Acta Botanica Brasilica 27(1): 195-204. 2013.

Phenological synchrony and seasonality of understory Rubiaceae in the Atlantic Forest, Bahia, Brazil

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Submitted: 9 October, 2012. Accepted: 23 November, 2012

ABSTRACT

In tropical forests with low seasonality, climatic variables generally exert a weak influence on the phenology of species. The seasonality of phenophases in closely related taxa can be controlled by phylogenetic constraints in such environments. In this study, our aim was to describe the phenology of Rubiaceae in the understory of the Atlantic Forest in the southern part of Bahia, Brazil, as well as to evaluate the seasonality and phenological synchrony of this family. For two years, we observed 90 individuals belonging to 13 species, in an area of 0.2 ha. Leaf flushing and leaf fall did not demonstrate any seasonality, were continuous for most species and correlated with few of the climatic variables. Flowering was seasonal and correlated positively with all climatic variables. Species exhibited seasonality for this phenophase with high flowering overlap among species of *Psychotria*, indicating an aggregated pattern for this genus. Fruiting was also seasonal and correlated with all the climatic variables, unripe fruit development peaking at the beginning of the season during which humidity is highest and fruit ripening peaking in the season during which humidity is slightly lower. The vegetative and flowering patterns observed in the study area are commonly seen in other tropical forests. The reproductive seasonality of this family can facilitate the attraction of biotic agents, as postulated in the facilitation hypothesis. Our results demonstrate that climatic variables influenced the phenological patterns observed here, although the high reproductive seasonality and interspecific synchrony, especially in congeneric species, raises the possibility that phylogenetic proximity plays a role in the pattern of the family Rubiaceae.

Key words: leaf flushing, phenology, flowering, fruiting, *Psychotria*

Introduction

Phenological studies in neotropical environments have traditionally been conducted in forests with a well-defined dry season (Frankie *et al.* 1974; Morellato *et al.* 1989), where changes in climatic variables directly or indirectly influence the phenological patterns of the community and synchronize events in a more favorable period of the year (Frankie *et al.* 1974; Rathcke & Lacey 1985). Subsequent studies indicate that plant communities exhibit phenological seasonality even in tropical forests without seasonality (Morellato *et al.* 2000; Zimmerman *et al.* 2007). Among the main factors that affect this pattern are abiotic factors, such as day length, precipitation and temperature (Hilty 1980; Wright & van Schaik 1994; Morellato *et al.* 2000; Borchert *et al.* 2005), as well as biotic factors, such as the interactions with herbivores, pollinators, and seed dispersers/predators (Rathcke & Lacey 1985; van Schaik *et al.* 1993). However, even in a low seasonal climate, forest stratification can result in different levels of influence of these factors among the strata (Marques *et al.* 2004). In the forest understory, specifically, among the abiotic factors, luminosity is usually the factor that exerts the strongest limiting effect on the phenology (Pearcy 1983; Williams-Linera 2003; Kudo *et al.* 2008).

Similar phenological patterns among related species can indicate a non-adaptive influence in their phenology, and phylogenetic constraints might be the main factor responsible for this similarity (Borchert 1983; Kochmer & Handel 1986; Wright & Calderón 1995; Staggemeier *et al.* 2010). Especially in congeneric plants, this phylogenetic constraint might result in an aggregate phenological pattern, which is considered a strategy that is favorable to plants because it increases the probability of pollination and seed or fruit dispersion (Poulin *et al.* 1999; Staggemeier *et al.* 2010), playing an essential role in species reproductive success (van Schaik *et al.* 1993). For example, studies involving species of

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[1] Based on the Master's dissertation of the first Author

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Piper and *Psychotria* indicate high interspecific synchrony of the fruiting events, indicating that an overlap in resource availability can act as a facilitating factor in the behavior of dispersers (Poulin *et al.* 1999; Thies & Kalko 2004). In contrast, synchrony tends to create competition between species, which could trigger a mechanism to avoid competition, such as the temporal segregation of phenophases (Wright & Calderón 1995; Günter *et al.* 2008).

Among vascular plant families in the understory of neotropical forests, Rubiaceae shows one of the highest levels of species richness (Gentry & Emmons 1987), and exhibits high representativeness in phenological studies involving the shrub community in such environments (Opler *et al.* 1980; Koptur *et al.* 1988). Studies carried out by San Martin-Gajardo & Morellato (2003a; 2003b) provided important information on the reproductive events in Rubiaceae in the Atlantic Forest in the state of São Paulo, Brazil, indicating interspecific differences in phenological behavior and low to medium values of interspecific synchrony. However, this is a natural group with evident variation in the geographical distribution of its species and consequent changes in the structure of the community along the Brazilian coast. Therefore, studies of different areas and species are needed in order to expand the discussion regarding the seasonality and synchrony that supposedly occur in the phenological events in this family.

