

Do vegetative and reproductive phenophases of deciduous tropical species respond similarly to rainfall pulses?

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Abstract: Variations in duration and intensity of rainfall pulses. Nevertheless, it remains unknown how phenophases of deciduous trees of the Brazilian semi-arid region respond to rainfall variations. The phenology of *Cordia oncocalyx* was monitored in deciduous thorny woodland (Caatinga), from April 2009 to March 2011, and was correlated with rainfall, soil humidity, temperature, and photoperiod. The rainy years 2009 and 2011 exhibited higher duration of rainfall pulses and lower frequency of interpulses, but in 2010 pulse duration and total rainfall were lower. Circular statistics showed leaf flush followed by flowering and fruiting in the rainy season, and leaf fall and seed dispersal in the dry season. Both the vegetative and reproductive phenophases respond similarly to variations in rain pulses, with adjustments in time, duration, and intensity, which were correlated with variations in rainfall and soil humidity, excluding photoperiod as a trigger. Total defoliation occurred in the driest months of each year, November to December 2009 and August to October 2010. A sporadic leaf flush in November 2010 was triggered by occasional rains. Vegetative and reproductive synchronies were high in rainy years, but in 2010 synchrony was low, flowering was delayed and reduced, and, despite the low fruiting, we recorded high

density in the seed bank. Lower synchrony, temporal separation of phenophases, and storage of fruits on the ground were risk-spreading strategies used by the population in the dry year, which suggest intrapopulation variability in responses to hydric stress. We believe that this plasticity contributes to high species density in the Caatinga.

Keyword: asynchrony; circular analysis; deciduous; phenology; risk spreading; seasonality.

Introduction

Plant growth and reproduction in tropical arid and semi-arid climates are limited by water availability, since rainfall is scarce and rainfall pulses exhibit high intra- and interannual variation (Chesson et al. 2004). Plant species that occur in these environments exhibit multiple risk-spreading strategies to assure their persistence and reproductive success. Among them we highlight: high reproductive rates in rainy years (Venable 2007) and storage in the soil seed bank of part of the seeds produced in years of higher rainfall (Facelli et al. 2005), in order to compensate for unfavorable years.

Phenological processes are important components of plant fitness, since the time and duration of vegetative and reproductive cycles affect the capacity of a plant species to establish itself in a given site (Pau et al. 2011). Therefore, when analyzing the relationship between the phenology and climatic factors, it is possible to infer how strongly the lack or abundance of resources affects reproduction and regeneration (Kelly and Sork 2002). This information is fundamental not only to understand the current behavior of a species, but also to predict its responses to future climatic changes (Walther et al. 2002), especially for plants of dry seasonal forests, which exhibit phenological patterns regulated mainly by abiotic factors (Sarmiento and Monasterio 1983; Van Schaik et al. 1993).

In the woody flora of these environments deciduous species predominate, whose production of leaves, flowers, and fruits is correlated with rainfall (Singh and Kushwaha 2005). However, there are species whose phenophases do not respond directly to rainfall pulses, but to variations, even slight, in photoperiod and

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temperature (Rivera et al. 2002; Borchert et al. 2005; Elliott et al. 2006). These species have deep roots, store water in the root or have low-density wood, characteristics that confer independence from rainfall pulses for triggering the start of phenophases (Reich and Borchert 1984; Borchert 1994; De Bie et al. 1998; Borchert et al. 2002).

Deciduous trees with high-density wood that occur in tropical regions with seasonal climates respond to rainfall seasonality with overlap between vegetative and reproductive phenophases (Bullock and Solis-Magallanes 1990) and intrapopulation synchrony of phenophases, as individuals must use quickly the water available during short periods of rain (Williams et al. 1997; Sayer and Newbery 2003; Mahall et al. 2010). However, these phenological strategies may be affected by interannual rainfall variations. Seghieri et al. (1995) observed that deciduous species decreased their flowering synchrony in years of reduced rainfall. Pavón and Briones (2001) and Yadav and Yadav (2008) observed that, in years with below average rainfall, there was delay and reduction in the production of leaves, flowers, and fruits, as well as a longer periods without leaves. Asynchrony in flowering or leaf flush appear as responses of savanna plant species to local disturbance, such as fire or water stress (Devineau 1999). However, there is no consensus about these phenological responses, since Seghieri et al. (2009) concluded from the production rate of leaves, flowers, and fruits that the vegetative phenophases are most affected by reduced rainfall.

Woody savanna (Woodward et al. 2004) is the predominant vegetation in the Brazilian semi-arid region, where it is known as caatinga, with physiognomies including savanna, scrubland and woodland (Cole 1960). Corroborating studies carried out in other seasonally dry regions, some authors have reported that, in the caatinga, the phenophases of deciduous species with high-density wood are triggered mainly by rainfall (Machado et al. 1997; Lima and Rodal 2010). The question that remains is: what are the effects of intra- and interannual rainfall variations on the phenodynamics of tree populations in the caatinga that express phenophases in the rainy season?

The caatinga occurs on shallow soils with low water storage capacity and highly variable rainfall (Sampaio 1995). Taking this into account, populations of deciduous species are expected to exhibit low synchrony in vegetative and reproductive phenophases and storage in the soil seed bank as a risk-spreading strategy in years of drought (i.e., when rainfall is below the historical annual average, and there are more interpulses in the rainy period) in opposition to high synchrony and high reproductive rates in rainy years. To test this hypothesis, the phenodynamic of an adult population of *Cordia oncocalyx*, a tree with high-density wood, which is endemic, abundant and characteristic of caatinga vegetation, was analyzed, aiming to answer the following questions: (1) which abiotic variables (rainfall, temperature and photoperiod) trigger the phenophases?; (2) do variations in the quantity and duration of rainfall pulses and interpulses affect similarly the beginning, duration, synchrony, and intensity of vegetative and reproductive phenophases?; and (3) how do interannual variations in rainfall affect the reproductive fitness of this species?

