Chapter 4
Reproductive Phenology of the Brazilian Mangrove Species

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4.1 Introduction

Phenology is the study of the occurrence of repetitive biological phenomena and their causes in terms of environmental factors as well as the interrelationship between phases of the same or different species (Lieth 1974). The phenological events studied in plants include vegetative phases (buds and leaf fall) and reproductive phases (flowering and fruiting).

Plant reproductive phenology is controlled by complex interactions between biotic and abiotic factors (Wolkovich et al. 2014). The biotic factors include interactions with pollinators, dispersers, and morphological and physiological adaptations (Van Schaik et al. 1993; Liebsch and Mikich 2009; Wolkovich et al. 2014), while abiotic factors include precipitation, air temperature, photoperiod, solar radiation, and soil water availability (Morellato et al. 2000; Engel and Martins 2005; Couralet et al. 2013; Wolkovich et al. 2014; Borchert et al. 2015). The reproductive patterns of tropical plants and their relationship with abiotic factors have been described for various ecosystems (Ballestrini et al. 2011; Nadia et al. 2012; Morellato et al. 2013; Rodríguez-Gallego and Navarro 2015; Ulsig et al. 2017).

The study of the reproductive phenology of plant species is fundamental to understanding the dynamics of ecosystems (Fournier 1974) since the periodicity and synchrony of phenological events influence the structure and functioning of

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communities (Williams et al. 1999; Encinas-Viso et al. 2012; Revilla et al. 2015). In addition, monitoring reproductive phenomena provides data on the quantity and quality of available wildlife resources (Bullock and Sollis-Magallanes 1990; Araújo et al. 2011), while also informing projects aiming at the recovery of degraded areas (Zamith and Scarano 2004; Garcia et al. 2009). Furthermore, phenological studies are currently being used to monitor climate change (Morellato 2008; Cleland et al. 2012) and can contribute to assessing and mitigating the consequences of land-use changes and other anthropogenic disturbances, such as fragmentation, fire, and invasive species (Morellato et al. 2010; Morellato et al. 2016).

Mangroves are highly ecologically important ecosystems (Adame et al. 2010; Mumby 2006; Donato et al. 2011) whose area has declined alarmingly in recent decades (Valiela et al. 2001; Giri et al. 2011; Hamilton and Casey 2016). The loss of mangrove forests has been caused by tourism, aquaculture, urban development, overexploitation of resources, agriculture, and industrialization (Alongi 2002), and the reminiscent mangroves remain under intense anthropogenic pressure, with an estimated global deforestation rate between 0.16% and 0.39% per year (Hamilton and Casey 2016) (see Chaps. 2 and 16).

Currently, mangroves are being affected by global climate changes that further aggravate anthropogenic pressures (Wong et al. 2014). Global changes in precipitation rates and air temperature as well as rising sea levels may modify reproductive phenology and reduce the production of flowers and fruits in addition to altering seed dispersal and seedling establishment (Alongi 2008; Ellison 2012; Van der Stocken et al. 2017). Thus, climate change is expected to have consequences for population dynamics and the biogeographical distribution of mangrove species (Perry and Mendelssohn 2009; Van der Stocken et al. 2017).

This chapter aims to assess the state-of-the-art research on reproductive phenology in mangroves in Brazil. We address methodological issues, describe patterns of flowering and fruiting, and highlight knowledge gaps on the phenology of mangrove species. The review was carried out by conducting a bibliographical survey of scientific journals and books as well as theses, dissertations, and monographs, since such references cover a large portion of the studies of the phenology of mangrove species in Brazil, namely, *Avicennia germinans* (L.) Stearn, *Avicennia schaueriana* Stapf & Leechm. ex Moldenke, *Laguncularia racemosa* (L.) Gaertn. f., *Rhizophora harrisonii* Leechman, *Rhizophora mangle* L., and *Rhizophora racemosa* G. F. Mayer.

