS, Hagen M, Borchsenius F. 2011. Twenty-five years of progress in understanding pollination mechanisms in palms (Arecaceae). *Annals of Botany* 108: 1503-1516.
- Batalha MA, Martins FR. 2004. Reproductive phenology of the cerrado plant community in Emas National Park (central Brazil). *Australian Journal of Botany* 52: 149-161.
- Bates D, Machler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: e1406. doi: 10.18637/jss.v067.i01.
- Barret SCH, Hough J. 2013. Sexual dimorphism in flowering plants. *Journal of Experimental Botany* 64:67-82.
- Begnini RM, Silva FR, Castellani TT. 2013. Fenologia reprodutiva de *Syagrus romanzoffiana* (Cham.) Glassman (Arecaceae) em Floresta Atlântica no sul do Brasil. *Revista Biotemas* 26: 53-60.
- Bencke CSC, Morellato LPC. 2002. Comparação de dois métodos de avaliação da fenologia de plantas, sua interpretação e representação. *Revista Brasileira de Botânica* 25: 269-275.
- Bijos NR, Eugênio CUO, Mello TRB, Souza GF, Munhoz CBR. 2017. Plant species composition, richness, and diversity in the palm swamps (veredas) of Central Brazil. *Flora* 236-237: 94-99.
- Blake GRB. 1996. Density. In: Blach CA, Evans DD, White JL, Esminger LE, Clark FE. (eds.) *Methods of soil analysis*. Madison, American Society of Agronomy. p. 371-390.
- Borchert R, Meyer SA, Felger RS, Porter-Bolland L. 2004. Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. *Global Ecology and Biogeography* 13: 409-425.
- Borchsenius F, Borgtoft PH, Balslev H. 1998. *Manual to the palms of Ecuador*. AAU Reports 37. Aarhus, Aarhus University, Universidad Católica del Ecuador.
- Castro ER, Galetti M, Morellato LPC. 2007. Reproductive phenology of *Euterpe edulis* (Arecaceae) along a gradient in the Atlantic rain forest of Brazil. *Australian Journal of Botany* 55: 725-735.
- Chagas KPT, Carvalho BLB, Guerra CAG, Silva RAR, Vieira FA. 2019. Fenologia do dendezeiro e correlações com variáveis climáticas. *Ciência Florestal* 29:1701-1711.
- Eiserhardt WL, Svenning JC, Kissling WD, Balslev H. 2011. Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Annals of Botany* 108: 1391-1416.
- Fenner M. 1998. The phenology of growth and reproduction in plants. *Perspectives in Plant Ecology, Evolution and Systematics* 1: 78-91.
- Freeman DC, Doust JL, El-Keblawy A, Miglia JK, McArthur ED. 1997. Sexual specialization and inbreeding avoidance in the evolution of dioecy. *The Botanical Review* 63: 65-92.



- Guedje NM, Zuidema PA, During H, Foahrom B, Lejoly J. 2007. Tree bark as a non-timber forest product: the effect of bark collection on population structure and dynamics of *Garcinia lucida* Vesque. *Forest Ecology and Management* 240: 1-12.
- Hall P, Bawa K. 1993. Methods to assess the impact of extraction of non-timber tropical forest products on plant populations. *Economic Botany* 47: 234-247.
- Hammer Ø, Harper DAT, Ryan PD. 2001. PAST: Paleontological statistics software package for education and data analysis. *Paleontologia Electronica* 4: 1-9.
- Henderson A. 2002. *Evolution and ecology of palms*. New York, The New York Botanical Garden Press.
- Henderson A, Fischer B, Scariot A, Pacheco MAW, Pardini R. 2000. Flowering phenology of a palm community in a central Amazon Forest. *Brittonia* 52: 149-159.
- Henderson A, Galeano G, Bernal R. 1995. *Field guide to the palms of Americas*. New Jersey, Princeton.
- Henderson A. 1986. Review of pollination studies in the Palmae. *The Botanical Review* 52: 221-259.
- Khorsand Rosa R, Koptur S. 2013. New findings on the pollination biology of *Mauritia flexuosa* (Arecaceae) in Roraima, Brazil: linking dioecy, wind, and habitat. *American Journal of Botany* 100: 613-62.