Material and methods

Species description and study area

Cordia oncocalyx Allemão (Boraginaceae) is a mesophanerophyte that occurs in lowlands (< 500 m a.s.l.) on shallow soils of the crystalline basement in the Brazilian semi-arid region. It has a restricted geographic distribution (3–7° S and 37–41° W), and presents flowers arranged in inflorescences of the thyrsus type; its fruit is of the nuculanum type (Spjut 1994), contains from one to four seeds, and is involved by a calyx, which is developed after the fecundation and helps in anemochoric dispersal (Silva and Machado 1997). *C. oncocalyx* is one the most abundant species in the study area (Costa and Araújo *in press*), has high-density wood (0.70 g·cm⁻³; Carvalho 2008), and is harvested for its timber, energetic, foraging, medicinal, and scenic values (Lorenzi 2009). The population analyzed is located in a caatinga (deciduous thorny woodland) fragment of the Serra das Almas Natural Reserve (5°6′58.1" S and 40°52′19.4" W), 368 m a.s.l.

The regional climate is classified as BSh (hot semi-arid, with rainy summer and dry winter) in the Köppen-Geiger system (Peel et al. 2007). The climatic diagram in the historical series (1978–2008) describes a well-defined rainy season (January to May) and a dry season (June to December) (Fig. 1). Average annual rainfall is 683 mm, but it varies greatly between years: recent years with above average rainfall were 2009 (1107 mm) and 2011 (877 mm), and years with below average rainfall were 2010 (441 mm) (Fig.1). Average annual temperature is 27 °C with low annual variation, from 21 °C in the coldest months (March to June) to 36 °C in the warmest months (October to December). Annual variation in photoperiod is around 36 min. The shortest day occurs in June (11:49 h) during winter and the longest day occurs in December (12:25 h) during summer. Data on rainfall and temperature were obtained from the climatological station of the National Institute of Meteorology (INMET), located in the municipality of Crateús, 25 km away from the study area and at a similar altitude. The daily and monthly photoperiods were calculated based on Lammi (2009). Water availability in the soil was analyzed through monthly sampling of deformed soil samples. The area of one hectare was divided in three portions: north, center, and south; in each portion three plots of 10 m × 10 m were randomly selected in order to distribute the sampling sites so that the whole area was well represented. Water content of the aliquots taken from the center of each plot was assessed by the difference between the fresh and dry weights. Average soil humidity was positively correlated with rainfall ($r_s = 0.8625$; $p < 0.001$), and reached the lowest values, below 6% water content, in the drought season.

Phenological monitoring

Thirty reproductive adult trees, of heights between 8.5 and 12 m and diameter at ground level between 13.7 and 70.1 cm were randomly selected from within the 1 ha area. The area was di-

vided in 100 contiguous plots of 10 × 10 m. The 30 trees were monitored monthly for 24 months, from April 2009 to March 2011, using binoculars during the day, from 7:00 to 17:00. For each individual, three vegetative phenophases were observed: leaf flush, adult leaf, and leaf fall; and three reproductive phenophases: open flower, unripe fruit, and ripe fruit. Leaf flush was identified as the presence of small light green leaves, both in the presence of adult leaves and after the period of total leaf fall.

Leaf fall was marked by visible canopy defoliation, presence of yellow leaves, and ease of leaf fall in the wind. The open flower phenophase was characterized as the period in which the tree exhibited flowers in anthesis. The unripe fruits phase was characterized by presence of developing fruits and by formation visible and green fruits. The ripe fruit phase was when diaspores were brown and ready to be dispersed.