4.2 Methodological Approaches

In Brazil, most studies of reproductive phenology monitor flowering (Fig. 4.1) and fruiting (Fig. 4.2), but the definition of phenophases varies according to the species. For *Rhizophora mangle*, for example, the recorded phenophases may be flower buds, flowers at anthesis, fruits, and propagules, while for *Avicennia schaueriana* and *Laguncularia racemosa*, they may be buds, flowers, and propagules (Nadia et al. 2012). Some authors also record immature and mature fruits (Matni 2007; Lima

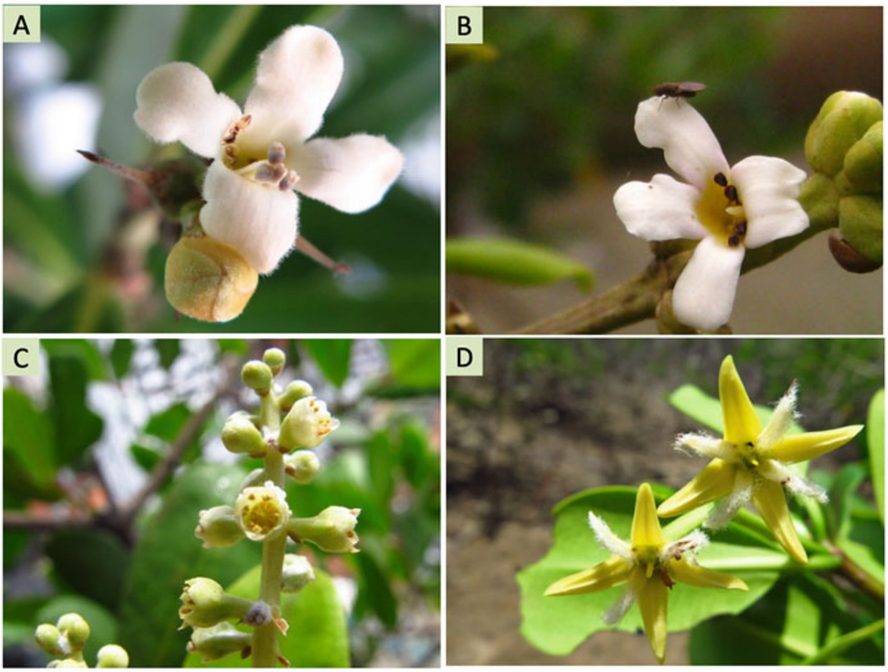

Fig. 4.1 Flowers of (**a**) *Avicennia germinans*, (**b**) *A. schaueriana*, (**c**) *Laguncularia racemosa*, and (**d**) *Rhizophora mangle*. (Photos: Clemente Coelho-Jr)

2012). The detailed monitoring of flowering (buds and flowers) and fruiting (immature fruits, mature fruits, and propagules) is useful to better plan recovery actions for degraded areas.

The research methodology can influence the analysis and interpretation of the phenological patterns, making it difficult to compare results among studies, so the choice of the evaluation method is of relevance (Bencke and Morellato 2002; D'Eça-Neves and Morellato 2004). A total count of flowers and fruits is virtually impossible for trees, so direct and indirect methods have been developed to monitor reproductive phenophases.

In Brazil, direct observation procedures for mangrove species include the semi-quantitative methods of canopy counting (Fernandes 1999) and Fournier intensity (Fournier 1974), in which the number of objects (e.g., flower buds or fruits) in different categories is recorded on an ordinal scale. Direct observation can be carried out by the quantitative method of branch counting (Christensen 1978), by which all the flowers or fruits on a branch are counted. Direct methods are faster than the indirect method (Stevenson et al. 1998; D'Eça-Neves and Morellato 2004).

The indirect method is conducted by quantifying the dry weight of phenophases, with the aid of litterfall collectors, which are baskets that come in different shapes and sizes. For mangrove species, the studies that have been carried out with collectors mainly emphasize the importance of phenological patterns in the