- Khorsand Rosa R, Barbosa RI, Koptur S. 2013. How do habitat and climate variation affect phenology of the Amazonian palm, *Mauritia flexuosa*? *Journal of Tropical Ecology* 29: 255-259.
- Kovach WL. 1994. Oriana for Windows, version 3.13. Pentraeth, UK: Kovach Computer Services.
- Kozlowski TT, Pallardy SG. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. *The Botanical Review* 68: 270-334.
- Kramer PJ, Kozlowski TT. 1979. *Physiology of woody plants*. New York, McGraw-Hill.
- Leitman P, Soares K, Henderson A, Noblick L, Martins RC. 2015. Arecaceae in lista de espécies da flora do Brasil. Jardim Botânico do Rio de Janeiro. <http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB15725>. 12 Jun. 2018.
- Listabarth C. 1999. The palms of the Surumoni area (Amazonas, Venezuela). II. Phenology and pollination of two flooded forest palms, *Mauritiella aculeata* and *Leopoldinia pulchra*. *Acta Botanica Venezuelica* 22: 153-165.
- Lorenzi H, Noblick LR, Kahn F, Ferreira E. 2010. *Flora brasileira: Arecaceae (Palmeiras)*. Plantarum, Nova Odessa, p. 368.
- Martins RC, Filgueiras T, Albuquerque UP. 2014. Use and diversity of palm (Arecaceae) resources in Central Western Brazil. *The Scientific World Journal* 3: 20-43.
- Mazzottini-dos-Santos HC, Ribeiro LM, Mercadante-Simões MO, Sant'Anna-Santos BF. 2015. Floral structure in *Acrocomia aculeata* (Arecaceae): evolutionary and ecological aspects. *Plant Systematics and Evolution* 301: 1425-1440.
- McLaren KP, McDonal MA. 2005. Seasonal patterns of flowering and fruiting in a dry tropical forest in Jamaica. *Biotropica* 37: 584-590.
- Mendes FN, Valente RM, Rêgo MMC, Esposito MC. 2017. Reproductive phenology of *Mauritia flexuosa* L. (Arecaceae) in a coastal restinga environment in northeastern Brazil. *Brazilian Journal of Biology* 77: 29-37.
- Mendonça RC, Felfili JM, Walter BMT et al. 2008. Flora vascular do bioma Cerrado: checklist com 12.356 espécies. In: Sano SM, Almeida SP, Ribeiro JF (eds.) *Cerrado: ecologia e flora*. Brasília, Embrapa Cerrados. 423-1279.
- Morellato LPC, Alberton B, Alvarado ST et al. 2016. Linking plant phenology to conservation biology. *Biological Conservation* 195: 60-72.
- Morellato LPC, Talora DC, Takahasi A, Bencke CC, Romera EC, Zipparro VB. 2000. Phenology of Atlantic rain forest trees: a comparative study. *Biotropica* 32: 811-823.
- Nadot S, Alapetite E, Baker WJ, Tregear JW, Barfod AS. 2016. The palm family (Arecaceae): a microcosm of sexual system evolution. *Botanical Journal of the Linnean Society* 182: 376-388.
- Newstrom LE, Frankie GW, Baker HG. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica* 26: 141-159.
- Nunes YRF, Bahia TO, Ávila MA, Veloso MDM, Santos RM. 2015. Florística e Fitossociologia das comunidades arbóreas de veredas: um estudo de caso no norte de Minas Gerais, Brasil. In: Eisenlohr PV, Felfili JM, Melo MMRE, Andrade LA, Meira Neto JAA. (eds.) *Fitossociologia do Brasil: métodos e estudos de casos*. Editora UFV, Viçosa. 264-287.
- Oliveira MSP, Couturier G, Beserra P. 2003. *Biologia da polinização da palmeira Tucumã (Astrocaryum vulgare Mart.) em Belém, Pará, Brasil*. *Acta Botanica Brasílica* 17: 343-353.
- Ostrorog DRV, Barbosa AAA. 2009. *Biologia reprodutiva de Geonoma brevispatha Barb. Rodr. (Arecaceae) em mata de galeria inundável em Uberlândia, MG, Brasil*. *Revista Brasileira de Botânica* 32: 479-488.