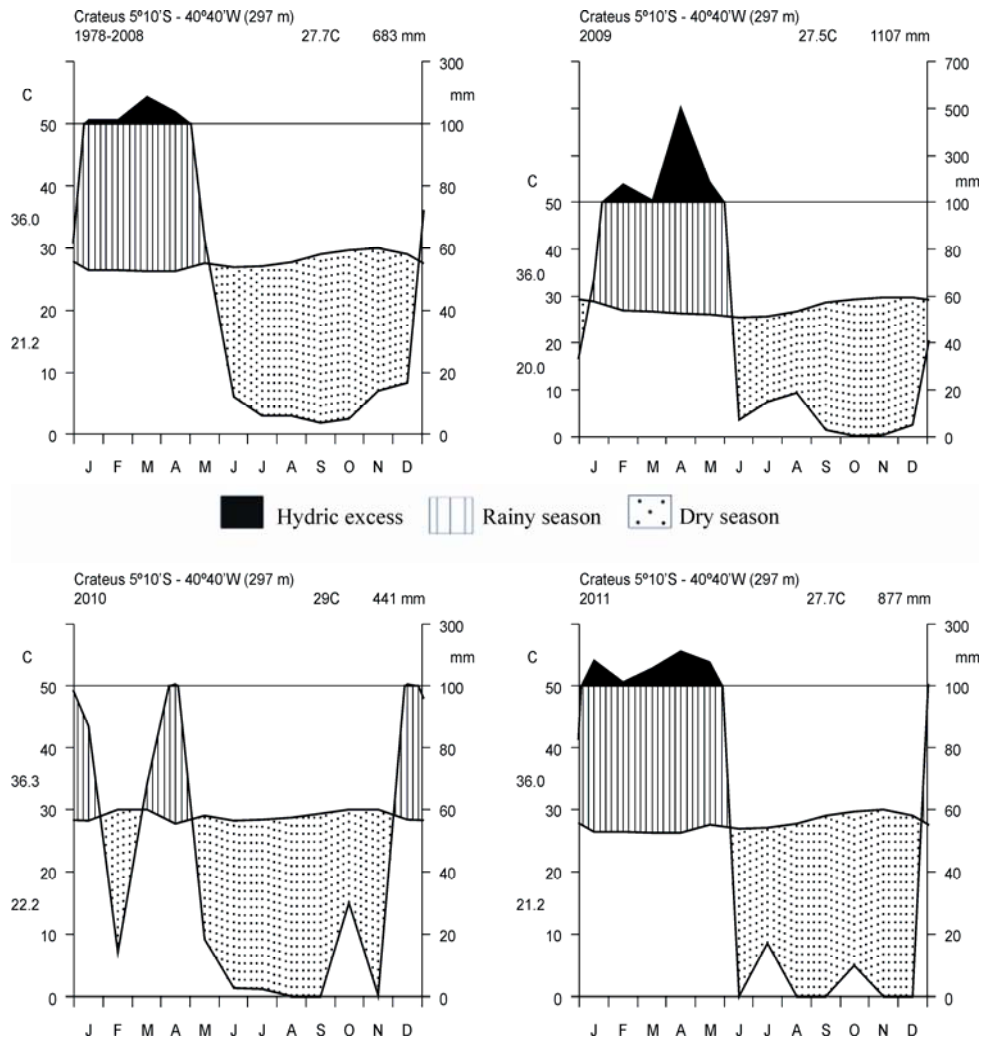


Fig. 1 Climatic diagram Walter and Lieth, during the historical average (1978-2008) and the study period (2009, 2010, 2011) for Crateús, state of Ceará, northeastern Brazil. R environment, package climatol (R Development Core Team 2010)

Data analysis

To assess which of the abiotic factors (rainfall, soil humidity, temperature, and photoperiod) was correlated with the vegetative and reproductive phenophases, the relationship between abiotic factors in the month of occurrence of the phenological event and in the month previous to the event, and the activity and intensity of each phenophase was analyzed, using a Spearman correlation test (rs).

To test whether the beginning, duration, synchrony, and inten-

sity of the vegetative and reproductive phenophases were similarly affected by variations in duration and distribution of rainfall pulses, Heideman was followed (1989). This author suggested using activity and intensity indexes, since an activity peak reflects the maximum number of individuals that exhibit the phenophase, but not necessarily with maximum intensity, as maximum intensity can occur even without the phenophase being expressed by all individuals. For the analysis of activity, we recorded only the presence or absence of each phenophase in each observation period. Synchrony of the phenophases was categorized as: (a) asynchrony, when < 20% of the individuals

were in the phenophase; (b) low synchrony, when 20%–60% of the individuals were in the phenophase; and (c) high synchrony, when >60% of the individuals were in the phenophase. To analyze the intensity of each phenophase, the semi-quantitative method of Fournier (1974) was used, which establishes five categories in ordinal and interval scale: 0 = 0%; 1 = 1%–25%; 2 = 26%–50%; 3 = 51%–75%; and 4 = 76%–100%. Activity and intensity were analyzed with phenograms.

To test for seasonality in vegetative and reproductive phenophases, circular histograms were made with the frequency distribution of phenophases for the 30 individuals in the periods (1) April 2009 to March 2010 and (2) April 2010 to March 2011. The frequency of occurrence was considered to be the proportion of individuals in each phenophase. The months were converted into angles, with intervals of 30°, and then the average angle or average date (μ), the circular concentration (r), and the circular standard deviation (sd) were calculated. The average angle (μ) is the period around which a determined phenophase was recorded in most individuals. A Rayleigh test (z) was used to determine the significance of the angle. When the average angle is significant, there is seasonality of the phenophase. The intensity of circular concentration around the average angle (r) varies from 0 (phenological activity uniformly distributed throughout the year) to 1 (phenological activity concentrated in a period of the year). We used the program ORIANA 3 (Kovach 2007) for these analyses.

To know if and how interannual rainfall variations affect the reproductive fitness of the species, the number of fruits recently dispersed in the seed rain, and the number of fruits accumulated on the ground (soil seed bank) were counted. For estimating the seed rain, 50 odd-numbered plots were selected. In the center of each plot a collector of 0.5 m \times 0.5 m was installed, suspended at 10 cm above the ground, and the number of fruits in each collector was counted monthly. For sampling the soil seed bank, the remaining 50 even-numbered plots were used. In the center of each plot, a subplot of 0.5 m \times 0.5 m was marked out for the sampling of leaf litter and soil layer of 0–2 cm depth. Two collections were carried out, one in December 2009 and the other in December 2010, before the period of seed germination.

Results

Vegetative phenophases

As expected for deciduous species of seasonal tropical environments, the vegetative phenophases were triggered by rainfall and, consequently, soil humidity. The phenophases ‘leaf flush’ and ‘adult leaf’ were positively correlated with rainfall and soil humidity, whereas ‘leaf fall’ was negatively correlated with soil humidity (Table 1). Although ‘leaf flush’ showed a positive correlation and ‘leaf fall’ a negative correlation with photoperiod, the interannual variability recorded at the beginning and on the average date (Fig. 2) exclude photoperiod as a trigger for these phenophases.

Table 1. Spearman correlations (r_s) between the abiotic factors and the phenophases of *Cordia oncocalyx* from April 2009 to March 2011.