Most phenological studies of the Atlantic Forest have been carried out in the southern and southeastern regions of Brazil, in areas of rain forest (Jackson 1978; Morellato *et al.* 2000; Talora & Morellato 2000; Bencke & Morellato 2002), seasonal semideciduous forest (Morellato *et al.* 1989; Morellato & Leitão-Filho 1992; Mikich & Silva 2001) and *restinga* (coastal woodland; Marques & Oliveira 2004; Marchioretto *et al.* 2007; Staggemeier *et al.* 2010). In the northeastern region, most studies have been conducted in areas of intense climatic seasonality (Funch *et al.* 2002; Locatelli & Machado 2004; Medeiros *et al.* 2007). For the Atlantic Forest *sensu stricto* in this region, the only available studies have been carried out in the southern part of Bahia, the objects of study ranging from tree populations to communities of tree species in submontane forests (Mori *et al.* 1982; Pessoa 2008; Santos 2011; Pessoa *et al.* 2012). However, there have been no studies evaluating the shrub component of the community in this region.

In the present study, impelled by the lack of phenological studies of the shrub community in the northeastern region of Brazil, together with the interest in natural groups with high species richness in the Atlantic domain, we analyzed the vegetative and reproductive phenology of Rubiaceae species in the understory of montane Atlantic Forest in the southern part of Bahia. Our objectives were: a) to describe the vegetative and reproductive phenological patterns of the family Rubiaceae; b) to correlate phenology with climatic variables; c) to test the degree of seasonality at the family and species levels and d) to determine the degree of overlap between individual species pairs. We expected that related species occurring in the same forest stratum would exhibit similar phenological patterns, with aggregate flowering and fruiting (Kochmer & Handel 1986). Because we studied a tropical forest with low seasonality, we also expected the environmental variables at the study site to exert less influence on the phenological behavior of Rubiaceae, such behavior being defined by the endogenous pattern of the various species (San Martin-Gajardo & Morellato 2003a).

Material and methods

Study Site

The study was carried out at the Serra Bonita Private Reserve (SBPR), part of the Serra Bonita mountain complex (15°22'50" to 15°24'16"S; 39°33'12" to 39°34'40"W), with a total of 7500 ha and located between the cities of Camacan and Pau Brasil, southern part of Bahia (Fig. 1). The SBPR comprises approximately 2000 ha, at altitudes ranging from 230 m to 1080 m.

According to the Köppen climate classification system, the climate of the region is type Af, which is characterized as humid tropical, with no dry season (Peel *et al.* 2007) and annual precipitation of 1500-1800 mm, evenly distributed through the year (Roeder 1975). Climatic data obtained from the CEPLAC (Comissão Executiva do Plano da Lavoura Cacaueira), collected between 2000 and 2010, indicate mean monthly precipitation of 100.5 mm (Camacan Station) and a mean monthly temperature of approximately 24.5°C (Ilhéus Station; Fig. 2). In the area of highest altitude within the SBPR (900 m), the climatic data were collected for only ten months between the years of 2009 and 2010 (Iuri Dias, personal communication), thus restricting the use of those data in this study. At the study site, two seasons can be defined: one (from November to April) during which temperatures are higher and precipitation is heavier, resulting in a wettest season; and one (from May to October) during which temperatures are lower and precipitation is somewhat lighter, resulting in a less wet season. At a latitude of 15°, the days are longest from December to February and shortest from June to August, with an annual variation of approximately 90 min (data obtained from: www.usno.navy.mil).

Throughout the mountain complex within which the SBPR is located, there is a predominance of fragments of montane rain forest, comprising areas in which, despite varying degrees of conservation, there is a high level of vascular plant richness (Amorim *et al.* 2009; Matos *et al.* 2010; Rocha & Amorim 2012). In a study of the structure of the SBPR community, high heterogeneity of woody species was detected, and the differences observed within the altitudinal gradient were strongly influenced by the families Fabaceae, Melastomataceae and Rubiaceae (Rocha & Amorim 2012). Among the vascular plant families in the area, Rubiaceae is second only to Orchidaceae in terms of species richness.