- Pires HCG, Rosa LS, Cabral BS, Silva VM, Nogueira GA, Ferreira PRN. 2016. Padrão fenológico de *Attalea amaripa* (Aubl.) Mart. em áreas de pastagens na Amazônia Oriental. *Floresta e Ambiente* 23:170-179.
- R Development Core Team. 2020. R: A language and environment for statistical computing. Version 4.0.1. R Foundation for Statistical Computing, Vienna, <https://www.R-project.org>. 29 Mar. 2020.
- Radford AE, Dickison WC, Massey JR, Bell CR. 1974. *Vascular plant systematic*. New York, H. R. Publishers.
- Reis SB, Mello ACMP, Oliveira DMT. 2017. Pericarp formation in early divergent species of Arecaceae (Calamoideae, Mauritiinae) and its ecological and phylogenetic importance. *Plant Systematics and Evolution* 303: 675-687.
- Ribeiro JF, Walter BMT. 2008. As principais fitofisionomias do bioma Cerrado. In: Sano SM, Almeida SP, Ribeiro JF (eds) *Cerrado: ecologia e flora*. Embrapa Informação Tecnológica, Brasília. 151-212.
- Royo VA, Rocha JA, Santos KT et al. 2019. Comparative studies between *Mauritia flexuosa* and *Mauritiella armata*. *Pharmacognosy Journal* 11: 32-36.
- Sampaio MB, Scariot A. 2008. Growth and reproduction of the understory palm *Geonoma schottiana* Mart. in the gallery forest in Central Brazil. *Revista Brasileira de Botânica* 31: 433-442.
- Scariot AO, Lleras E, Hay JD. 1991. Reproductive biology of the palm *Acrocomia aculeata* in Central Brazil. *Biotropica* 23: 12-22.
- Silva FAM, Assad ED, Steinke ET, Müller AG. 2008. *Clima do bioma Cerrado*. In: Albuquerque ACS, Silva AG (eds) *Agricultura tropical: quatro décadas de inovações tecnológicas, institucionais e políticas*. Acre, Embrapa Informações Tecnológicas. 93-148.
- Silva PAD, Scariot A. 2013. Phenology, biometric parameters and productivity of fruits of the palm *Butia capitata* (Mart.) Beccari in the Brazilian cerrado in the north of the state of Minas Gerais. *Acta Botanica Brasílica* 27: 580-589.
- Souza AT, Junio RF, Neuba LM, et al. 2020a. Caranan fiber from *Mauritiella armata* palm tree as novel reinforcement for epox composites. *Polymers* 12. doi: 10.3390/polym12092037.
- Souza FG, Araújo FF, Farias DP, Zanotto AW, Neri Numa IA, Pastore GM. 2020b. Brazilian fruits of Arecaceae family: an overview of some representatives with promising food, therapeutic and industrial applications. *Food Research International* 138. doi: 10.1016/j.foodres.2021.110260.
- Souza FG, Náthia Neves G, Araújo FF, et al. 2021. Evaluation of antioxidant capacity, fatty acid profile, and bioactive compounds from buritirana (*Mauritiella armata* Mart.) oil: a little-explored native Brazilian fruit. *Food Research International* 142. doi: 10.1016/j.foodres.2020.109690.
- Storti EF. 1993. *Biologia floral de Mauritia flexuosa* Lin. Fil. na região de Manaus, AM, Brasil. *Acta Amazônica* 23: 371-381.
- Ticktin T. 2004. The ecological implications of harvesting non-timber forest products. *Journal of Applied Ecology* 41: 11-21.
- Tomlinson PB. 1990. *The structural biology of palms*. Oxford, Clarendon Press.
- Vogel S. 1983. Ecophysiology of zoophilic pollination. In: Lange OL, Nobel PS, Osmond CB, Ziegler H. (eds.) *Physiological plant ecology III*. Encyclopedia of Plant Physiology, Berlin, Springer-Verlag. 559-624.
- Wang X. 2015. *Flower: tools for characterizing flowering traits*. R package version 1.0. <https://CRAN.R-project.org/package=flower>. 15 Oct. 2020.
- Willson MF. 1979. Sexual selection in plants. *The American Naturalist* 113: 777-790.
- Zar JH. 2010. *Biostatistical analysis*. 5th ed, Prentice-Hall, New Jersey.