Phenophases	R0	R1	H0	H1	T0	T1	P0	P1	
Leaf flush	0.72	0.44	0.71	*	*	*	*	0.60	
Adult leaf	0.53	0.72	*	0.53	-0.66	-0.44	*	*	
Activity	Leaf fall	*	*	-0.40	*	*	*	-0.45	-0.45
Index	Open flower	*	0.46	0.41	0.41	*	*	*	*
	Unripe fruit	*	0.57	0.47	0.63	-0.71	-0.67	-0.51	*
	Ripe fruit	-0.62	-0.39	-0.45	*	*	*	*	-0.62
	Leaf flush	0.65	*	0.66	*	*	*	0.43	0.61
	Adult leaf	0.68	0.79	0.53	0.58	-0.59	*	*	*
Intensity	Leaf fall	*	*	-0.40	*	*	*	-0.44	-0.45
Index	Open flower	*	0.46	0.41	0.40	*	*	*	*
	Unripe fruit	*	0.56	0.47	0.62	-0.72	-0.66	-0.54	*
	Ripe fruit	-0.63	-0.44	-0.49	*	*	*	*	-0.60

R = rainfall; H = soil humidity; T = temperature; P = photoperiod; 0 = month of occurrence of the phenological event; and 1 = month previous to the occurrence of the phenological event. * Non-significant results ($p > 0.05$).

The beginning, duration, synchrony, and intensity of the vegetative phenophases were manifested according to intra- and interannual variations in rain pulses and interpulses (Figures 2a and 2b). In the years of higher rainfall, 2009 and 2011, leaf flush was continuous and in high synchrony throughout the rainy months. However, in 2010, a year with below average rainfall, three discontinuous leaf flush events were recorded: two during the rainy season (one in January and the other in April) that were interrupted by an interpulse (drought) in February, and another at the end of the dry season (November and December), coinciding with short rain pulses outside the expected rainy season. During this atypical leaf flush period in November 2010, low synchrony was recorded, as only 57% of the individuals re-sprouted (Fig. 2a).

The adult leaf phenophase exhibited a high activity index and, therefore, high synchrony during the rainy season, in both years. In 2009, the year of highest annual total rainfall and longest rainfall duration, intensity decreased only in August, whereas in 2010, it occurred prematurely in June; both periods coincided with the end of rains. In 2009, leaf fall occurred from June to October, when it reached 100%. In 2010, leaf fall occurred earlier, from February to December, and trees remained in complete defoliation for three months, from August to October (Fig. 2 A; B).

Trees that lost their leaves later in 2010 emitted leaves prematurely in November, triggered by an occasional rain pulse at the end of the dry season ($r_s = -0.4824$, $p = 0.0069$), and showed higher flowering intensity in the following rainy season, in February and March 2011 ($r_s = -0.3815$, $p = 0.0375$; $r_s = -0.4251$, $p = 0.0191$). However, there was no correlation between the size of the tree (height and diameter) and the beginning, duration and intensity of the phenophases ($p > 0.05$).

All vegetative phenophases were seasonal (Rayleigh Z, $p < 0.01$), and ‘leaf flush’ was the phenophase with highest seasonality and shortest duration compared to the phenophases ‘adult

leaf' and 'leaf fall'. The phenophase adult leaf in 2009, a year with above average rainfall, exhibited the lowest seasonality index ($r = 0.21$) among vegetative phenophases (Fig. 2 C).

