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Original Paper

Reproductive phenology and influence of abiotic variables for two mangrove species in northeastern Brazil

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Abstract

Information on plant phenological patterns aids in understanding the structure and functioning of ecosystems and support restoration projects in degraded areas. The aim of this study was to characterize the reproductive phenology of *Avicennia germinans* and *Laguncularia racemosa* in a mangrove forest in the Mamanguape River estuary in northeastern Brazil. The characterization was performed monthly from July 2016 to June 2017. We applied circular statistics to detect seasonal trends, calculated intra-specific synchrony, and performed regressions between the reproductive phenophases and the abiotic variables. *Avicennia germinans* exhibits seasonal responses to floral buds, flowers at anthesis, and fruit, with one reproductive episode per year (annual pattern). *Laguncularia racemosa* has no seasonal response, with one reproductive episode per year for floral buds (annual pattern) and two episodes for flowers at anthesis and fruits (subannual pattern). Reproductive phenophases of *A. germinans* exhibited higher intra-specific synchrony than *L. racemosa*. We provide evidence that temperature, solar radiation and rainfall are important drivers of the flowering rhythm in both species. In conclusion, the results of this study showed that the species exhibited different phenological responses, even though they were subjected to the same abiotic conditions.
Key words: *Avicennia germinans*, flowering, fruiting, *Laguncularia racemosa*.

Resumo

Informações sobre padrões fenológicos das plantas ajudam a entender a estrutura e o funcionamento dos ecossistemas e apóiam projetos de restauração em áreas degradadas. O objetivo deste estudo foi caracterizar a fenologia reprodutiva em indivíduos de *Avicennia germinans* e *Laguncularia racemosa* em uma floresta de mangue no estuário do rio Mamanguape, Nordeste do Brasil. O registro foi realizado mensalmente de Julho 2016 a Junho 2017. Aplicamos estatística circular para detectar tendências sazonais, calculamos a sincronia intra-específica e realizamos regressões entre fenofases e variáveis abióticas. *Avicennia germinans* exibiu respostas sazonais para botões florais, flores em antese e frutos, com um episódio reprodutivo por ano (padrão anual). *Laguncularia racemosa* não mostrou resposta sazonal, com um episódio por ano para botões florais (padrão anual) e dois episódios para flores em antese e frutos (padrão subanual). As fenofases reprodutivas de *A. germinans* apresentaram maior sincronia intra-específica do que *L. racemosa*. Fornecemos evidências de que a temperatura, a radiação solar e a precipitação são fatores importantes para o ritmo da floração em ambas as espécies. Em conclusão, os resultados deste estudo mostraram que as espécies exibiram diferentes respostas fenológicas, mesmo estando submetidas às mesmas condições abióticas.
Palavras-chave: *Avicennia germinans*, floração, frutificação, *Laguncularia racemosa*.

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Introduction

Reproductive phenology of tropical plants and its dependence on abiotic factors have been analyzed for several ecosystems (Morellato *et al*. 2013; Rodríguez-Gallego & Navarro 2015; Ulsig *et al*. 2017). Knowledge on phenological patterns provides information on the quality and quantity of available resources for fauna (Fenner 1998; Morellato *et al.* 2016), aids in understanding ecosystems structure and functioning (Encinas-Viso *et al*. 2012; Revilla *et al*. 2014), support restoration projects in degraded areas (Zamith & Scarano 2004; Garcia *et al*. 2009), and can be used to monitor climate change (Morellato 2008).

Complex interactions between abiotic and biotic factors control plant reproductive phenology (Wolkovich *et al*. 2014). Abiotic factors include rainfall, the air temperature, and solar radiation (Nadia *et al*. 2012; Couralet *et al*. 2013; Wolkovich *et al*. 2014; Borchert *et al*. 2015), whereas biotic factors are related to pollinators, dispersers, and morphological/physiological adaptations (Liebsch & Mikich 2009; Wolkovich *et al*. 2014).

Reproductive phenology of the mangrove species has been successfully associated with abiotic factors. Nadia *et al.* (2012) showed that rainfall and temperature drive the flowering and fruiting rhythm of the mangrove species. Van der Stocken *et al*. (2017) demonstrated significant correlations between mangrove propagule release and rainfall, with 72% of the studies showing propagule release during the wet season, except for southernmost latitudes. However, in some cases the reproductive phenophases of mangrove species has exhibited little or no relationship with abiotic variables (Wang'ondu *et al.* 2013; Kamruzzaman *et al*. 2019).

