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Reproductive phenology of Brazilian savannas and riparian forests: environmental and phylogenetic issues

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Abstract

· **Introduction** The reproductive phenology of plants is expected to be influenced by climatic factors and by the phylogenetic history of the species. In savannas, the peaks of flowering and fruiting are associated with climate seasonality. However, there is still a controversy about the reproductive phenology of plants in riparian forests, a vegetation type that does not experience a severe water shortage.
· **Methods** We tested whether the reproductive peaks in riparian forests are different from those of the savannas. We also tested if the number of species in flower is correlated with rainfall and day length. We sought evidence of phylogenetic signals in the reproductive periods of the species.
· **Results** Most of species in savannas and riparian forests flowered and fruited in the wet season. The number of flowering species was positively correlated with monthly rainfall and day length. However, we did not find phylogenetic signals in the reproductive periods.
· **Conclusions** The phenological pattern of riparian forests was similar to that of savannas. At the community level, the reproductive periods of plants may not be under phylogenetic constraints, as observed in forests under nonseasonal climate. Sun-related variables seem to be the main cues for the reproductive phenology of plants in savannas and riparian forests.

Keywords Cerrado · Flowering · Phenology · Phylogeny · Seasonality

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1 Introduction

Flowering and fruiting are important stages of the life history of plants, with both ecological and evolutionary consequences (Rathcke and Lacey 1985; Sakai 2001). The seasonal timing of flowering and fruiting, i.e. the reproductive phenology of plants, is directly associated with resource availability to animals and consequently has effects on herbivory, pollination and seed dispersal (Mduma et al. 2007; Stevenson et al. 2009; van Schaik et al. 1993). For these reasons, phenological synchronisation among individuals of a population is directly related to the reproductive success of the species (Sakai 2001).

The importance of phenological synchronisation for species survival may have led plants to link reproductive events to predictable environmental factors, such as rainfall, temperature, and day length (Borchert et al. 2002; Borchert et al. 2005). Some phenological studies of plant communities under seasonal climate have found that the reproductive phenology usually follows moisture availability (Batalha and Martins 2004; Boulter et al. 2006; Williams et al. 1999). However, it is still disputed whether climatic variables are the exclusive triggers of phenological events (Wright and Cornejo 1990). Other studies have also demonstrated that phenological events are under phyloge-

netic constraints (Kochmer and Handel 1986; Staggemeier et al. 2010; Wright and Calderon 1995), because plant species commonly present a high degree of evolutionary stasis (Qian and Ricklefs 2004) and niche conservatism (Prinzing et al. 2001). Consequently, phylogenetically related plants are expected to have similar flowering and fruiting periods, i.e. a phylogenetic signal (sensu Blomberg et al. 2003) in their reproductive times.

In South America, the largest savanna region is the Brazilian cerrado, which once covered 22% of the land surface of the country (22 million ha), mainly in the central region (Gottsberger and Silberbauer-Gottsberger 2006). The cerrado is strongly seasonal, with a dry season, from April to September, and a wet season, from October to March, which define the growth patterns of plant species (Gottsberger and Silberbauer-Gottsberger 2006). Riparian forests occur commonly along rivers and streams crossing the cerrado landscape. Depending on the soil moisture availability along rivers, riparian forests include from permanent waterlogged vegetation (i.e. swamp forests) to rarely waterlogged vegetation (i.e. gallery forests; Naiman and Décamps 1997). Although riparian forests within cerrado areas are under the same seasonal regional climate, the drought in the winter is believed to have a small influence over the plant community, since riparian areas are influenced by elevated water tables or flooding and by the ability of the soils to hold water (Naiman and Décamps 1997). For this reason, riparian forests have a distinct flora (Felfili et al. 2001).

Phenological studies in cerrado have found that the flowering and fruiting of plants are markedly associated with rainfall periods. The flowering generally occurs year round with peaks at the late wet season (February and March) for herbaceous species, and at the late dry and early wet seasons (August and September) for woody species (Batalha and Mantovani 2000; Batalha and Martins 2004; Oliveira and Gibbs 2000). In riparian forests, however, the seasonality of phenological events seems to be less pronounced. Whereas in some riparian forests the phenological events of the woody species are uniform along the year (e.g. Gouveia and Felfili 1998), in others they seem to be also associated with rainfall, with peaks in the wet season (e.g. Funch et al. 2002).