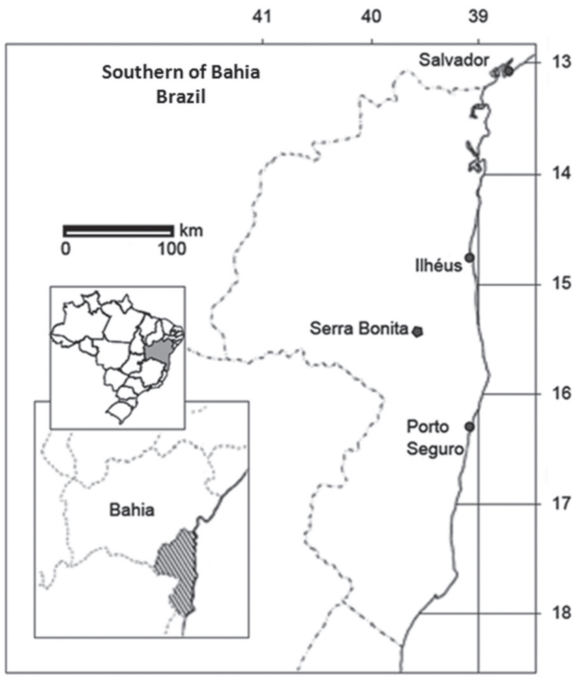

Figure 1. Geographical location of the Serra Bonita Private Reserve, Bahia, Brazil. Source: Adapted from Amorim *et al.* (2009).

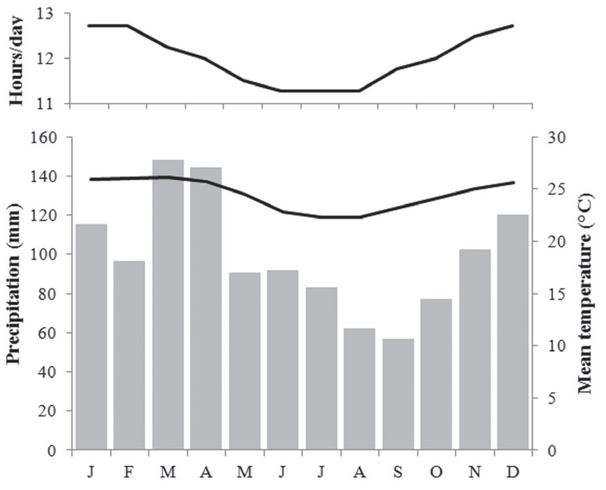

Figure 2. Climatic data for the period from 2000 to 2010 for the region of Camacan, Bahia, Brazil.
Source: Executive Commission on Cocoa Crop Plans for the State of Bahia—Camacan Station (for precipitation data) and Ilhéus Station (for temperature data).

Of the 58 Rubiaceae species sampled in the area by Rocha *et al.* (unpublished data), eight represented new records for northeastern Brazil. In addition to high representativeness in the overstory, Rubiaceae also had the largest number of species in the understory, followed by Piperaceae and Melastomataceae.

Species observation

To sample the Rubiaceae species, we selected a fragment of mature forest at approximately 900 m of altitude and used some of the plots of a study on the woody community for the sampling design, in a total of 0,2 ha (Rocha & Amorim 2012). We used the method proposed by Gentry (1982), in which each of the plots (n = 2) consists of 10 parallel subplots of 50 × 2 m, spaced at 20-m intervals. All Rubiaceae individuals between 1.3 m and 8 m in height (here defined as understory species) were sampled and tagged. Juveniles of overstory species were excluded from the sampling. Initially, 18 Rubiaceae species were observed in the understory in the SBPR, of which five were later classified as juveniles of overstory species and removed from the analyses (*Amaioua intermedia* Mart., *Bathysa cuspidata* (A. St.-Hil.) Hook.f. ex K. Schum., *B. mendoncae* K. Schum., *Psychotria mapourioides* DC. and *P. pleiocephala* Müll. Arg.). Therefore, we sampled a total of 90 individuals belonging to 13 species. Voucher material was deposited at the CEPEC herbarium.

The phenological observations (n = 24) were conducted monthly between March 2010 and February 2012. We used the semi-quantitative method proposed by Fournier (1974), scoring each phenophase on a scale of 0 to 4, by the magnitude of the event: 0 = no events; 1 = 1-25%; 2 = 26-50%; 3 = 51-75%; and 4 = 76-100%. We observed the vegetative phenophases (leaf flushing and leaf fall) and the reproductive phenophases, including flowering (flower buds and anthesis) and fruiting (unripe and ripe fruits).

Data analysis

All species were categorized according to the duration and periodicity of the vegetative and reproductive events using the system proposed by Newstrom *et al.* (1994). The vegetative events, when occurring continuously, were classified as regular (when individuals contributed jointly) and irregular (when individuals contributed randomly). Because the reproductive events were observed on an annual basis for all species, those with a duration of less than five months were classified as short, whereas those with a duration of five months or longer were classified as extended. We used the proportion of individuals and the Fournier proportion, respectively, to calculate the indices of species activity and intensity for each phenophase, on a month-by-month basis:

$$\%\,Individuals=\frac{\sum Individuals}{n}\cdot 100 \quad \%\,Fournier=\frac{\sum Fournier}{4\cdot n}\cdot 100$$

The activity and intensity indices did not differ over the course of the study period, and the former was used in order to describe the phenological patterns of Rubiaceae. To determine whether the species presented a longer response time to the variables, as tested by Morellato *et al.* (2000) in Atlantic Forest fragments with low climatic seasonality, we applied the Spearman correlation (r_s) in comparing the activity index for each phenophase of the family with the abiotic factors (day length, precipitation and mean temperature) present during the last three months before the phenological event.