Adaime (1985) conducted the first study in Brazil on the flowering and fruiting patterns of the mangrove species and their relationship with abiotic factors to estimate mangrove primary productivity. A growing number of studies on reproductive phenology and its relationship with abiotic (*e.g.*, Fernandes 1999; Nadia *et al*. 2012; Medeiros & Sampaio 2013; Alvarenga 2015; Cardoso *et al*. 2015) and biotic factors (Nadia *et al*. 2012) have subsequently been published, although the study areas have been distributed irregularly along the coast.

The mangrove forests of the Mamanguape River estuary are considered the largest and best-preserved mangrove forests in Paraíba state in northeastern Brazil. This ecosystem is within the Barra de Mamanguape Environmental Protection Area but has been degraded by vegetation removal for the installation of shrimp farming tanks, resource overexploitation, intruding livestock production, urbanization, and intensive selective cutting. In the upper Mamanguape River estuary, a large clearing has resulted from intensive selective cutting. Severe defoliation of *Avicennia germinans* (L.) L. (Acanthaceae) by the caterpillars of a lepidopteran species led the local population to conclude that the plants were dead and begin logging. The *Laguncularia racemosa* (L.) C.F. Gaertn. (Combretaceae) trees that also occurs in this area were not affected by severe defoliation but they were also targeted for selective cutting. The conservation unit management plan recommends the restoration of this degraded forest (ICMBio 2014), but studies are needed to support forest restoration actions.

Within this context, the objective of this study was to characterize of the reproductive phenology of *A. germinans* and *L. racemosa* in the mangroves of the Mamanguape River estuary to answer the following questions: (1) Do these species flower and fruit seasonally? (2) Do reproductive patterns vary between species? (3) Do reproductive phenophases exhibit intraspecific synchrony and depend on abiotic factors? Phenological information, which is required to understand the geographic variability of phenological responses to environmental factors, remains scarce for many tropical trees. The results from this study represent the first record of the reproductive phenology of mangrove species in Paraíba state.

Materials and Methods

Study area and species studied

This study was conducted in a mangrove forest in the upper Mamanguape River estuary (06°49'16''S, 35°03'44''W) in the Barra do Rio Mamanguape Environmental Preservation Area (Decree No. 924/93), on the northern coast of Paraíba state, northeastern Brazil. The regional climate is tropical and humid (Am, in the Köppen classification), and the average annual temperature varies between 24 ºC and 26 ºC (Alvares *et al*. 2013). Total annual precipitation ranges between 1,600 and 1,900 mm (Alvares *et al*. 2013), and the rainy season spreads from February to August.

The mangrove forest in the Mamanguape River estuary covers approximately 45.6 km^2 and is composed of *Avicennia germinans*, *A. schaueriana* Stapf & Leechm. *ex* Moldenke, *L. racemosa*, and *Rhizophora mangle* L. Only *A. germinans* and *L. racemosa* were recorded in the study area, which form forests with a mean canopy height ranging from 1.4 to 11.1 m, a mean diameter at breast height ranging from 0.8 to 21.6 cm, a mean basal area ranging from 1.5 to 16.2 m^2/ha, and mean density of 15 to 1,331 individuals/ha (Nascimento-Costa 2015). The *Avicennia germinans* tree is known the black mangrove and thrives under a wide variety of topographic conditions and interstitial salinity. The *Laguncularia racemosa* tree is known as white mangrove and develops mainly at high elevations with low flood frequencies.

Phenological monitoring

Reproductive phenology was monitored monthly from July 2016 to June 2017. Sixteen individuals of each species (> 2 m tall) were tagged along a track (following Morellato *et al.* 2010). The intensity of each reproductive phenophase was assessed by the Fournier intensity index (Fournier 1974), wherein a value of 0 was assigned in the absence of a phenophase, and phenophases were assigned values from 1 to 4 in 25% intervals (1 = 1–25%; 2 = 26–50%; 3 = 51–75%; 4 = 76–100%). The following phenophases were considered: floral buds, flowers at anthesis, and fruits (immature and mature).

Precipitation and temperature data for the study area (06°49'16''S, 35°03'44''W) were obtained from the Climatic Research Unit at the University of East Anglia (Harris & Jones 2020). Solar radiation data were obtained from the NASA website (NASA 2020).