Although phenological patterns in savannas have been well reported throughout South America (see Morellato 2003 and references therein), as far as we know there is a lack of studies considering the phylogenetic relatedness of plants. In this study, we assessed the reproductive events of 366 plant species in cerrado and riparian forest sites. We tried to answer whether the (1) soil moisture availability, (2) climatic variables, or (3) phylogenetic relatedness are the dominant determinants of the phenological patterns of the plant community. Several alternative outcomes can be predicted. First, if soil moisture is the limiting factor that determines the timing of flowering, then the riparian forest species are expected to flower and fruit in different periods than the cerrado species, as water is available to riparian forest plants year round. By contrast, cerrado species would be expected to have peaks of flowering and fruit that coincide with moisture availability. However, if other climatic variables determine the phenology of plants, then the number of species in flower in cerrado and riparian forest might be expected to be correlated with rainfall or day length. Finally, if the phylogenetic signal in the flowering and fruiting is the dominant determinant of flowering, then phylogenetically related species are expected to have similar phenological periods, regardless of water availability and seasonality.

To sum up, we addressed the following specific questions: (1) Do the riparian forest species present reproductive peaks different from the cerrado species? (2) Are the reproductive peaks of the herbaceous and woody species in riparian forests different from each other and from those in cerrado? (3) Is the number of species in flower related to precipitation or day length? (4) Do the closely related species have similar periods of flowering and fruiting?

2 Methods

2.1 Study areas

We carried out this study in a fragment of woodland cerrado of about 125 ha at the Federal University of São Carlos, São Paulo countryside, southeastern Brazil (21°58′–22°00′ S, 47°51′–47°52′ W). Regional climate is markedly seasonal, with wet summers and dry winters (Cwa; Köppen 1931). The average annual rainfall is 1,339 mm, and the average annual temperature is 22.1°C. The soil is dystrophic on a flat topography, and the water table is reached 10 m below the surface. In the western portion of the cerrado fragment, there is a 50-m wide swamp forest in width along the Fazzari stream, which has 1.0 m in width and 0.3 m in depth approximately. The swamp forest presents a continuous canopy cover about 15 m high. The understory is composed by a mix of herbs, ferns and dwarf shrubs sparsely distributed.

In February 2007, we systematically placed five parallel transects in the swamp forest, two on one side of the stream, three on the other. In each transect, we established 20 contiguous plots of 25 m². About 500 m distant from the swamp forest, we also systematically placed five parallel transects in a cerrado site, where we established 20 contiguous plots of 25 m² in each transect. From February 2007 to January 2008, we visited monthly the two sites, where we observed all individuals of angiosperms in the

plots. In the swamp forest, we used binoculars to search for flowers and fruits in the canopy of trees. The individuals at reproductive stage were identified in the field or collected for comparison with vouchers lodged at the herbarium of the Escola Superior Luiz Antônio de Queiroz. The observations were qualitative: for example, if at least one individual of a determined species was found producing flowers, the species was considered to be on its flowering period. We increased the phenological data with observations on trails of approximately 1.5 km within these sites of cerrado and riparian forests. Then, we classified the species in families according to a recent phylogenetic classification of angiosperms (Davies et al. 2004) and in growth forms according to Cornelissen et al. (2003). We considered the tree, shrub, climber, and palmoid species as belonging to woody component and the species with other growth forms as belonging to herbaceous component (see Electronic Appendix 1 in the Electronic supplementary material (ESM)).

To compare our results, we also analysed published flowering periods of woody species in a gallery forest at the Onça stream, in Brasília, central Brazil, approximately 15°50′ S, 47°50′ W (Oliveira and Paula 2001), comparing them with the flowering periods of woody species in a nearby woodland cerrado site in the Brasília Botanical Garden reserve, approximately 15°58′ S, 47°51′ W (Oliveira and Gibbs 2000). These nearby sites are also under a marked seasonal climate, with dry winters and wet summers (Aw; Köppen 1931).