To test the degree of seasonality of the phenological events in Rubiaceae, we performed the Rayleigh testof circular statistics analysis using the software Oriana, version 4.0 (see Morellato *et al.* 2000; 2010 for details). In the analysis of the reproductive events, we used the variables beginning of event and frequency of events, converting their values from dates to angles that represent the months of the year, from January (15°) to December (345°), at intervals of 30° for each month. Because the vegetative phenophases occurred through the year, with little variation, we opted not to use this test for their events. When seasonality was confirmed ($p<0.05$), we obtained the vector r, used as a measure of the degree of seasonality and synchrony, and also the mean angle and mean date of the phenological events. To test the degree of interspecific seasonality, we used the frequency of reproductive events only of the species with at least five individuals. To compare the significantly seasonal pairs of species, we used the Watson-Williams test (F).

Results

Vegetative phenophases

Leaf flushing and leaf fall were continuous for the majority of species observed (Tab. 1), with at least one of the individuals displaying the phenophases through the study. Species with annual pattern exhibited leaf flushing with a maximum duration of three months, whereas *P. nemorosa* was the only species with five months. The peak of leaf production occurred between September and October (in the transition between the two seasons, at the equinox; Fig. 3A), with a maximum of 92.3% of species in this phenophase during the two years studied. Leaf fall occurred irregularly, without peaks (Fig. 3B), with a maximum of 84.6% of species in October 2010. In November 2011, period of increased precipitation and longer day length, there was an acute decrease in leaf fall, only 34.7% of individuals participating in the event. All species were classified as evergreen, except for *Randia armata*, which was classified as deciduous, because 66.7% of its individuals shed their leaves completely at some point during of the year, albeit asynchronously. Leaf flushing correlated negatively with precipitation and day length, whereas leaf fall correlated positively with precipitation only (Tab. 2).

Reproductive phenophases

The only flowering strategy observed was annual (Tab. 1), with a mean duration of 2.5 ± 0.9 months for flower buds and 1.6 ± 0.8 months for anthesis. Flowering was concentrated in the wettest season, flower buds peaking in December 2010 and January 2012 (observed in 69.2% and 61.5% of species, respectively; Fig. 3C) and anthesis in January for both years (observed in 76.9% and 53.8% of species, respectively; Fig. 3D). Flower buds and anthesis both correlated positively with mean temperature and day length, exhibiting the strongest correlation with the data for the current month (Tab. 2). Flower buds correlated negatively with precipitation data for the month three months prior to the event, whereas anthesis correlated positively with precipitation data for the current month.

Fruiting occurred in all months during the study, with evident peaks for unripe fruits from March to May, at the end of the wettest season (maximum of 53.8% of species in 2010 and 69.2% in 2011; Fig. 3E), and for ripe fruits from June to August, during the less wet season (maximum of 46% of species in 2010 and 53.8% in 2011; Fig. 3F). The mean duration per individual was of 5.7 ± 2.1 months for unripe fruits and 2.7 ± 1.1 months for ripe fruits. Only four species did not exhibit extended fruiting (Tab. 1). Unripe fruits correlated positively with the three climatic variables, exhibiting the strongest correlation with the data for the three months prior to the event; whereas ripe fruits correlated negatively with those same variables, exhibiting the strongest correlation with the data for the current month (Tab. 2).

Seasonality

Rubiaceae exhibited a seasonal pattern for the beginning and frequency of the flowering and fruiting events, with nearly one month of difference between the initiation of flower buds and the onset of anthesis, and more than five months between the beginning of unripe fruits and the beginning of ripe fruits (Tab. 3). The phenophases were highly seasonal for all species, except for the fruit production of *Chomelia pubescens* (Tab. 4).

Interspecific synchrony

For all phenophases, the majority of the species studied here differed significantly, indicating that there are interspecific differences in the period of occurrence of the phenophases, especially for the non-congeneric species, as evidenced by the high values of F (Tab. 5). Conversely, the highest interspecific synchrony, here indicated by the absence of significant differences between the mean angles, occurred between pairs of species of the same genus. For example, there were only two species pairs, both from the genus *Psychotria*, that did not exhibit significant differences for anthesis. However, none of the *Psychotria* species, except for *P. suterella*, exhibited differences for flower buds and ripe fruits. In addition to the aforementioned pairs of species, *Chomelia pubescens* and *P. suterella* did not differ significantly in terms of unripe fruit development.

Discussion

Vegetative phenological patterns

Leaf flushing occurring through the year, as we observed for most of the Rubiaceae species in the SBPR, is common in

Table 1. Phenology of 13 Rubiaceae species in the understory of a montane rain forest in the southern part of Bahia, Brazil.