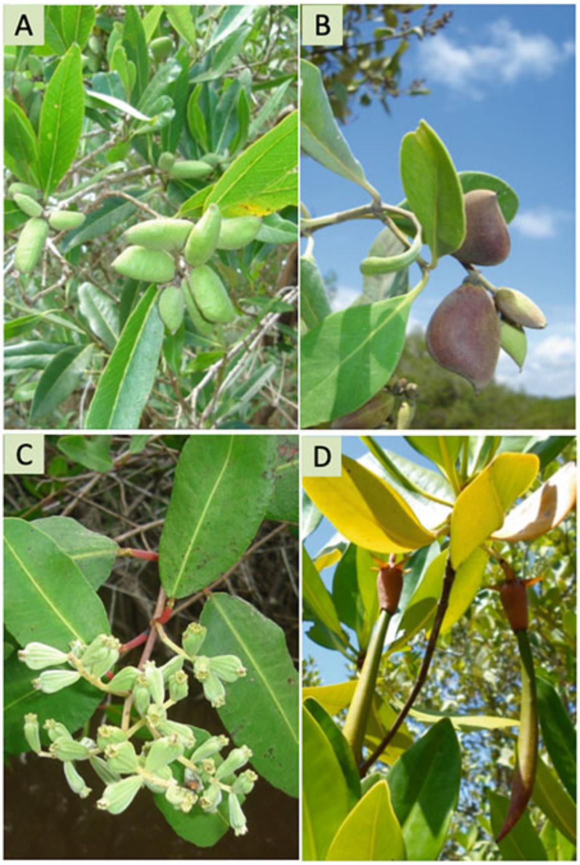

Fig. 4.2 Fruits of (**a**) *Avicennia germinans*, (**b**) *A. schaueriana*, (**c**) *Laguncularia racemosa*, and (**d**) *Rhizophora mangle*. (Photos: Elaine Bernini)

production of forest biomass. Such studies do not always separate reproductive structures into categories (flowers and fruits) and/or species. We found only one study (Mehlig 2006) that specifically used collectors to evaluate phenology in Brazil. However, studies that employed collectors to quantify primary production and that specified the occurring phenophases/mangrove species were also included in our data compilation.

Studies comparing direct and indirect observation methods in tropical forests have found different results. Morellato et al. (2010) reported differences in seasonal patterns, while Stevenson et al. (1998) reported similar seasonal patterns for both methods. Morellato et al. (2010) drew attention to the following deviations when estimating phenology using collectors: (1) species composition may vary between methods; (2) there is a time interval between the direct observation of a phenophase in a tree and the record of it in the collectors; and (3) there is sensitivity to local effects, such as the presence of large quantities of flowers and fruits of a certain species in the collectors or flowers or heavy fruits that overestimate production. As mangrove species exhibit significant differences in propagule weight, the evaluation of phenology using collectors should be avoided.

Fernandes et al. (2005) studied the reproductive phenology of *L. racemosa* through the direct methods of canopy and branch counting. The authors noted the difficulty of recording more than 100 items in higher trees using the canopy counting method. It is possible to quantify the absolute number of each item more easily using the branch counting method, but this is logistically more complicated in forests with very high trees. However, the results of the two methods showed a significant correlation with both the flower phenophase ($r = 0.94$, $p < 0.001$) and the fruit phenophase ($r = 0.93$, $p < 0.001$), indicating that the indirect method is efficient for monitoring and describing reproductive phenological patterns.

The Fournier intensity (1974) has been the most-used method for mangrove species in Brazil followed by canopy counting, branch counting, and collectors (see Tables 4.1, 4.2, 4.3 and 4.4). In the northern region of the country, the most used method is canopy counting, while the Fournier method (1974) is more common in the other regions.

Sample size may also influence the characterization of phenological patterns. Fournier et al. (1975) suggested a sample size of 10 individuals to analyze the phenology of tropical tree species, but Morellato et al. (2010) recommend at least 15 trees to better estimate the pattern of a sampled population. Considering the most-used evaluation methods in Brazilian mangrove forests (Fournier 1974; Fernandes 1999), the sample number was 15 or more trees in 70% and 10 trees in 30% of the surveys analyzed, indicating an adequate sample number.

The frequency of observations is another important aspect of phenological studies. Morellato et al. (2010) showed that larger sample numbers describe phenological patterns with increasing accuracy as the frequency of observations increases, while small samples lose information and accuracy. Thus, biweekly observations (i.e., every 15 days) provide reasonable accuracy regardless of sample size. For the studies analyzed here, only Mehlig (2006) and Bernini and Rezende (2010) made biweekly observations, while the other studies performed monthly observations (see Tables 4.1, 4.2, 4.3 and 4.4). This result can be partly attributed to a lack of financial resources and logistical issues but considering that the number of sampled individuals has been adequate in most studies, the monthly observation frequency would not represent a severe loss of information (Morellato et al. 2010) that might compromise the phenological characterization by the studies here presented.