Since the plant communities were sampled in different regional climates and with different methods, we first established a design for comparisons within Brazilian regions: we compared (1) the cerrado and swamp forest we sampled in southeastern Brazil (Cwa; Köppen 1931) and (2) the cerrado and gallery forest sampled by Oliveira and Gibbs (2000) and by Oliveira and Paula (2001) in central Brazil (Aw; Köppen 1931). Thus, we did not combine the data on the same vegetation type.

2.2 Data analysis

2.2.1 Phenological data

As our data were normally distributed (Shapiro–Wilk test), we used parametric circular statistics to analyse the number of species in flower and in fruit in each month in cerrado and in riparian forest. Circular statistics allow us to study seasonality in reproduction, being particularly useful in southern climates where flowering has not a logical starting point and reproducing events can occur almost continuously in an annual cycle (Morellato et al. 2010). Circular statistics can be used to characterise peaks in reproductive events and is recommended to formally compare and test hypotheses in

plant phenology (Morellato et al. 2010). In our dataset, peaks are related to months that correspond to the average of the reproductive period and can be tested for differences in ecological dynamics between vegetation types. Our phenological data corresponded to one year cycle; therefore, they are better analysed with circular statistics (Morellato et al. 2010).

First, we applied the Rayleigh test of uniformity (Zar 1999) in which the 1st of January corresponded to 15°, 1st of February corresponded to 45°, 1st of March corresponded to 75°, and so on, to answer whether there were reproductive peaks in cerrado and riparian forests. We also used this statistical test to answer whether the herbaceous and woody species flowered and fruited uniformly throughout the year. Then, to answer the first and second questions, we used the Watson–Williams test (Zar 1999) to evaluate whether the mean angles (i.e. the months that represent the average of the reproductive period) were different. We did these analyses with the 'circular' package (version 0.3-8, http://cran.r-project.org/web/packages/circular/) for the R environment (http://www.R-project.org).

2.2.2 Climatic data

To answer our third question, we correlated (1) the monthly rainfall (based on a 30-year record) in Brasília and in São Carlos, and (2) the average day length for each month to the number of herbaceous and woody species in flower in the cerrado and riparian forest sites. We estimated the Pearson's correlation coefficient and applied the t test to evaluate if the correlation was different from zero (Zar 1999). We obtained the monthly rainfall data from records of the Brazilian Agricultural Research Corporation (Embrapa, http://www.bdclima.cnpm.embrapa.br/) and computed the day length with tools from The United States Naval Observatory (USNO, http://www.usno.navy.mil/USNO/astronomical-applications/data-services/rs-one-year-world).

2.2.3 Phylogenetic data

To answer our last question, we first constructed a phylogenetic tree for the species sampled in São Carlos and another for the species sampled in Brasília with the Phylomatic software, a phylogenetic toolkit for the assembly of phylogenetic trees (Webb and Donoghue 2005). We included in these phylogenetic trees only those species classified at least to the genus level. The node ages of families were estimated from the dated angiosperm super-tree of Davies et al. (2004). We assigned branch lengths to genus and species of the phylogenetic tree by using the Branch Length Adjustment averaging algorithm of the Phylocom software package (version 4.0.1, http://

www.phylodiversity.net/phylocom/). The algorithm spaces undated nodes evenly between dated nodes in the tree. When a family node presented polytomies, we distributed the genera into their subfamilies following the last angiosperms relationship (Angiosperm Phylogeny Website, Version 9, http://www.mobot.org/MOBOT/research/APweb/). We assigned branch lengths of these genera by spacing undated nodes evenly above family node.

We calculated the phylogenetic distances from the estimated intervening branch length distances (measured in millions of years) between all species pairs with the Phydist module of the Phylocom software (version 4.0.1, http://www.phylodiversity.net/phylocom/). We estimated the mean angles of flowering and fruiting periods and calculated the difference between mean angles of all species pairs. Then, we compared the correlation coefficient between phylogenetic distances and mean angle differences of all species pairs to a null model, in which the differences in mean angles were randomised (Mantel test; Manly 2004). We also applied Mantel tests to compare the phylogenetic distances between genera and families with the differences between mean angles of genera and families.