Species	n	Flowering	Fruiting	Leaf flushing	Leaf fall
Chomelia pubescens Cham. & Schltdl.	13	extended	extended	c. regular	c. regular
Coussarea contracta Müll. Arg.	1	short	extended	annual	annual
Faramea martiana Müll. Arg.	6	short	short	annual	annual
Faramea multiflora A. Rich. ex DC.	2	short	short	c. irregular	c. irregular
Margaritopsis chaenotricha (DC.) C.M. Taylor	8	short	extended	annual	c. irregular
Psychotria cupularis Müll. Arg.	15	short	extended	c. irregular	c. irregular
Psychotria hoffmannseggiana (Willd. Ex. Roem. & Schult.) Müll. Arg.	3	short	*	annual	annual
Psychotria minutiflora Müll. Arg.	8	short	extended	c. irregular	c. irregular
Psychotria nemorosa Gardner	2	short	short	annual	c. regular
Psychotria platypoda DC.	1	short	extended	*	*
Psychotria schlechtendaliana (Müll. Arg.) Müll. Arg.	10	short	extended	c. irregular	c. irregular
Psychotria suterella Müll. Arg.	12	short	extended	c. regular	c. regular
Randia armata (Sw.) DC.	9	short	short	c. irregular	c. irregular

n – number of individuals observed; c. regular – continuous regular pattern; c. irregular – continuous irregular pattern.
*Event not observed.

Table 2. Spearman correlations between the phenophases and the climatic variables available for the Serra Bonita Private Reserve region, Bahia, Brazil.

Variable	Flower buds	Anthesis	Unripe fruit	Ripe fruit	Leaf flushing	Leaf fall
Temp	0.69(0)*	0.75(0)* 0.65(1)*	0.62(2)* 0.80(3)*	−0.79(0)* −0.63(1)*	n.s.	n.s.
Precip	−0.71(3)*	0.65(0)*	0.70(2)* 0.77(3)*	−0.80(0)*	−0.65(2)*	0.53(3)**
DayL	0.89(0)* 0.69(1)*	0.86(0)* 0.85(1)* 0.59(2)**	0.80(3)*	−0.79(0)* −0.86(1)* −0.68(2)*	−0.57(3)*	n.s.

Temp – mean temperature; Precip – monthly precipitation; DayL – day length; n.s. – not significant.
Numbers in parentheses represent the months of the correlation: 0 = current month; 1 = previous month; 2 = month two months prior to the event; 3 = month three months prior to the event.
*p<0.05; **p<0.001.

Table 3. Seasonality in the reproductive events of understory Rubiaceae in a montane rain forest in the southern part of Bahia, Brazil.

	Flower bud development		Anthesis		Unripe fruit development		Fruit ripening	
Variable	Beginning	Freq.	Beginning	Freq.	Beginning	Freq.	Beginning	Freq.
Observations, n	72	344	66	210	55	540	44	227
Mean angle*	332.35°	357.22°	1.66°	17.03°	49.25°	127.88°	185.42°	214.05°
(mean date)	(02 Dez)	(28 Dec)	(01 Jan)	(17 Jan)	(18 Feb)	(09 May)	(06 Jul)	(05 Aug)
Circular standard deviation	48.89°	63.71°	40.37°	61.29°	48.02°	83.87°	81.77°	83.19°
Mean vector length (r)	0.69	0.53	0.78	0.56	0.7	0.34	0.36	0.35
Rayleigh test (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.003	< 0.001

Freq. – frequency of individuals.
*Values were converted from dates to angles that represent the months of the year, from January (15°) to December (345°), at intervals of 30° for each month.

Table 4. Results of the Rayleigh test for the occurrence of seasonality in the reproductive events of seven Rubiaceae species with at least 5 sampled individuals in the understory of a montane rain forest in the southern part of Bahia, Brazil.*

Species	Flower bud development			Anthesis			Unripe fruit development			Fruit ripening		
	n obs.	Angle (date)	Vector r	n obs.	Angle (date)	Vector r	n obs.	Angle (date)	Vector r	n obs.	Angle (date)	Vector r
Chomelia pubescens	64	93.94° (05 Apr)	0.66	48	104.58° (16 Apr)	0.66	69	174.82° (26 Jun)	0.50	14	n.s.	n.s.
Faramea martiana	23	258.72° (19 Sep)	0.92	19	280.48° (11 Oct)	0.92	30	353.88° (24 Dec)	0.89	10	42.10° (11 Feb)	0.99
Margaritopsis chaenotricha	41	306.64° (06 Nov)	0.86	21	339.27° (10 Dec)	0.96	53	72.17° (14 Mar)	0.72	25	131.52° (13 May)	0.91
Psychotria cupularis	42	358.87° (29 Dec)	0.90	30	1.14° (01 Jan)	0.96	119	128.87° (10 May)	0.55	60	235.28° (26 Aug)	0.75
Psychotria minutiflora	45	357.48° (29 Dec)	0.68	23	13.41° (13 Jan)	0.78	47	112.81° (24 Apr)	0.45	19	216.20° (07 Aug)	0.81
Psychotria schlechtendaliana	29	353.39° (24 Dec)	0.94	15	16.96° (17 Jan)	0.97	46	115.74° (27 Apr)	0.62	26	213.14° (04 Aug)	0.63
Psychotria suterella	54	27.79° (28 Jan)	0.89	32	46.49° (16 Feb)	0.92	142	183.52° (05 Jul)	0.40	41	276.78° (07 Oct)	0.63