Data analysis

The phenological response of the phenophases was classified according to Newstrom *et al.* (1994), and the synchrony index was calculated according to Augspurger (1983) using the 'flower' package (Wang 2015) of R software (R Development Core Team 2018).

Bencke & Morellato (2002) have recommended the combined use of two methods to estimate and represent species-level phenological data and accurately differentiate between activity and intensity peaks. Therefore, Fournier intensity index data were used to quantify the activity index (in terms of presence and absence). To test the null hypothesis that the phenophases were uniformly distributed through time, Rao's spacing test was used because it is less sensitive to multimodal data (Jammalamadaka & SenGupta 2001). After visual analysis of data distribution, seasonality was assessed by Rayleigh test (Morellato *et al*. 2000; Zar 2010) only for *A. germinans* that presented unimodal data. Circular statistics were performed by R software, using functions from the 'circular' package (Agostinelli & Lund 2017). Circular distributions were visualized using Oriana 4.02 software (Kovach 2011).

A stepwise multiple regression analysis was performed to determine whether the activity index data for each phenophase were related to the following abiotic factors: solar radiation, temperature, and rainfall (considering no time lag, a one-month time lag, and a two-month time lag). Final model selection was accomplished in R software through forward or backward elimination stepwise regression ($\alpha = 0.05$) that generated the lowest Akaike information criterion (AIC) score.

Results

During the study period, the most intense solar radiation was recorded from September to November (Fig. 1). The lowest and highest mean air temperatures were recorded in July (24.9 °C) and February (27.5 °C; Fig. 1), respectively. The lowest rainfall values were recorded from September to November, and the highest rainfall values were recorded from April to June (Fig. 1).

Avicennia germinans exhibited high intra-specific synchrony (Tab. 1). This species showed an annual (only one reproductive episode per year) and a seasonal response for floral buds, flowers at anthesis, and fruits (Fig. 2). The highest flowering

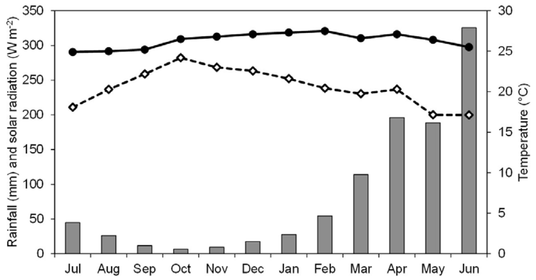

Figure 1 – Precipitation and temperature data (Harris & Jones 2020), and solar radiation data (NASA 2020) obtained for the study area in a mangrove in the Mamanguape River estuary (July/2016 to June/2017). Open diamonds = solar radiation; Closed circles = air temperature; Gray bars = rainfall.

Table 1 – Synchrony index and results of the circular statistical analysis for the activity index calculated for the reproductive phenophases of two mangrove species in the Mamanguape River estuary.

	Avicennia germinans			*Laguncularia racemosa*		
	Bud	**Flower**	**Fruit**	**Bud**	**Flower**	**Fruit**
Synchrony index (Z)	0.90	0.94	0.94	0.82	0.73	0.85
Mean angle	305.36°	311.26°	65.67°	-	-	-
Angular standard deviation	46.99°	49.92°	37.54°	-	-	
Mean date	6 Nov	12 Nov	7 Mar	-	-	-
Length of the mean vector (r)	0.71	0.68	0.81	-	-	-
Rao test (*P*)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Rayleigh test (*P*)	< 0.001	< 0.001	< 0.001	-	-	-

intensity occurred during the dry season, whereas fruiting was more intense in the transition period between the dry and rainy seasons (Fig. 2). The total duration of flowering was eight months and that of fruiting was six months; in both cases this duration is classified as extended (Newstrom *et al.* 1994). The phenophases showed non-uniform distribution (Tab. 1). The mean activity index for floral buds, flowers at anthesis, and fruits showed significant seasonality, with mean dates in November, November and March, respectively (Tab. 1; Fig. 3). Phenophases were associated with at least two of the abiotic variables, either in the month of their occurrence or in the previous months in *A. germinans* (Tab. 2). The floral bud and fruits were associated with all abiotic variables, whereas flowers at anthesis were associated with temperature and solar radiation.