Phenological patterns may vary over time due to climate variations and differential flower and fruit production, so long-term studies (three years or more) are recommended. For Brazilian mangroves, most of the data refer to one year of observation with sampling periods exceeding two years in rare cases (see Tables 4.1, 4.2, 4.3 and 4.4). The reasons for the short study duration can be the limitation of resources, as above, as well as a short period of time available to perform the monitoring and/or achieve the study objectives since most studies are linked to dissertations and theses. Monitoring for three or more annual cycles is mainly important for studies aimed at investigating climate change, as it will have

Table 4.1 Data on reproductive phenology of *Avicennia germinans* in Brazilian mangroves in different locations (coastal state and coordinates)

Location	Method and sample number	Periodicity and duration (months)	Flowering duration (months)	Fruiting duration (months)	Flowering pattern	Fruiting pattern	Period of highest flowering intensity				Period of highest fruiting intensity			
							D	R	DRT	RDT	D	R	DRT	RDT
Amapá[a] 02°10′ N	Semiquantitative[i] ($n = 50$)	Monthly (12)	8	9–11	Annual	Annual	•					•		
Pará[b] 00°50′ S	Semiquantitative[i] ($n = 15$)	Monthly (12)	5–7	1–4	Annual	Annual	•				•			
Pará[c] 00°50′ S	Semiquantitative[i] ($n = 20$)	Monthly (36)	12	9–10	Continuous	Annual	•					•		
Pará[d] 00°53′ S	Semiquantitative[i] ($n = 20$)	Monthly (12)	11	11	Continuous	Continuous	•					•		
Pará[e] 01°00′ S	Semiquantitative[i] ($n = 20$)	Monthly (12)	9	8	Annual	Annual	•				•			
Paraíba[f] 06°49′ S	Semiquantitative[j] ($n = 16$)	Monthly (12)	8	7	Annual	Annual	•					•		
Rio de Janeiro[g] 21°17′ S	Quantitative[k] ($n = 4$)	Monthly (12)	10	8–9	Annual	Annual		•				•		
Rio de Janeiro[h] 21°36′ S	Quantitative[k] ($n = 7$)	Biweekly (24)	5–6	4–5	Annual	Annual		•				•		

D dry, *R* rainy, *DRT* dry and rainy transition, *RDT* rainy and dry transition
[a]Fernandes (1999); [b]Matni (2007); [c]Rodrigues (2015); [d]Silva and Fernandes (2011); [e]Gardunho (2009); [f]Lage-Pinto et al. (unplublished data); [g]Bernini et al. (2014); [h]Bernini and Rezende (2010); [i]Fernandes (1999); [j]Fournier (1974); [k]Baskets. See Chap. 3, Maps: 1 – Amapá, 2 – Pará, 7 –Paraíba, 8 – Pernambuco, 13 – Rio de Janeiro, 14 – São Paulo, and 15 – Paraná

Table 4.2 Data on reproductive phenology of *Avicennia schaueriana* in Brazilian mangroves in different locations (coastal state and coordinates)

Location	Method and sample number	Periodicity and duration (months)	Flowering duration (months)	Fruiting duration (months)	Flowering pattern	Fruiting pattern	Period of highest flowering intensity				Period of highest fruiting intensity			
							D	R	DRT	RDT	D	R	DRT	RDT
Pernambuco[a] 07°47′S	Quantitative[h] ($n = 7$)	Monthly (12)	5	–	Annual	–	●							
Pernambuco[b] 07°50′S	Semiquantitative[i] ($n = 10$)	Monthly (48)	4–7	5–6	Annual	Annual	●				●			
Rio de Janeiro[c] 22°42′S	Semiquantitative[i] ($n = 20$)	Monthly (24)	10	9	Annual	Annual	●					●		
Rio de Janeiro[d] 23°00′S	Quantitative[j] ($n = 6$)	Monthly (36)	–	6–9	–	Annual						●		
São Paulo[e] 25°00′S	Quantitative[j] ($n = 5$)	Monthly (38)	8	4	Annual	Annual		●				●		
Paraná[f] 25°29′S	Semiquantitative[i] ($n = 10$)	Monthly (13)	13	12	Sub-continuous	Sub-continuous	●	●			●			
Paraná[f] 25°49′S	Semiquantitative[i] ($n = 10$)	Monthly (13)	13	12	Sub-continuous	Continuous	●	●			●			
Paraná[g] 25°49′S	Semiquantitative[i] ($n = 20$)	Monthly (12)	8	3	Sub-annual	Sub-annual	●	●				●		

D dry, *R* rainy, *DRT* dry and rainy transition, *RDT* rainy and dry transition
[a]Medeiros and Sampaio (2013); [b]Nadia et al. (2012); [c]Rodrigues (2015); [d]Cardoso et al. (2015); [e]Adaime (1985); [f]Lima (2012); [g]Alvarenga (2015); [h]Christensen (1978); [i]Fournier (1974); [j]Baskets

Table 4.3 Data on reproductive phenology of *Laguncularia racemosa* in Brazilian mangroves in different locations (coastal state and coordinates)