3 Results

We analysed the flowering and fruiting periods of 196 species belonging to 56 families in the cerrado and of 97 species belonging to 47 families in the swamp forest, in southeastern Brazil. We also analysed the flowering period of 43 woody species belonging to 26 families in the cerrado and of 84 woody species belonging to 45 families in the gallery forest, in central Brazil (see Electronic Appendix 1 in the ESM). The results of these analyses are presented below.

3.1 Uniformity test

Considering all sampled plants in southeastern Brazil, the number of flowering and fruiting species was not uniformly distributed throughout the year (Fig. 1; Table 1; $P<0.05$). In general, most of the species in cerrado as well as in swamp forest flowered and fruited in the wet season (Table 1). However, the peaks of flowering and fruiting of the species in swamp forests occurred before those of the species in cerrado ($F=0.33$; $P<0.01$ for flowering, $F=0.46$; $P<0.01$ for fruiting).

When we independently analysed the herbaceous and woody plants, the number of flowering and fruiting species was also not uniformly distributed throughout the year (Fig. 2; Table 2; $P<0.05$). In general, the peaks of flowering and fruiting of the herbaceous species occurred

after those of the woody species in both vegetation types ($F<1.10$; $P<0.05$ for all comparisons). Most of the herbaceous species flowered and fruited at the end of the wet season, whereas most of the woody species flowered and fruited at the end of the dry season and at the beginning of the wet season (Table 2).

3.2 Comparisons between cerrado and riparian forests within regions

When we compared the flowering and fruiting patterns of both herbaceous and woody species between cerrado and swamp forest, the only significant pattern was in the fruiting peaks. The fruiting peaks of the herbaceous and woody species in the swamp forest were not different from those of the herbaceous and woody species in the cerrado (Table 2, $F=1.13$ for woody species, $F=0.54$ for herbaceous species, $P>0.05$ for both comparisons). In the southeastern sites, the flowering peaks of the herbaceous and woody species in the swamp forest occurred before those of the herbaceous and woody species in the cerrado ($F<0.50$, $P<0.05$ for both comparisons). By contrast, in central Brazil, the flowering peak of woody species in the gallery forest occurred after the flowering peak of woody species in the cerrado (Table 2; $F=13.25$, $P<0.01$).

3.3 Correlations between flowering and climatic variables

The number of flowering species was not strongly correlated with climatic variables. Most of the correlations with the monthly rainfall and day length were not significant (Table 3; $R^2<0.25$, $P>0.05$). Nevertheless, the number of flowering herbaceous species in the swamp forest was positively correlated with monthly rainfall ($R^2=0.73$, $t=5.26$, $P<0.01$) and day length ($R^2=0.45$, $t=2.87$, $P<0.01$), and the number of flowering woody species in the cerrado was positively correlated with day length ($R^2=0.31$, $t=2.19$, $P=0.05$), in southeastern Brazil.

3.4 Phylogenetic signal test

The comparison between phylogenetic distances and differences of mean angle of the flowering and fruiting periods of the species was not significantly correlated ($r=0.004$, $P=0.336$ for flowering; $r=-0.014$ for fruiting, $P=0.773$ in southeastern sites and $r=-0.029$ for flowering, $P=0.995$ in central sites). When we considered the differences of mean angle of genera and families, we also did not observe significant correlations ($-0.05<r<0.06$, $P>0.05$ for all comparisons). Thus, we did not find a phylogenetic signal in the reproductive periods of plants in cerrado and riparian forest sites.