n obs. – number of observations; n.s. – not significant.
*Unless otherwise noted, all results were significant (p<0.05).

Table 5. Results of the Watson-Williams test (F*) for the occurrence of seasonality in the reproductive events of seven Rubiaceae species with at least 5 sampled individuals in the understory of a montane rain forest in the southern part of Bahia, Brazil.

Anthesis Flower buds	*Chomelia pubescens*	*Faramea martiana*	*Margaritopsis chaenotricha*	*Psychotria cupularis*	*Psychotria minutiflora*	*Psychotria schlechtendaliana*	*Psychotria suterella*
Chomelia pubescens	---	146.59	116.19	115.66	52.50	46.36	36.82
Faramea martiana	170.86	---	72.59	166.32	74.08	172.67	289.57
Margaritopsis chaenotricha	241.52	39.99	---	17.52	13.02	46.34	123.59
Psychotria cupularis	123.36	211.36	64.37	---	2.64**	10.98***	78.61
Psychotria minutiflora	83.69	80.15	30.38	0.002**	---	0.115**	14.51
Psychotria schlechtendaliana	107.55	211.71	46.36	0.916**	0.287**	---	21.18
Psychotria suterella	70.78	323.76	172.46	30.01	14.19	37.97	---
Ripe fruit Unripe fruit	*Chomelia pubescens*	*Faramea martiana*	*Margaritopsis chaenotricha*	*Psychotria cupularis*	*Psychotria minutiflora*	*Psychotria schlechtendaliana*	*Psychotria suterella*
Chomelia pubescens	---	u.r.	u.r.	u.r.	u.r.	u.r.	u.r.
Faramea martiana	169.49	---	101.25	107.07	118.07	83.06	60.97
Margaritopsis chaenotricha	83.20	69.54	---	117.44	54.25	40.82	145.12
Psychotria cupularis	19.86	133.13	35.43	---	2.79**	2.51**	16.58
Psychotria minutiflora	19.07	72.54	10.08***	1.69**	---	0**	18.01
Psychotria schlechtendaliana	23.93	117.06	16.06	1.78**	0.019**	---	16.41
Psychotria suterella	0.61**	135.36	101.50	34.73	26.58	33.08	---

u.r.. – unrealized.
*Lower values of F translate to higher values of p; **p>0.05; ***p>0.001.

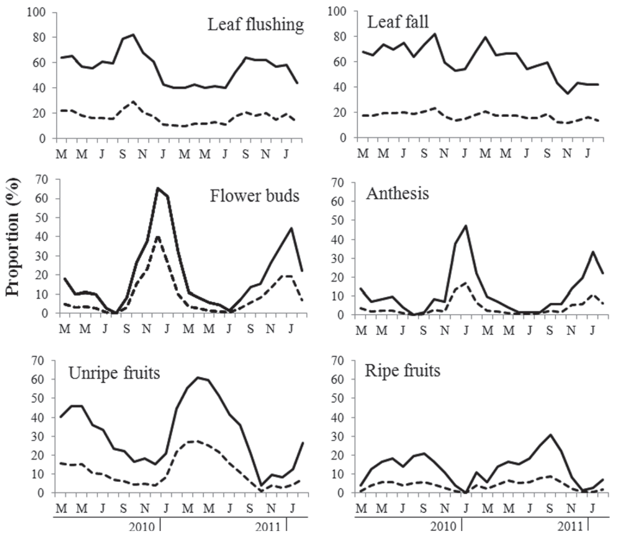

Figure 3. Activity and intensity indices (– and ---, respectively) for the vegetative and reproductive phenophases of understory Rubiaceae in a montane rain forest in the southern part of Bahia, Brazil.

tropical wet forests with low climatic seasonality (Koptur *et al.* 1988; San Martin-Gajardo & Morellato 2003b). In these environments, there is never a water shortage. Therefore, luminosity is considered the only limiting factor for vegetative growth in the understory, and a small variation in its availability is enough to induce the production of new leaves (Pearcy 1983; Barone 1998; Williams-Linera 2003). In the SBPR, although leaf renewal occurs continuously through the year, we observed an evident peak of leaf flushing during the transition to the period of longer days, suggesting that light availability has a marked influence on this phenophase. Although this peak occurred at the beginning of the wettest season, we observed a negative correlation between leaf flushing and precipitation. This correlation suggests that in environments with low seasonality abiotic factors are weak limiters of the occurrence of the phenophase through the year, especially because water is never in short supply. In fact, experimental studies indicate that the species in the family Rubiaceae are poorly influenced by variations in water availability. In a study controlling the irrigation of four *Psychotria* species, Wright (1991) observed no increase in leaf production with an increase in irrigation, demonstrating the weak connection between water availability and leaf flushing in these species.