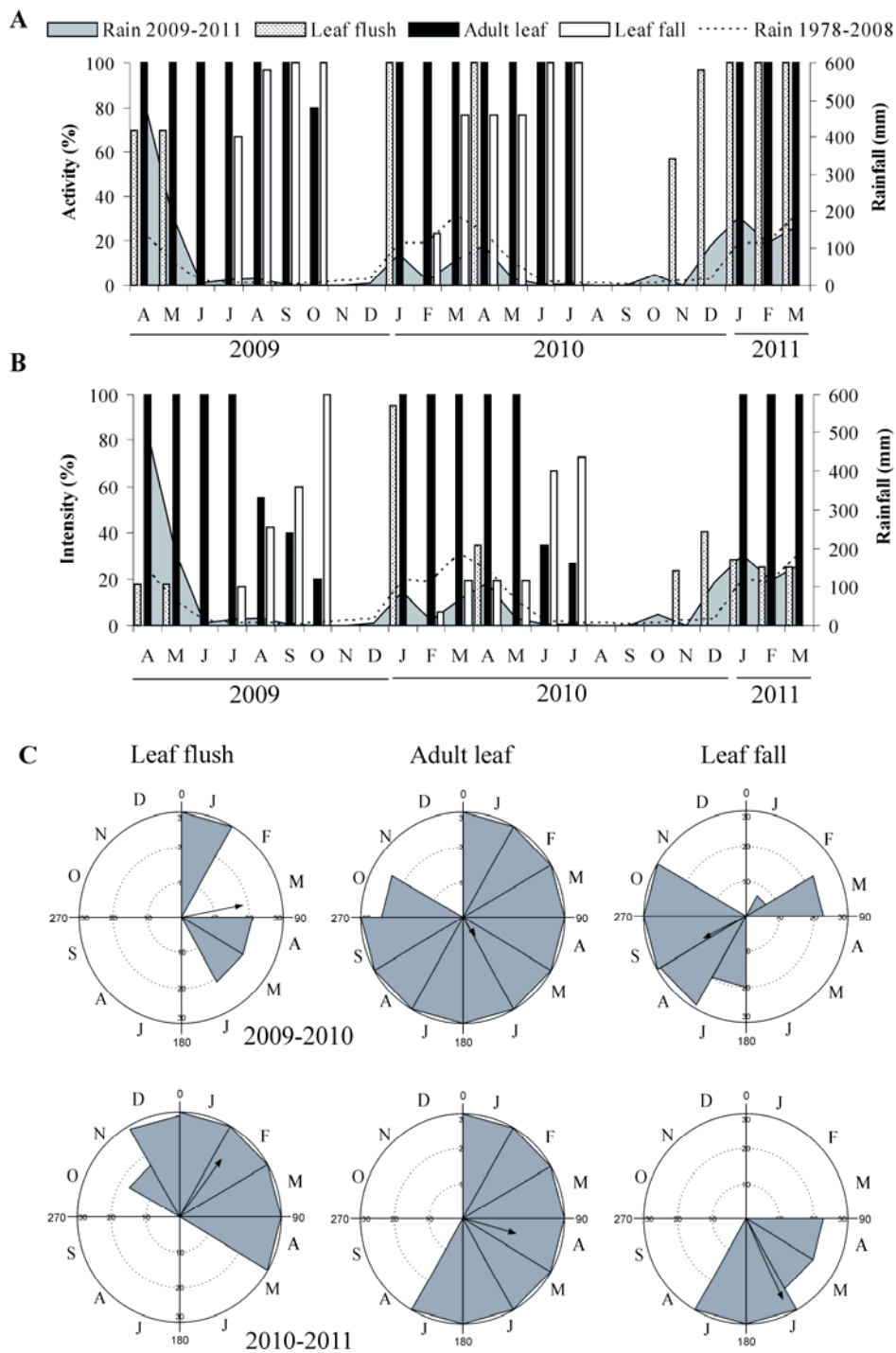


Fig. 2 (A) Activity index and (B) intensity index of Fournier measured for the vegetative phenophases, and monthly rainfall during the study and the historical average. (C) Circular histograms of the phenophases indicating the average date. Leaf flush (2009-2010: $r = 0.62$, $sd = 56.50^\circ$; 2010-2011: $r = 0.69$, $sd = 49.72^\circ$), adult leaf (2009-2010: $r = 0.21$, $sd = 100.54^\circ$; 2010-2011: $r = 0.54$, $sd = 63.67^\circ$) and leaf fall (2009-2010: $r = 0.46$, $sd = 71.23^\circ$; 2010-2011: $r = 0.84$, $sd = 32.83^\circ$), where r = length of the average vector and sd = circular standard deviation

Reproductive phenophases

The reproductive phenophases of this species were also triggered by rainfall. The phenophases 'open flower' and 'unripe fruit'

were positively correlated with rainfall in the month previous to the event and with soil humidity both in the month of the event and in the previous month. As expected, the phenophase 'ripe fruit' was negatively correlated with rainfall and soil humidity

(Table 1), since fruit ripening occurs at the end of the rainy season and anemochoric dispersal occurs in the dry season.

The phenophases ‘flowering’ and ‘fruiting’ (unripe fruit) were short (Rayleigh Z , $p < 0.01$); the open flower lasted two months and the unripe fruit, from two to four months, but the occurrence of ripe fruits was more evenly distributed during the year (Fig.

3c). Flowering and fruiting exhibited high synchrony and intensity in the rainy years 2011 and 2009, but in 2010, the year with shortest duration of rain pulses and lowest total rainfall, there was delay in the beginning of flowering and fruiting, low intrapopulation synchrony, and low intensity (Fig. 3 A, B).