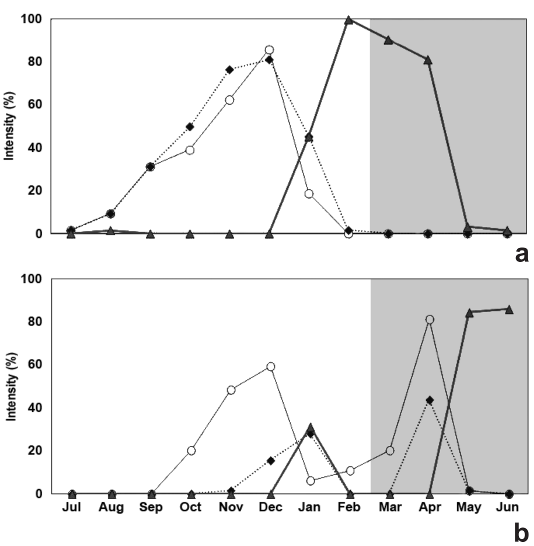

Figure 2 – a-b. Fournier intensity percentage for reproductive phenophases in a mangrove in the Mamanguape River estuary – a. of *Avicennia germinans*; b. of *Laguncularia racemosa*. Open circles = floral buds; Closed diamonds = flowers at anthesis; Gray triangles = fruits; the shaded area indicates the rainy season.

The synchrony values for *Laguncularia racemosa* were high, albeit smaller than those for *A. germinans* (Tab. 1). An annual phenological pattern for floral buds and a subannual pattern (two reproductive episodes per year) for flowers at anthesis and fruits were observed for *L. racemosa* (Fig. 2). Although flowering and fruiting occurred in both the rainy and dry seasons, the highest intensity was recorded in the rainy season. Floral buds were produced during eight months, which again is classified as a extended duration (Newstrom *et al.* 1994). Flowers in anthesis episodes were present for a period lasting between two and three months, and fruiting episodes lasted between one and two months. Although the reproductive phenophases did not exhibit seasonality, flowering and fruiting were concentrated in certain periods, indicating a non-uniform distribution of buds, flowers and fruits throughout the year (Tab. 1; Fig. 3). Phenophases were associated with at least one of the abiotic factors, either in the month of their occurrence or in the previous months in *L. racemosa* (Tab. 2). The floral bud and flowers at anthesis were associated with all abiotic factors, whereas fruits were associated with rainfall in the current month.