Leaf fall was not seasonal for Rubiaceae in the SBPR, similarly to the results obtained by San Martin-Gajardo & Morellato (2003b) for Rubiaceae in the Atlantic Forest in southeastern Brazil. This pattern has usually been found in studies carried out in tropical forests for the tree community (Morellato *et al.* 2000; Talora & Morellato 2000) and the shrub community (Opler *et al.* 1980; Koptur *et al.* 1988). In addition, this phenophase was the one least correlated with the climatic variables and exhibited a significant correlation only with precipitation. Albeit leaf fall occurred in a irregular way, without an evident peak, there was a reduction in leaf fall, there was a reduction in its activity coincident with the period of increased precipitation and longer days, which might be a response of the species to these associated factors. Especially in the understory, where luminosity is limited, individuals usually keep their leaves for a longer time when water is available and take advantage of this period of increased light availability, a strategy that enables greater photosynthetic activity and carbohydrate storage (Barone 1998).

Reproductive phenological patterns

The higher number of species flowering at the beginning of the hotter and wettest season, is consistent with the observations of San Martin-Gajardo & Morellato (2003b). Flowering occurring in the wettest season or during the transition to the dry season has also been observed for *Psychotria* species in other tropical forests (Wright 1991; Almeida & Alves 2000; Lopes & Buzato 2005) and is a common pattern for the shrub communities in these environments (Opler *et al.* 1980; Koptur *et al.* 1988). In forests with low climatic seasonality, the longer day length is considered a determinant of the synchronization of flowering (Wright & van Schaik 1994; Morellato *et al.* 2000; Marques *et al.* 2004; Borchert *et al.* 2005), a relationship we also noted for Rubiaceae species in the SBPR, due to the positive correlations with observed data with the two months preceding the phenological event. Similarly, Williams-Linera (2003) reported a positive correlation between flowering and photosynthetically active radiation for understory species in a dense montane rain forest in Mexico.

We found that flowering of Rubiaceae in the SBPR was aggregate among species, with high seasonality and positive correlations with the climatic variables, and exhibited the highest concentration during the wettest season. The high seasonality observed in the present study contradicts the observations of San Martin-Gajardo (2003a; 2003b), who detected two flowering peaks in the same year, with no evident seasonality for this phenophase. According to the authors, that fact is explained by the absence of significant correlations with the climatic variables, associated with the variation in the flowering patterns of species. In the present study, we obtained positive correlations between flowering and the climatic variables. However, we cannot dismiss the phylogenetic hypothesis of phenological grouping as being co-responsible for this event, because the interspecific synchrony was high, especially for *Psychotria* species. The aggregate phenological patterns observed here are commonly found in related species in tropical forests, as in those of the genera *Ilex* (Corlett 1993) and *Piper* (Thies & Kalko 2004), as well as in those of the tribe Myrteae (Staggemeier *et al.* 2010) and the family Myrtaceae (Smith-Ramírez *et al.* 1998). According to the facilitation hypothesis, a seasonal, aggregate pattern, as we observed in the SBPR, increases the visibility of flowers and greatly influences the attraction of pollinators and consequent higher probability of pollination (Augspurger 1983; Staggemeier *et al.* 2010).

Although the Rubiaceae in the SBPR were found to produce fruit through the year, we observed seasonality in unripe and ripe fruits, which peaked at the end of the wettest season and during the less wet season, respectively. This pattern of fruit production throughout the year, with higher frequency at the end of the wettest season, has also been reported for Rubiaceae species in other tropical forests (Opler *et al.* 1980; Poulin *et al.* 1999). Despite the fact that we observed a greater number of species also fruiting during the period with less precipitation, San Martin-Gajardo & Morellato (2003b) did not observe seasonality for this event. This finding was attributed by the authors to the fact that there are no restrictions for the development of Rubiaceae fruit through the year in environments with low climatic seasonality. Similarly, we found that unripe fruits of Rubiaceae in the SBPR correlated with the three climatic variables for three month-period prior to the event, underscoring the idea that, after fruit development (regardless of the period of the year), a climate with low seasonality is favorable for its development.