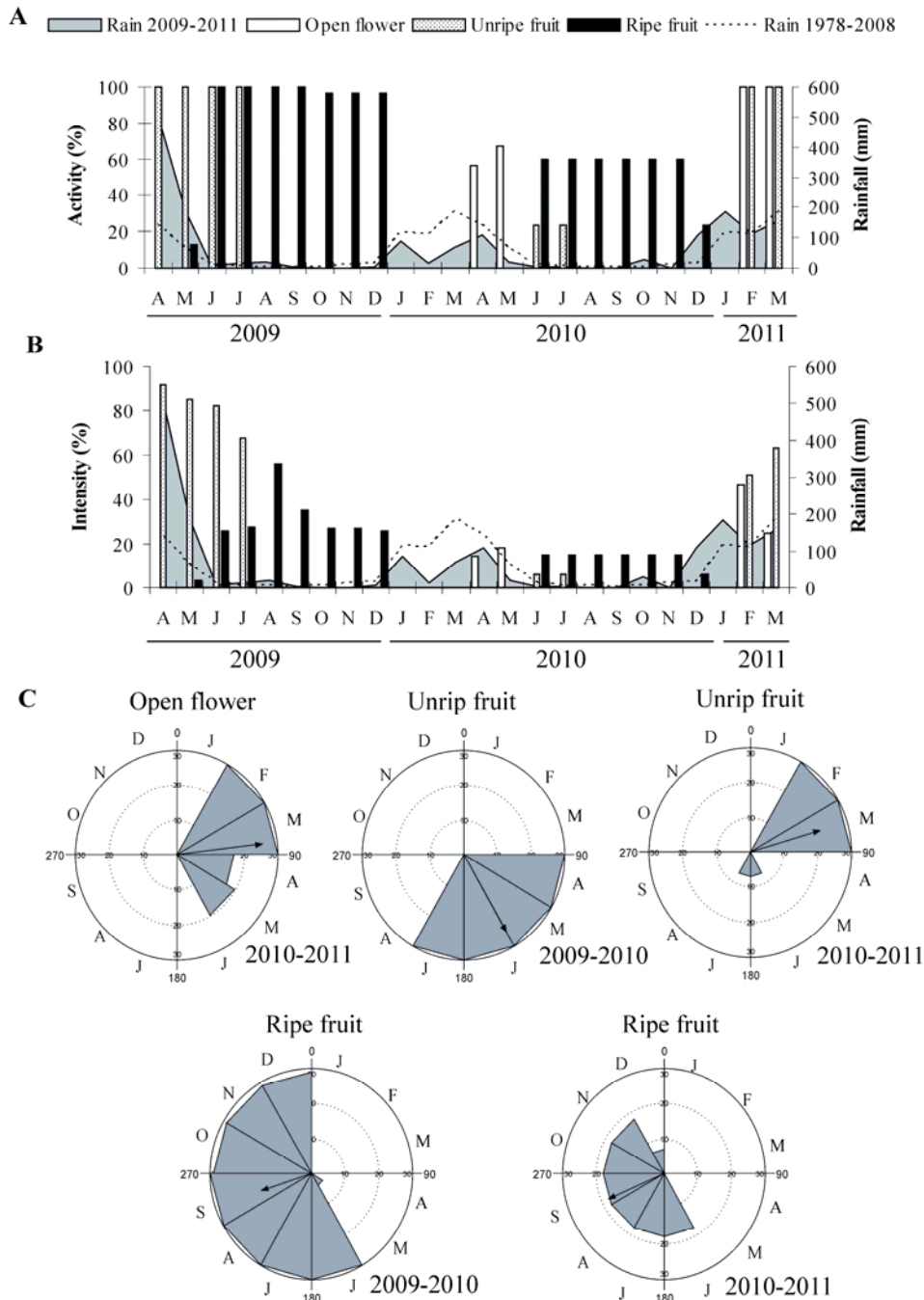


Fig. 3 (A) Activity index and (B) intensity index of Fournier measured for reproductive phenophases, and monthly rainfall during the study and the historical average. (C) Circular histograms of the phenophases indicating the average date. Open flower (2010-2011: $r = 0.85$, $sd = 32.77^\circ$), unripe fruit (2009-2010: $r = 0.85$, $sd = 33.12^\circ$; 2010-2011: $r = 0.72$, $sd = 46.65^\circ$), and ripe fruit (2009-2010: $r = 0.52$, $sd = 65.40^\circ$; 2010-2011: $r = 0.59$, $sd = 58.03^\circ$), where r = length of the average vector and sd = circular standard deviation.

In total 429 fruits were counted in the seed rain of 2009 (17 fruits/m²) and only four fruits were counted in 2010 (0.16

fruits/m²). In 2009, 1,330 fruits (53 fruits/m²) were counted in the leaf litter and 228 fruits (9 fruits/m²) in the soil layer of 0–2

cm. In 2010, despite the low fruit production, 762 fruits were counted in the leaf litter (30 fruits/m²) and 268 fruits (10 fruits/m²) in the soil layer at 0–2 cm depth.

In the dry year of 2010, lower overlap between reproductive phenophases (flowering and fruiting) and between vegetative phenophases was observed (Figs. 2 and 3). In the rainy year of 2009, a longer period of overlap of unripe and ripe fruits (three months) was observed compared to the dry year (two months). In the rainy year of 2011, overlap was also recorded between the phenophases ‘open flower’ and ‘unripe fruit’, and between ‘leaf flush’, ‘flowering’, and ‘beginning of fruiting’ (in February and March). However, in the dry year of 2010, overlap was not observed between the phenophases ‘leaf flush’ (January and April), ‘open flower’ (May), and ‘beginning of fruiting’ (June).

Discussion

Vegetative phenology

The beginning of ‘leaf flush’ in *C. oncocalyx* after the leaf-fall period and in positive correlation with rainfall and soil humidity suggests that the first rains activated the vegetative buds and triggered the production of new leaves. In addition, the sporadic leaf flush associated with an occasional rain pulse at the end of the dry season in 2010 might have been a response to increased soil moisture resulting from occasional rains, as reported by Sarmiento and Monasterio (1983), Borchert (1994), De Bie et al. (1998), Singh and Kushwaha (2005) and Elliot et al. (2006). Although in 2010 leaf flush coincided with an increase in photoperiod, in 2009 there was no sporadic rain in the dry season and no leaf flush was observed; hence, a possible influence of the photoperiod was excluded. These results corroborate those of Rivera et al. (2002), who reported variations in photoperiod triggered ‘leaf flush’ and ‘leaf fall’ at low latitudes only when there were no interannual variations in the timing of these phenophases.

The fact that leaf flush in *C. oncocalyx* occurred throughout the rainy months indicates that, despite the quick leaf flush and development of adult leaves during the first rains, trees produce new leaves sequentially. This sequential leaf production in deciduous species occurs due to the low production cost and the high initial photosynthetic capacity, the latter decreasing with leaf aging (Kikuzawa 1995). According to the same author, the non-simultaneous development of leaves minimizes shading and increases photosynthetic production. Therefore, the sequential leaf production in *C. oncocalyx*, associated with spiral phyllotaxy, should minimize shading and maximize photosynthesis during the short rainy season.

In *C. oncocalyx*, the relationship between leaf fall and increased duration and severity of the dry season results in leafless trees for progressively longer periods, as reported by Pavón and Briones (2001), Elliott et al. (2006) and Yadav and Yadav (2008) for other species of seasonally dry tropical environments. However, Borchert et al. (2002) showed that, in deciduous species with high-density wood, severe drought reduced the lifespan of

older leaves from eight to four months. Although leaf lifespan was not monitored here, the leaf fall recorded in February 2010, one month after leaf flush, resulting from a drought pulse during the rainy season, indicates that hydric stress and not leaf age was the main trigger of leaf abscission in *C. oncocalyx*.

Although high synchrony in vegetative phenophases among deciduous species of dry seasonal climates is expected (Williams et al. 1997; Devineau 1999; Mahall et al. 2010), we observed that this synchrony varied in *C. oncocalyx* according to interannual rainfall variations. The low synchrony recorded at the beginning of leaf fall and in the sporadic leaf flush at the end of the dry season in 2010 caused intrapopulation variations in response to hydric stress, as reported by De Bie et al. (1998) and Singh and Kushwaha (2005). They stated that early leaf production increases fitness because the production of new leaves at the end of the dry season probably provides a photosynthetic apparatus ready to work in the following rainy season. Hence, this intrapopulation plasticity recorded in *C. oncocalyx* may confer an adaptive advantage to this species that faces variable and unpredictable conditions of water availability.

Our results show that the timing of vegetative phenophases is correlated with seasonal variations in rainfall, including a longer duration of adult leaves in the rainy year compared with the dry year. Our results corroborate those of Borchert et al. (2002), who considered the expression of vegetative phenophases in deciduous species with hard wood to be opportunistic.