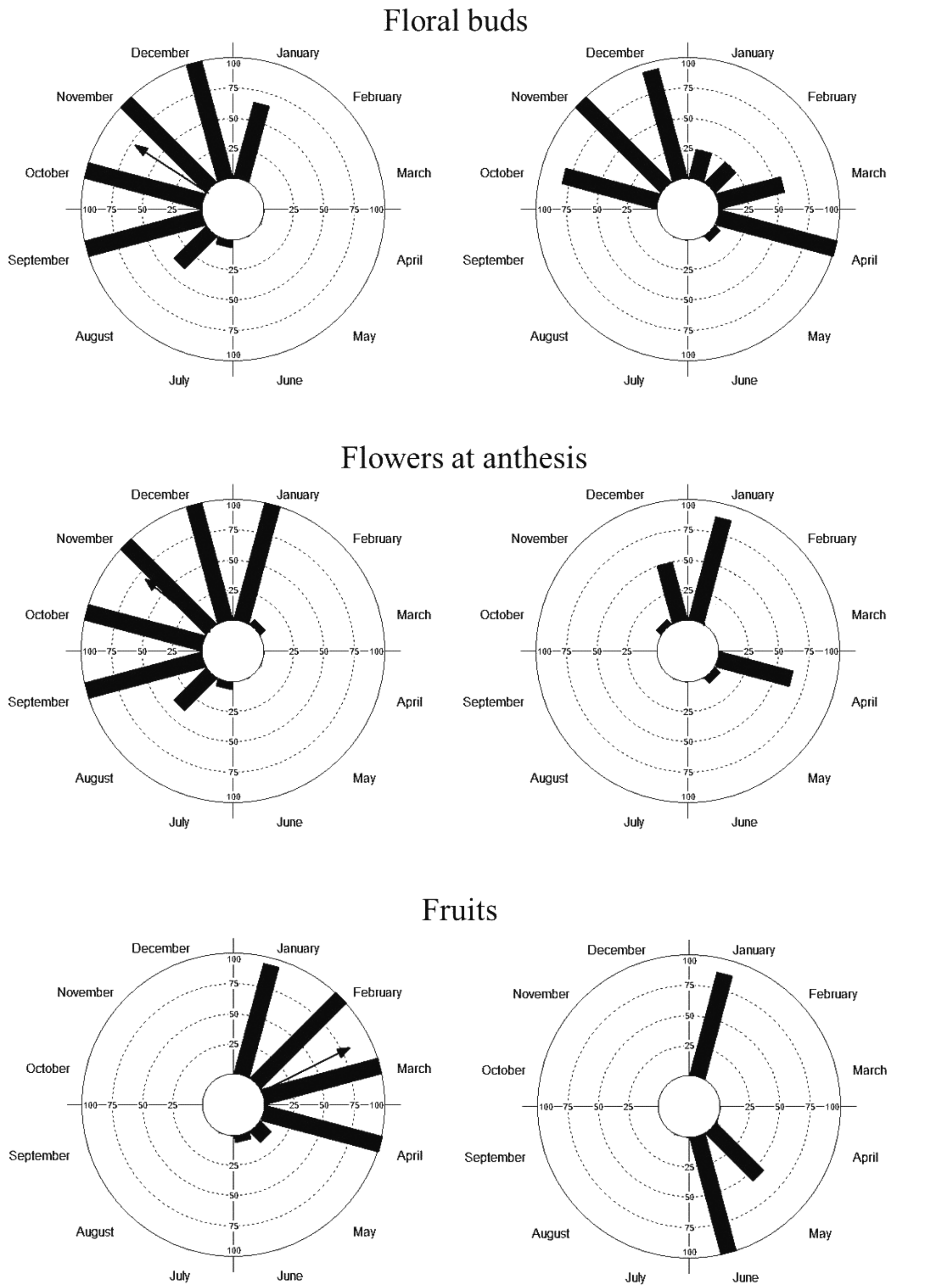

Figure 3 – Circular histograms of activity index of reproductive phenophases of *Avicennia germinans* (left) and *Laguncularia racemosa* (right) in a mangrove forest in the Mamanguape River estuary; arrow length reflects r value from 0 to 1. Arrow direction indicates mean date (mean angle); monthly observations were conducted from July 2016 to June 2017.

Table 2 – Models used to evaluate the association between abiotic factors and the reproductive phenophases of of *Avicennia germinans* and *Laguncularia racemosa* in a mangrove in the Mamanguape River estuary. Numbers after each variable refer to the time lag used in the analyses. AIC = Akaike information criterion; temp = mean temperature; rain = rainfall; rad = solar radiation.

Species / Phenophase	Full Model	AIC	Selected Model	AIC
Avicennia germinans				
Bud	bud ~ temp0+temp1+temp2+rain0+ rain1+rain2+ rad0+rad1+rad2	96.0	bud ~ temp0+temp1+temp2+rain1+ rain2+rad2	56.0
Flower	flo ~ temp0+temp1+temp2+rain0+ rain1+rain2+ rad0+rad1+rad2	117.8	flo ~ temp0+temp1+rad1+rad2	74.9
Fruit	fr ~ temp0+temp1+temp2+rain0+ rain1+rain2+ rad0+rad1+rad2	108.6	fr ~ temp0+temp1+temp2+rain0+ rain1+rad2	66.7
Laguncularia racemosa				
Bud	bud ~ temp0+temp1+temp2+rain0+ rain1+rain2+ rad0+rad1+rad2	124.0	bud ~ temp2+rain0+rain2+rad0+ rad1 +rad2	83.6
Flower	flo ~ temp0+temp1+temp2+rain0+ rain1+rain2+ rad0+rad1+rad2	118.6	flo ~ temp0+temp1+temp2+rain0+ rain2+ rad0+rad1	79.0
Fruit	fr ~ temp0+temp1+temp2+rain0+ rain1+rain2+ rad0+rad1+rad2	133.3	fr ~ rain0	85.2

Discussion

The results of this study showed that intraspecific synchrony was high for both species, though it was higher in *A. germinans* than in *L. racemosa*. In the case of flowering, this is important because pollinator attraction and cross-pollination intensify when individuals exhibit high synchrony during flowering (Augspurger 1983). High synchrony in flowering was observed for *A. schaueriana* populations in another mangrove in northeastern Brazil (Nadia *et al*. 2012) and for *A. germinans* in mangroves in the north and northeast of Brazil (Fernandes 1999; Matni 2007; Silva & Fernandes 2011; Rodrigues 2015), suggesting that high phenological synchrony is a common characteristic of this genus. Unlike the results of the present study, low (Nadia *et al*. 2012) or no (Fernandes 1999; Matni 2007) synchrony has been reported for flowering in *L. racemosa*.