Location	Method and sample number	Periodicity and duration (months)	Flowering duration (months)	Fruiting duration (months)	Flowering pattern	Fruiting pattern	Period of highest flowering intensity				Period of highest fruiting intensity			
							D	R	DRT	RDT	D	R	DRT	RDT
Amapá[a] 02°10′N	Semiquantitative[p] ($n = 50$)	Monthly (12)	9–12	9–12	Sub-annual	Sub-annual	●					●		
Pará[b] 00°50′S	Semiquantitative[p] ($n = 15$)	Monthly (12)	1–5	2–9	Annual	Annual	●					●		
Pará[c] 00°50′S	Semiquantitative[p, q] ($n = 20$; $n = 5$)	Monthly (12)	11	12	Continuous	Continuous		●				●		
Pará[d] 01°00′S	Semiquantitative[p] ($n = 20$)	Monthly (12)	12	12	Continuous	Continuous		●				●		
Pernambuco[e] 07°47′S	Quantitative[r] ($n = 7$)	Monthly (12)	5	–	Annual	Annual		●						
Pernambuco[f] 07°50′S	Semiquantitative[p] ($n = 10$)	Monthly (48)	6–9	5–10	Sub-annual	Sub-annual		●				●		
Pernambuco[g] 08°43′S	Quantitative[s] ($n = 8$)	Monthly (12)	7	7	Annual	Annual		●				●		
Paraíba[h] 06°49′S	Semiquantitative[r] ($n = 16$)	Monthly (12)	8	3	Annual	Sub-annual		●				●		
Rio de Janeiro[i] 21°17′S	Quantitative[s] ($n = 4$)	Monthly (12)	3	2–4	Annual	Annual		●				●		
Rio de Janeiro[j] 21°36′S	Quantitative[s] ($n = 7$)	Biweekly (24)	4	4	Annual	Annual		●				●		
Rio de Janeiro[k]	Semiquantitative[r] ($n = 20$)	Monthly (24)	8	8–10	Annual	Annual		●				●		

22°42′S														
Rio de Janeiro[l] 23°00′S	Quantitative[s] ($n = 6$)	Monthly (36)	–	2–6	–	Sub-annual						●		
São Paulo[m] 25°00′S	Quantitative[s] ($n = 5$)	Monthly (38)	3	7	Annual	Annual		●				●		
Paraná[n] 25°29′S	Semiquantitative[r] ($n = 10$)	Monthly (13)	12	7	Sub-continuous	Annual	●	●				●		
Paraná[n] 25°49′S	Semiquantitative[r] ($n = 10$)	Monthly (13)	11	7	Sub-continuous	Annual	●	●				●		
Paraná[o] 25°49′S	Semiquantitative[r] ($n = 20$)	Monthly (12)	8	3	Annual	Annual		●				●		

D dry, *R* rainy, *DRT* dry and rainy transition, *RDT* rainy and dry transition

[a]Fernandes (1999); [b]Matni (2007); [c]Fernandes et al. (2005); [d]Gardunho (2009); [e]Medeiros and Sampaio (2013); [f]Nadia et al. (2012); [g]Longo (2009); [h]Lage-Pinto et al. (unplublished data); [i]Bernini et al. (2014); [j]Bernini and Rezende (2010); [k]Rodrigues (2015); [l]Cardoso et al. (2015); [m]Adaime (1985); [n]Lima (2012); [o]Alvarenga (2015); [p]Fernandes (1999); [q]Christensen (1978); [r]Fournier (1974); [s]Baskets. See Chap. 3, Maps: 1 – Amapá, 2 – Pará, 7 – Paraíba, 8 – Pernambuco, 13 – Rio de Janeiro, 14 – São Paulo, and 15 – Paraná

Table 4.4 Data on reproductive phenology of *Rhizophora mangle* in Brazilian mangroves in different locations (coastal state and coordinates)