Reproductive phenology

The high flowering synchrony in the rainy year recorded for *C. oncocalyx* should favor allogamy, as reported by Borchert et al. (2005) for species of different functional types. However, in the dry year, fitness was reduced, considering the synchrony and quantity of fruits produced. This refutes Seghieri et al. (2009), who concluded that, in savannas, a reduction in rainfall more strongly affected leaf production than flower and fruit production. However, these results corroborate those of Pavón and Briones (2001), Borchert et al. (2004) and Singh and Kushwaha (2005), who observed that the timing of flowering is determined by rainfall and water availability in the soil. These results suggest that the endogenous processes that regulate the timing of vegetative and reproductive phenophases in *C. oncocalyx* are similarly affected by a decrease in rainfall and soil humidity.

Negative effects of years of drought on flowering have been observed in several species in environments subject to water stochasticity. These negative effects include: abscission of flower buds before anthesis (Borchert et al. 2002), reduction in the number of flowers produced (Pavón and Briones 2001), flowering delay (Yadav and Yadav 2008), reduction in the proportion of flowering individuals, and flowering inhibition (Seghieri et al. 1995). However, the high flowering and fruiting rates in rainy years, together with seed storage in the soil seed bank in the dry year, derived from a part of the fruits produced in rainy years as observed in *C. oncocalyx*, corroborate Venable (2007) and Pau et al. (2011), who concluded that this is a risk-spreading strategy, since in species that occur in environments with high interannual

resource variations, high reproductive rates in years of higher water availability can compensate low rates in years of scarcity.

A sequence of several dry years (Seghieri et al. 1995) or of several pulses of drought during the rainy season, which is common in seasonal dry forests (Vieira and Scariot 2006), can cause population decline due to seedling death. In this case, even a seed stock in the soil may not be enough to lessen the effects of frequent drought periods. Hence, if the forecasts of climate change in arid and semi-arid ecosystems in the southern hemisphere result in even drier climates (Walther et al. 2002; Miles et al. 2006), a reduction in the rates of fruit and seed production may cause population decline and compromise the recruitment and maintenance of endemic species such as *C. oncocalyx*. To make more conclusive forecasts, however, our study needs to be complemented by study of population dynamics.

Whereas the high synchrony of vegetative and reproductive phenophases in rainy years (2009 and 2011) suggests an adaptation of *C. oncocalyx* to water seasonality, a decrease in synchrony in the dry year (2010), during interpulses of drought in the rainy season and during rainfall pulses at the end of the dry season, reflects intrapopulation variability. In this case, the individuals that express the phenophases under these conditions are probably the least demanding in terms of water availability. However, this result was not related to the size of the tree as there was no correlation between tree size (height and diameter) and the beginning, duration and intensity of the phenophases, similar to the findings of Sayer and Newbery (2003) and Singh and Kushwaha (2005), but was probably due to the genetic heterogeneity of this population in a highly variable environment.

It is important to note that the vegetative and reproductive phenophases of *C. oncocalyx* respond similarly to annual and interannual variations in rainfall pulses and interpulses, with high synchrony and overlap of phenophases in rainy years, whereas in dry years there is low intrapopulation synchrony of phenophases, reduction in reproductive rates, and smaller overlap of phenophases. This corroborates the results of Singh and Kushwaha (2005), who stated that hydric stress is not only reflected in longer leaf-fall periods, but also in the temporal segregation between the vegetative and reproductive phenophases.

Hence, the plasticity recorded in *C. oncocalyx* in terms of adjustments in the beginning, duration, synchrony, and intensity of the vegetative and reproductive phenophases in response to interannual variations in rainfall, and intrapopulation variations in phenology in the dry year, support our hypothesis that, in deciduous species, both the vegetative and the reproductive phenophases are adjusted to variations in rainfall pulses. We believe that this phenological variation confers an adaptive advantage to these plants, mainly under variable and unpredictable conditions of water availability, and contributes to the high density of this species in the caatinga of northeastern Brazil. However, despite the phenological plasticity and the current local abundance of *C. oncocalyx*, if the climate of the Brazilian semi-arid region becomes even drier as predicted due to climatic change, the soil seed bank, together with the asynchrony and smaller overlap in phenophases, considered as risk-spreading strategies in dry years, and recorded in the present study, may be

not enough to maintain population sizes or distributions.

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References

- Borchert R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology*, **75**: 1437–1449.
- Borchert R, Meyer SA, Felger RS, Porter-Bolland L. 2004. Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. *Global Ecology and Biogeography*, **13**: 409–425.
- Borchert R, Renner SS, Calle Z, Vavarrete D, Tye A, Gautier L, Spichiger R, Hildebrand P. 2005. Photoperiodic induction of synchronous flowering near the Equator. *Nature*, **433**: 627–629.
- Borchert R, Rivera G, Hagnauer W. 2002. Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. *Biotropica*, **34**: 27–39.
- Bullock SH and Solis-Magallanes A. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica*, **22**: 22–35.
- Carvalho PER. 2008. Pau-Branco-do-Sertão (*Auxemma oncocalyx*). *Circular Técnica Embrapa*, **153**: 1–6.
- Chesson P, Gebauer RLE, Schwinning S, Huntly N, Wiegand K, Ernest SKM, Sher A, Novoplansky A, Weltzin JF. 2004. Resource pulses, species interactions and diversity maintenance in arid and semi-arid environments. *Oecologia*, **141**: 236–253.
- Cole MM. 1960. Cerrado, Caatinga and Pantanal: the distribution and origin of the savanna vegetation of Brazil. *The Geographical Journal*, **126**: 168–179.
- Costa RC and Araújo FS. 2012. Physiognomy and structure of a caatinga with *Cordia oncocalyx* (Boraginaceae), a new type of community in Andrade-Lima's classification of caatingas. *Rodriguésia*, **63**(2): 269–276.
- De Bie S, Ketner P, Paasse M, Geerling C. 1998. Woody plant phenology in the west Africa savanna. *Journal of Biogeography*, **25**: 883–900.
- Devineau JL. 1999. Seasonal rhythms and phenological plasticity of savanna woody species in a fallow farming system (south-west Burkina Faso). *Journal of Tropical Ecology*, **15**: 497–513.
- Elliott S, Baker JP, Borchert R. 2006. Leaf flushing during the dry season: the paradox of Asian monsoon forests. *Global Ecology and Biogeography*, **15**: 248–257.
- Facelli JM, Chesson P, Barnes N. 2005. Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. *Ecology*, **86**: 2998–3006.
- Fournier LA. 1974. Um método quantitativo para la medición de características fenológicas en arboles. *Turrialba*, **24**: 422–423.
- Heideman PD. 1989. Temporal and spatial variation in the phenology of