An annual pattern (*sensu* Newstrom *et al*. 1994) was observed in the reproductive phenophases of *Avicennia germinans*, which is common in other Brazilian mangrove forests (Tab. 3). *Laguncularia racemosa* exhibited annual and subannual patterns for flowering (bud + flower) and fruiting, respectively. To confirm this pattern, monitoring should be carried out for at least two years, because other flowering patterns have been documented for this species (Tab. 4).

In general, *A. germinans* and *L. racemosa* showed similar associations to abiotic factors. Solar radiation, temperature and rainfall with a two-month lag triggered flowering in both species studied. At low latitudes, in the absence of a distinct day length signature, this result indicates an adaptation of tropical tree phenology to the annual course of solar radiation (Borchert *et al.* 2015).

The flowering of mangrove species has been associated with air temperature (Fernandes 1999; Kamruzzaman *et al*. 2013, 2016; Wang'ondu *et al*. 2013), as observed in the present study. Latitudinal trends have been observed for the flowering of *Avicennia marina* in Australian mangroves, because high air temperature was the determining factor stimulating this phenophase and the duration of the reproductive cycle of the species (Duke 1990). However, studies conducted in northeastern Brazil indicated that *L. racemosa* flowering is not associated with temperature (Nadia *et al.* 2012; Medeiros & Sampaio 2013).

Water deficiency with a two-month lag triggered the flowering of *A. germinans* and *L.*

Table 3 – Reproductive phenological patterns of *Avicennia germinans* in Brazilian mangrove forests. D = dry; R = rainy. [1] = Fernandes (1999); [2] = Matni (2007); [3] = Rodrigues (2015); [4] = Silva & Fernandes (2011); [5] = Gardunho (2009); [6] = Bernini *et al.* (2014); [7] = Bernini & Rezende (2010). Flowering = floral buds + flower at anthesis. Fruiting = mature and immature fruits.

Site / latitude	Methods	Flowering duration	Fruiting duration	Flowering	Fruiting	Period with greater intensity of flowers		Period with greater intensity of fruits	
		in the year (months)	in the year (months)	pattern	pattern	D	R	D	R
Amapá[1] 02°10'N	Semi-quantitative (Fernandes 1999)	8	9 to 11	Annual	Annual	●			●
Pará[2] 00°50'S	Semi-quantitative (Fernandes 1999)	5 to 7	1 to 4	Annual	Annual	●		●	
Pará[3] 00°50'S	Semi-quantitative (Fernandes 1999)	12	9 to 10	Continuous	Annual	●			●
Pará[4] 00°53'S	Semi-quantitative (Fernandes 1999)	11	11	Continuous	Continuous	●			●
Pará[5] 01°00'S	Semi-quantitative (Fernandes 1999)	9	8	Annual	Annual	●		●	
This study 06º49'S	Quantitative (Fournier 1974)	8	7	Annual	Annual	●			●
Rio de Janeiro[6] 21°17'S	Quantitative (collectors)	10	8 to 9	Annual	Annual		●		●
Rio de Janeiro[7] 21°36'S	Quantitative (collectors)	5 to 6	4 to 5	Annual	Annual		●		●

racemosa, showing that hormonal regulation can be an endogenous regulator of flowering (Sánchez-Nuñez & Mancera-Pineda 2011). Flowering was gradually induced in *A. germinans* by water deficit and it was more intense in the dry season, which coincides with the moment when there is a tendency to reduce interstitial salinity. This species has high photosynthetic water use efficiency (Lovelock & Feller 2003) and can maintain photosynthetic activity with high interstitial salinity, although with a reduced carbon gain (Sobrado 2006). Thus, during flowering, energy reservoirs or reallocated resources must be utilized to form flowers, with reduced vegetative growth (Sánches-Nuñez & Mancera-Pineda 2011). On the other hand, flowering was more intense during the rainy season in *L. racemosa*, as reported by several authors (Tab. 4). Unlike that of *A. germinans*, there is a greater intensity of *L. racemosa* flowering during the seasonal growth of the aerial part of the plant and during periods of increased water availability, which allows allocating more resources to flower development (Sánchez-Nuñez & Mancera-Pineda 2011).