Location	Method and sample number	Periodicity and duration (months)	Flowering duration (months)	Fruiting duration (months)	Flowering pattern	Fruiting pattern	Period of highest flowering intensity				Period of highest fruiting intensity			
							D	R	DRT	RDT	D	R	DRT	RDT
Amapá[a] 02°10′N	Semiquantitative[o] ($n = 50$)	Monthly (12)	12	12	Continuous	Continuous	•					•		
Pará[b] 00°50′S	Semiquantitative[o] ($n = 15$)	Monthly (12)	6–7	6–12	Annual	Annual	•				•			
Pará[c] 00°50′S	Semiquantitative[o] ($n = 20$)	Monthly (36)	12	12	Continuous	Continuous				•		•		
Pará[d] 00°52′S	Quantitative[p, q] ($n = 15$; $n = 14$)	Biweekly (24)	12	12	?	?				•		•		
Pernambuco[e] 07°47′S	Quantitative[p] ($n = 7$)	Monthly (12)	5	–	Annual	Annual			•					
Pernambuco[f] 07°50′S	Semiquantitative[r] ($n = 10$)	Monthly (48)	9–12	11–12	Annual	Continuous		•			•			
Pernambuco[g] 08°43′S	Quantitative[p] ($n = 8$)	Monthly (12)	8–12	8–12	Annual	Annual		•			•	•		
Rio de Janeiro[h] 21°17′S	Quantitative[p] ($n = 4$)	Monthly (12)	12	10–12	Continuous	Annual	•	•				•		
Rio de Janeiro[i] 21°36′S	Quantitative[p] ($n = 7$)	Biweekly (24)	7–8	6–11	Annual	Annual		•				•		
Rio de Janeiro[j] 22°42′S	Semiquantitative[r] ($n = 20$)	Monthly (24)	5–7	11	Annual	Continuous	•					•		
		Monthly (36)	–	10	–	Annual						•		

Rio de Janeiro[k] 23°00′S	Quantitative[p] ($n = 6$)													
São Paulo[l] 25°00′S	Quantitative[p] ($n = 5$)	Monthly (38)	5	11	Annual	Continuous				●		●		
Paraná[m] 25°29′S	Semiquantitative[r] ($n = 10$)	Monthly (13)	11	13	Sub-continuous	Sub-continuous	●	●			●	●		
Paraná[m] 25°49′S	Semiquantitative[r] ($n = 10$)	Monthly (13)	13	12	Sub-continuous	Sub-continuous	●	●			●	●		
Paraná[n] 25°49′S	Semiquantitative[r] ($n = 20$)	Monthly (12)	9	10	Annual	Annual		●				●		

D dry, *R* rainy, *DRT* dry and rainy transition, *RDT* rainy and dry transition

[a]Fernandes (1999); [b]Matni (2007); [c]Rodrigues (2005); [d]Mehlig (2006); [e]Medeiros and Sampaio (2013); [f]Nadia et al. (2012); [g]Longo (2009); [h]Bernini et al. (2014); [i]Bernini and Rezende (2010); [j]Rodrigues (2015); [k]Cardoso et al. (2015); [l]Adaime (1985); [m]Lima (2012); [n]Alvarenga (2015); [o]Fernandes (1999); [p] Baskets; [q] Christensen (1978); [r] Fournier (1974). See Chap. 3, Maps: 1 – Amapá, 2 – Pará, 7 – Paraíba, 8 – Pernambuco, 13 – Rio de Janeiro, 14 – São Paulo, and 15 – Paraná

long-term effects that may alter the phenological patterns of mangrove plants (Alongi 2008; Ellison 2012).

One variable that may change over time is the synchrony of reproductive phenophases. Synchrony refers to a simultaneous occurrence of a given phenophase between individuals and populations, but it has received little attention in phenological studies of mangrove species. In Brazil, synchrony has mainly been evaluated without the use of quantitative methods. Nadia et al. (2012) and Lage-Pinto et al. (2021) evaluated synchrony using the index proposed by Augspurger (1983). This synchrony index is a quantitative method that estimates the overlap in the flowering or fruiting period between individuals of the same species, but it does not consider the differences in the intensities of the phenophases. Freitas and Bolmgrem (2008) suggested an index that includes the total duration of the phenophase of an individual and the variation in the number of flowers and fruits within this interval. This index corrects the overestimation of synchrony when the measurement does not account for the differences in the intensity of the phenophase. The use of quantitative methods to evaluate the flowering and fruiting synchrony of mangrove species would facilitate data comparison, especially when long-term monitoring is required to evaluate phenological responses to climate change.

4.3 Phenological Patterns

Adaime (1985) was the first researcher to describe the flowering and fruiting phenological patterns of mangrove species in Brazil (São Paulo state), even though the focus was on the primary productivity of the ecosystem. Since then, studies of reproductive phenology have become more frequent but have been unevenly distributed along the Brazilian coast (Tables 4.1, 4.2, 4.3 and 4.4). This scenario reflects the distribution of both species and researchers.