The existence of a period of higher fruit availability in the SBPR suggests an aggregate condition that enables dispersers to specialize in the consumption of a wide variety of fruits from different species (Poulin *et al.* 1999). The aggregated fruiting pattern in the rainiest season is common, especially in forests with a well-defined dry season, because that is when disperser activity increases (Rathcke & Lacey 1985; Morellato & Leitão-Filho 1992). Although the Rubiaceae species evaluated here are exclusively zoochoric, the lack of a dry season seems to have favored the occurrence of fruiting throughout the year. It makes ripe fruits constantly available to the understory component of the community, as evidenced by the negative correlation between ripe fruits and precipitation in the current month.

Intraspecific synchrony

Flowering synchrony, as was observed in the present study, is frequently associated with evolutionary interactions with pollinators and dispersers. According to Ramos & Santos (2005), the high flowering synchrony in *P. tenuinervis* Müell. Arg., for example, induces higher attraction of pollinators, thus increasing the quantity and quality of the seeds produced. Similarly, populations of *P. suterella* in a submontane rain forest in the state of São Paulo exhibited high flowering synchrony (Lopes & Buzato 2005), which suggests the selective pressure among the bees that pollinate this species is a determinant of this synchrony. In the SBPR, we observed that *Chomelia pubescens* showed the lowest interspecific synchrony, which we attributed to the extended pattern and low individual intensity of flowering. Augspurger (1983) demonstrated that massive flowering results in higher levels of synchrony, whereas, as previously mentioned, less massive flowering decreases synchrony. Although the majority of SBPR species evaluated in the present study exhibited extended patterns, fruiting was highly synchronized. That was not observed by San Martin-Gajardo & Morellato (2003a), who considered low synchrony to be a reflection of the long duration of the reproductive phenophases. Because the reproductive potential of individuals out of population synchrony is usually reduced by the low level of pollination and high seed predation (Augspurger 1981), the synchrony observed for the flowering and fruiting of Rubiaceae species in the SBPR might have occurred as a result of the factors cited above.

Interspecific synchrony

Of the four *Psychotria* species we analyzed in the SBPR, three exhibited high overlap in flowering. In general, monophyletic groups limit the response of their taxa to directional selection, that is, to a similar pattern of flowering (Kochmer & Handel 1986). The fact that only species of the same genus were synchronic in our study suggests this phylogenetic constraint in the pattern. For example, Staggemeier *et al.* (2010) also found aggregate flowering in species of the tribe Myrteae. Those authors stated that this behavior corroborates the facilitation hypothesis, in which such synchrony favors the attraction of more pollinators to the species. Although there are no available ecological data on the reproductive system of the Rubiaceae species in the SBPR, the fact that synchrony was observed only for *Psychotria* species allows us to consider the idea of facilitation.

Even with extended periods of fruiting, we observed a high overlap between the *Psychotria* species monitored in the SBPR, resulting in aggregated fruiting. This pattern might increase the activity of dispersers, as observed by Poulin *et al.* (1999), who evaluated 21 *Psychotria* species in Panama and found that the capture rate for frugivorous birds in the understory was highest during the fruiting peak, and that the species evaluated showed an aggregate phenological pattern. That pattern increases mutualistic interactions with dispersers in comparison with species fruiting separately, especially for congeneric plants (Rathcke & Lacey 1985).

Although our study site was in a forest with low climatic seasonality, the seasonality observed for the reproductive events of Rubiaceae, together with the high number of significant correlations with the climatic variables, demonstrated that the species studied are influenced by this slight climatic variation. This is in contrast with results previously obtained for different Rubiaceae species in another forest with low climatic seasonality in southeastern Brazil. In addition, because we observed aggregated patterns of reproductive events in Rubiaceae species in the SBPR, , and mainly because the interspecific synchrony was found almost exclusively for *Psychotria* species, we cannot exclude the influence of phylogenetic hypotheses in the studied species, indicating that a higher degree of relatedness increases the similarity among phenological events.

Acknowledgments

This study received financial support from the Graduate Program in Botany of the Universidade Estadual de Feira de Santana (UEFS), for the field work, as well as from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, master's scholarship to HSL), the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq - ; Research Grant no. 309303/2009-5 to AMA and Universal Project no. 481592/2009-1) and the Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB - Research Project no. APP0041/2009). We would like to thank Dr. Vitor Becker and Clemira Souza, owners of the Serra Bonita Private Reserve, for the logistic support provided. We are also grateful to Dr. Jomar G. Jardim (Universidade Federal do Rio Grande do Norte), and Dr. Charlotte Taylor (Missouri Botanical Garden), for the identification of Rubiaceae species, as well as to Dr. Luis F. Alberti (Universidade Estadual de Santa Cruz), and Dr. Lígia S. Funch (UEFS), for the suggestions and discussions related to this work. We also thank the two anonymous referees for their valuable criticism and suggestions for improving the final version of the manuscript.

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