Table 3 shows the phenological pattern of *A. germinans* in Brazilian mangrove forests, in which we verified the tendency for flowering during the dry season in low latitudes and in the rainy season in high latitudes. However, the small number of studies at low latitudes prevents the translation of these trends into a latitudinal pattern. On the other hand, in general, *L. racemosa* flowering occurs during the rainy season along the Brazilian coast (Tab. 4).

The species showed an association between fruiting and rainfall in this study. Higher fruiting intensity was observed for *L. racemosa* during the rainy season than during the dry season, as previously reported (Tab. 4). *Avicennia germinans*

Table 4 – Reproductive phenological patterns of *Laguncularia racemosa* in Brazilian mangrove forests. D = dry; R = rainy. [1] = Fernandes (1999); [2] = Matni (2007); [3] = Fernandes *et al.* (2005); [4] = Gardunho (2009); [5] = Medeiros & Sampaio (2013); [6] = Nadia *et al.* (2012); [7] = Bernini *et al.* (2014); [8] = Bernini & Rezende (2010); [9] = Rodrigues (2015); [10] = Cardoso *et al.* (2015); [11] = Adaime (1985); [12] = Lima (2012); [13] = Alvarenga (2015). Flowering = floral buds + flower at anthesis. Fruiting = mature and immature fruits.

Site / latitude	Methods	Flowering duration in the year (months)	Fruiting duration in the year (months)	Flowering pattern	Fruiting pattern	Period with greater intensity of flowers		Period with greater intensity of fruits	
						D	R	D	R
Amapá[1] 02°10'N	Semi-quantitative (Fernandez 1999)	9 to 12	9 to 12	Subannual	Subannual	●			●
Pará[2] 00°50'S	Semi-quantitative (Fernandez 1999)	1 to 5	2 to 9	Annual	Annual	●			●
Pará[3] 00°50'S	Semi-quantitative (Fernandez 1999)	11	12	Continuous	Continuous		●		●
Pará[4] 01°00'S	Semi-quantitative (Fernandez 1999)	12	12	Continuous	Continuous		●		●
Pernambuco[5] 07°47'S	Quantitative (Christensen 1978)	5	-	Annual	Annual		●	-	-
Pernambuco[6] 07°50'S	(Fournier 1974)	6 to 9	5 to 10	Subannual	Subannual		●		●
This study 06º49'S	Quantitative (Fournier 1974)	8	3	Annual	Subannual		●		●
Rio de Janeiro[7] 21°17'S	Quantitative (collectors)	3	2 to 4	Annual	Annual		●		●
Rio de Janeiro[8] 21°36'S	Quantitative (collectors)	4	4	Annual	Annual		●		●
Rio de Janeiro[9] 22° 42'S	Quantitative (Fournier 1974)	8	8 to 10	Annual	Annual		●		●
Rio de Janeiro[10] 23° 00'S	Quantitative (collectors)	-	2 to 6	-	Subannual	-	-		●
São Paulo[11] 25° 00'S	Quantitative (collectors)	3	7	Annual	Annual		●		●
Paraná[12] 25°29'S	Quantitative (Fournier 1974)	12	7	Continuous	Annual		●		●
Paraná[13] 25°49'S	Quantitative (Fournier 1974)	8	3	Annual	Annual		●		●

showed greater intensity of fruiting during the transition between dry and rainy seasons. Other studies have shown greater intensity during the rainy season (Tab. 4). Latitudinal patterns in fruit production have been described for 47 mangrove species, with significant association between fruiting and rainfall (Van der Stoken *et al*. 2017). As mangrove species are hydrocoric, the rainy season is favorable for fruit dispersion, survival, and seedling establishment (Duke *et al*. 1984).

The results of the present study of a degraded mangrove forest may be useful for restoration initiatives that require propagule collection for no-till or seedling production. We recommend that these propagules be collected when fruiting intensity is high, that is, mainly from February to May for *A. germinans* and from May to June for *L. racemosa*.

In conclusion, the present study demonstrated that *A. germinans* exhibits seasonal responses to floral buds, flowers at anthesis, and fruit and *L. racemosa* has no seasonal response. The results showed that the species exhibited different phenological responses, even though they were subjected to the same abiotic conditions.

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