In Brazil, the northern limit of the distribution of mangrove species is in Amapá State, and the southern boundary varies according to the species (Cintrón and Schaeffer-Novelli 1992) (see Chap. 1). From the northernmost portion of Brazil, *Rhizophora harrisonii* and *R. racemosa* occur until Maranhão State (Santos 1986), and *Avicennia germinans* occurs until Rio de Janeiro State (Maciel and Soffiati-Netto 1998). The state of Santa Catarina is the southern limit of occurrence of *A. schaueriana*, *L. racemosa*, and *R. mangle* (Cintrón-Molero and Schaeffer-Novelli 1981, 1992) (see Chap. 3, Maps).

Mangroves in the westmost part of the Amazonian Equatorial Coast (Amapá and Pará states) (see Chap. 1) are the subject of most of the studies since they have been the focus of a research group that aims to determine the reproductive phenological patterns of mangroves in that region (Fernandes 2016). However, there continues to be a lack of information on the phenology of the mangroves in Maranhão State, at the eastmost part of the coastal segment. Concerning the other studied mangrove areas in the country, the states of Pernambuco, Rio de Janeiro, and Paraná are the ones presenting more data on flowering and fruiting (Tables 4.1, 4.2, 4.3 and 4.4).

In terms of species, most of the data correspond to *L. racemosa* and *R. mangle*, reflecting their wider distributions, but there are no records for several Brazilian states. Despite the wide geographic distribution of *A. schaueriana*, the number of studies on this species is relatively low. There are fewer studies of *A. germinans*, *R. harrisonii*, and *R. racemosa*, reflecting the smaller biogeographic range of these species in Brazil.

The reproductive phenology data of the typical mangrove species in Brazil are summarized in Tables 4.1, 4.2, 4.3 and 4.4. The frequency of the phenological patterns was classified according to Newstrom et al. (1994). The phenological patterns of *R. harrisonii* and *R. racemosa* are described throughout the text, but *Conocarpus erectus* was not included in this chapter, because, according to Lugo (1998), this species is erroneously listed as a typical mangrove species as it can tolerate salt but not flooding.

Avicennia germinans presents marked seasonality in its formation of flowers and fruits, whose pattern is mainly annual (Table 4.1). According to 75% of the studies analyzed, the presence of flowers and fruits extends for eight or more months of the year. Flowering shows a tendency toward greater intensity during the dry season, and the fruiting peak mainly occurs during the rainy season. *Avicenna schaueriana* exhibits a seasonal pattern and is mainly characterized by the annual pattern (Table 4.2). Flower production is typically highest during the dry season and was recorded as occurring over eight or more months of the year in 71% of the studies. Fruiting may occur in the dry or rainy season, but the duration of this phenomenon varies widely throughout the year along the Brazilian coast (3–12 months).

Flowering and fruiting in *L. racemosa* show mainly annual patterns, being characterized as seasonal or not (Table 4.3). Reproductive phenophases exhibit peaks in the rainy season. In most studies, flowering occurs in more than seven months, while fruiting occurs in less than eight months throughout the year.

Rhizophora mangle exhibits continuous or annual patterns for flowering and fruiting (Table 4.4). Peak flower production mainly occurs during the rainy season but can also occur in the dry season, in the transition between the dry and rainy seasons, or the transition between the rainy and dry seasons. Fruiting shows greater intensity during the rainy season. *Rhizophora harrisonii* and *R. racemosa* exhibit phenological patterns like those of *R. mangle*. In Amapá State, *R. harrisonii* presented continuous flowering and fruiting throughout the year, but flowering is more intense during the transition from the dry to the rainy season and fruiting is more intense during the rainy season (Fernandes 1999). Similar results were recorded for *R. harrisonii* and *R. racemosa* in Pará State, but the flowering peak occurred in the rainy season (Gardunho 2009).

While the reproductive phenophases of mangrove species are more intense during the dry or rainy seasons, significant correlations with precipitation may be weak or absent (Fernandes 1999; Matni 2007; Bernini and Rezende 2010; Nadia et al. 2012). Most studies have related flowering and fruiting with precipitation and air temperature, but the intensity of solar radiation, photoperiod, relative humidity, evapotranspiration, and interstitial salinity also play important roles in the reproductive phenology of mangrove species (Nadia et al. 2012; Alvarenga 2015; Cardoso et al. 2015; Rodrigues 2015; Lage-Pinto et al. 2021).