- flowering and fruiting in a tropical rainforest. *Journal of Tropical Ecology*, **77**: 1059–1079.
- Kelly D, Sork VL. 2002. Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics*, **33**: 427–447.
- Kikuzawa K. 1995. Leaf phenology as an optimal strategy for carbon gain in plants. *Canadian Journal of Botany*, **73**: 158–163.
- Kovach WL. 2007. *Oriana for Windows 3*. Wales, Kovach Computing Services.
- Lammi J. 2009. Online photoperiod calculator. Available at: <http://www.nic.fi/wbenefon/sun.php3> [accessed on: 20/05/2011].
- Lima ALA, Rodal MJN. 2010. Phenology and wood density of plants growing in the semi-arid region of northeastern Brazil. *Journal of Arid Environments*, **74**: 1363–1373.
- Lorenzi H. 2009. *Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil*. v 1. 5 ed. São Paulo: Plantarum, p.384.
- Machado ICS, Barros LM, Sampaio EVSB. 1997. Phenology of caatinga species at Serra Talhada, Northeastern Brazil. *Biotropica*, **29**: 57–68.
- Mahall BE, Thwing LK, Tyler CMA. 2010. Quantitative comparison of two extremes in chaparral shrub phenology. *Flora*, **205**: 513–526.
- Miles L, Newton AC, Defries RS, Ravilious C, May I, Blyth S, Valerie VK, Gordon JE. 2006. A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, **33**: 491–502.
- Pau S, Elizabeth MW, Benjamin IC, Jonathan D, Nathan JBK, Kjell B, Julio LB, Elsa EC. 2011. Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology*, **17**: 3633–3643.
- Pavón NP, Briones O. 2001. Phenological patterns of nine perennial plants in an intertropical semi-arid Mexican scrub. *Journal of Arid Environments*, **49**: 265–277.
- Peel MC, Finlayson BL, McMahon TA. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, **11**: 1633–1644.
- R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reich PB, Borchert R. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology*, **72**: 61–74.
- Rivera G, Elliott S, Caldas LS, Nicolossi G, Coradin VTR, Borchert R. 2002. Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. *Trees*, **16**: 445–456.
- Sampaio E. 1995. Overview of the Brazilian caatinga. In: Bullock SH, Mooney HA, Medina E. (eds.), *Seasonally dry tropical forests*. New York: Cambridge University Press, pp. 35–63.
- Sarmiento G, Monasterio M. 1983. Life forms and phenology. In: Bourlière F. (ed.), *Ecosystems of the world: tropical savannas*. Amsterdam: Elsevier, pp. 79–108.
- Sayer EJ, Newbery DM. 2003. The role of tree size in the leafing phenology of a seasonally dry tropical forest in Belize, Central America. *Journal of Tropical Ecology*, **19**: 539–548.
- Seghier J, Floret CH, Pontanier R. 1995. Plant phenology in relation to water availability: herbaceous and woody species in the savannas of northern Cameroon. *Journal of Tropical Ecology*, **11**: 237–254.
- Seghier J, Vescovo A, Padel K, Soubie R, Arjounin M, Boulain N, Rosnay P, Galle S, Gosset M, Mouctar AH, Peugeot C, Timouk F. 2009. Relationships between climate, soil moisture and phenology of the woody cover in two sites located along the West African latitudinal gradient. *Journal of Hydrology*, **375**: 78–89.
- Silva MAP, Machado ICS. 1997. Biologia da reprodução e morfologia polínica de *Auxemma Miers*. *Boletim da Sociedade Broteriana*, **68**: 73–88.
- Singh KP, Kushwaha CP. 2005. Emerging paradigms of tree phenology in dry tropics. *Current Science*, **89**: 964–975.
- Spjut RW. 1994. *A systematic treatment of fruit types*. New York: New York Botanic Garden, p. 182.
- Van Schaik CP, Terborgh JW, Wright JS. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, **24**: 353–377.
- Venable DL. 2007. Bet hedging in a guild of desert annuals. *Ecology*, **88**, 1086–1090.
- Vieira DLM and Scariot A. 2006. Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology*, **14**: 11–20.
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebe TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F. 2002. Ecological responses to recent climate change. *Nature*, **416**: 389–395.
- Williams RJ, Myers BA, Muller WJ, Duff GA, Eamus D. 1997. Leaf phenology of woody species in a North Australian tropical savanna. *Ecology*, **78**: 2542–2558.
- Woodward FI, Lomas MR, Kelly CK. 2004. Global climate and the distribution of plant biomes. *Philosophical Transactions of the Royal Society B*, **359**: 1465–1476.
- Yadav RK, Yadav AS. 2008. Phenology of selected woody species in a tropical dry deciduous forest in Rajasthan, India. *Tropical Ecology*, **49**: 25–34.