Studies conducted at different latitudes show different results. For example, Alvarenga (2015) showed that variations in interstitial salinity promote marked seasonality in reproductive phenophases in a mangrove in Paraná State, while Matni (2007) did not find an effect of salinity on the flowering and fruiting of the mangrove species in Pará State. Bernini and Rezende (2010), who studied a mangrove in Rio de Janeiro State, and Lima (2012), who evaluated a mangrove in Paraná State, demonstrated that the flowering of *L. racemosa* and *R. mangle* mangroves was positively correlated with mean air temperature, but Nadia et al. (2012) did not find such a correlation in a mangrove in Pernambuco State. The flowering of *A. schaueriana* was significantly correlated with photoperiod in Pernambuco State (Nadia et al. 2012), but no correlation was recorded in Paraná State (Lima 2012). The phenological records of Adaime (1985) showed the seasonal influence of low temperatures on flower and fruit formation in the three mangrove species that are typical of the Cananéia region (São Paulo State). On the other hand, Fernandes (1999) found no significant relationship between flowering and abiotic factors and suggested that endogenous factors are responsible for stimulating the formation of mangrove species in Pará State.

Duke (1990) found latitudinal trends in the flowering and fructification of *Avicennia marina* Vierh in Australian mangroves, where the duration of each phenophase increased with higher latitudes. The air temperature was the main factor responsible for stimulating the reproductive cycle, playing a fundamental role in flower formation. Van der Stocken et al. (2017) found clear latitudinal patterns in the release of the fruits and propagules of 47 species of mangroves in the northern and southern hemispheres, with significant positive correlations with precipitation. The authors observed that the propagules/fruits fall from the trees during most of the year without pronounced production peaks in the equatorial zone, but at higher latitudes, the release of propagules is variable and significantly correlated with air temperature.

In general, as mangrove species exhibited a lot of variation in phenological patterns (Tables 4.1, 4.2, 4.3 and 4.4), it is not possible to establish a latitudinal pattern related to abiotic variables. However, phenological data on the species are insufficient to establish a general pattern for the Brazilian coast.

Nadia et al. (2012) showed that biotic factors also shape phenology, as they observed that mangrove species that share the same pollinators present distinct flowering strategies, but the fruiting pattern is similar among species with the same dispersal syndrome. These authors also found that precipitation, air temperature, and day length play an important role in the formation of flowers and fruits. Thus, the reproductive phenological patterns of mangrove species represent a complex response to abiotic and biotic factors. However, the results of the studies remain unclear, so further research on the correlations with these factors is needed to better understand the phenological patterns of Brazilian mangrove species since the climatic variables vary widely along the coast.

Another biotic factor that has been related to reproductive phenology is the forest structure. Silva and Fernandes (2011) evaluated the influence of structural characteristics (height, density, and basal area) on the reproductive phenology of *A. germinans* in Pará State. The authors concluded that the structural attributes do not affect the reproductive phenology of this species, because the phenological events were synchronized, in both quantity and periodicity, in forests with distinct structural characteristics.

Regarding the timing of reproductive phenological phases, some studies have indicated flowering synchrony in populations of *A. germinans* (Fernandes 1999; Rodrigues 2005; Matni 2007; Silva and Fernandes 2011; Lage-Pinto et al. 2021), whereas asynchrony in fruit production is more common in populations of this species (Fernandes 1999; Matni 2007). In *A. schaueriana*, high intraspecific synchrony was observed in flower and fruit production (Nadia et al. 2012), but the reproductive phenophases show lack of synchrony (Fernandes 1999; Matni 2007) or low synchrony in *L. racemosa* (Nadia et al. 2012). In *R. mangle*, synchrony has not been analyzed, because this species exhibits continuous production throughout the year (Nadia et al. 2012) or has been assessed at the peak of flower or fruit production (Rodrigues 2005; Matni 2007), which indicated a lack of synchrony between populations.

4.4 Final Remarks

Direct observation methods have been used mostly to evaluate the reproductive phenology of mangrove species in Brazil. The number of individuals sampled and the frequency of observations of reproductive phenophases have been adequate in most studies, but long-term studies (more than three years) are scarce.

Further studies on reproductive phenology are needed, mainly for *A. germinans* and *A. schaueriana*. There was no record of studies to evaluate the effects of climate change on the reproductive phenology of mangrove species. Therefore, long-term studies are needed and could be made possible through collaboration among scientists who simultaneously collect data along the Brazilian coast. The information may contribute to understanding the responses of mangrove species to climate changes and establishing the reproductive phenological patterns of Brazilian mangrove forests. In addition, the inclusion of a synchrony index would facilitate data comparison.

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