Fig. 1 Proportion of species **a** flowering in the cerrado, **b** flowering in the swamp forest, **c** fruiting in the cerrado and **d** fruiting in the swamp forest, in southeastern Brazil (approximately, 22°00′ S, 47°51′ W)
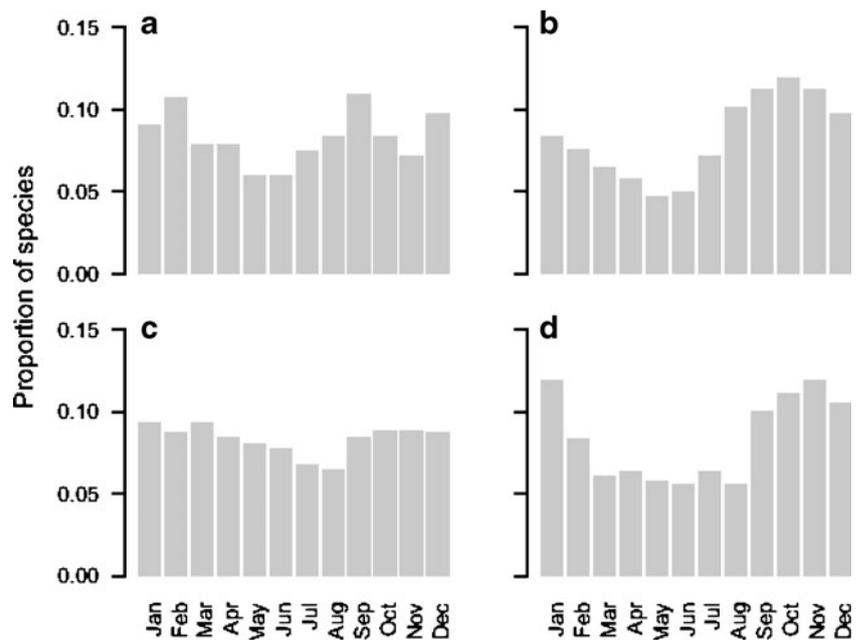
4 Discussion

4.1 Reproductive peaks in the wet season

The riparian forests had annual flowering and fruiting peaks. These phenological periods were in general similar to those found in cerrado, i.e. the species flowered and fruited predominantly in the wet season. There was no evidence from our data that the small seasonal variation in soil moisture in riparian forests influenced the reproductive periods of plants. However, we did not observe any strong correlations between the number of flowering species and climatic variables we considered or a phylogenetic signal in the reproductive periods of species.

In the absence of a phylogenetic signal, the cue to flowering is likely to be environmental. While we did not find any evidence of this relationship, this may be because several environmental factors are at work or we did not test for the appropriate environmental factor. The cerrado plants show a multitude of phenological strategies that are to a certain extent independent of rainfall and soil moisture (Monasterio and Sarmiento 1976; Sarmiento and Monasterio 1983). The phenology of riparian forest species also appear

to respond weakly to soil moisture availability (Funch et al. 2002; Wright and Calderon 1995; Wright and Cornejo 1990). Thus, other factors such as sun-related variables (Borchert et al. 2005), could predominantly trigger flowering and fruiting in cerrado and riparian forests.

4.2 Comparisons between cerrado and riparian forests

Considering all species, the peaks of flowering and fruiting occurred in the wet season in both cerrado and riparian forest sites. In other seasonally dry communities (savannas: Williams et al. 1999; Batalha and Martins 2004; dry forests: Borchert et al. 2002) or even in communities with weak climatic variation (Atlantic rain forests: Morellato et al. 2000; gallery forests: Funch et al. 2002), there are also seasonal peaks of reproductive events in the late dry or early wet season. Although seasonally dry communities are under moisture seasonality, sun-related environmental factors, such as day length and insolation, seem to be the only reliable environmental cues for synchronisation of reproductive events, since they do not vary over the years (Borchert et al. 2005). Our results demonstrated some support for

Table 1 Rayleigh test of uniformity (Z), mean angles (in degrees) of flowering and fruiting periods and the months that correspond to the average of the reproductive period distributions in cerrado and swamp forest sites in São Carlos, southeastern Brazil

Vegetation type	Phenological data	Mean angle	Month	Z	P
Cerrado	Flowering	320.4	November	0.077	0.031
Cerrado	Fruiting	3.5	January	0.062	0.053
Swamp forest	Flowering	281.2	October	0.199	0.001
Swamp forest	Fruiting	312.7	November	0.198	0.001

Fig. 2 Proportion of **a** herbaceous and **b**, **c** woody species flowering in cerrado, **d** herbaceous and **e**, **f** woody species flowering in riparian forest, **g** herbaceous and **h** woody species fruiting in cerrado and **i** herbaceous and **j** woody species fruiting in riparian forest in **a**, **b**, **d**, **e**, **g**–**j** southeastern Brazil (approximately, 22°00′ S, 47°51′ W) and **c**, **f** central Brazil (**c** approximately, 15°58′ S, 47°51′ W; Oliveira and Gibbs 2000; **f** approximately, 15°50′ S, 47°50′ W; Oliveira and Paula 2001)
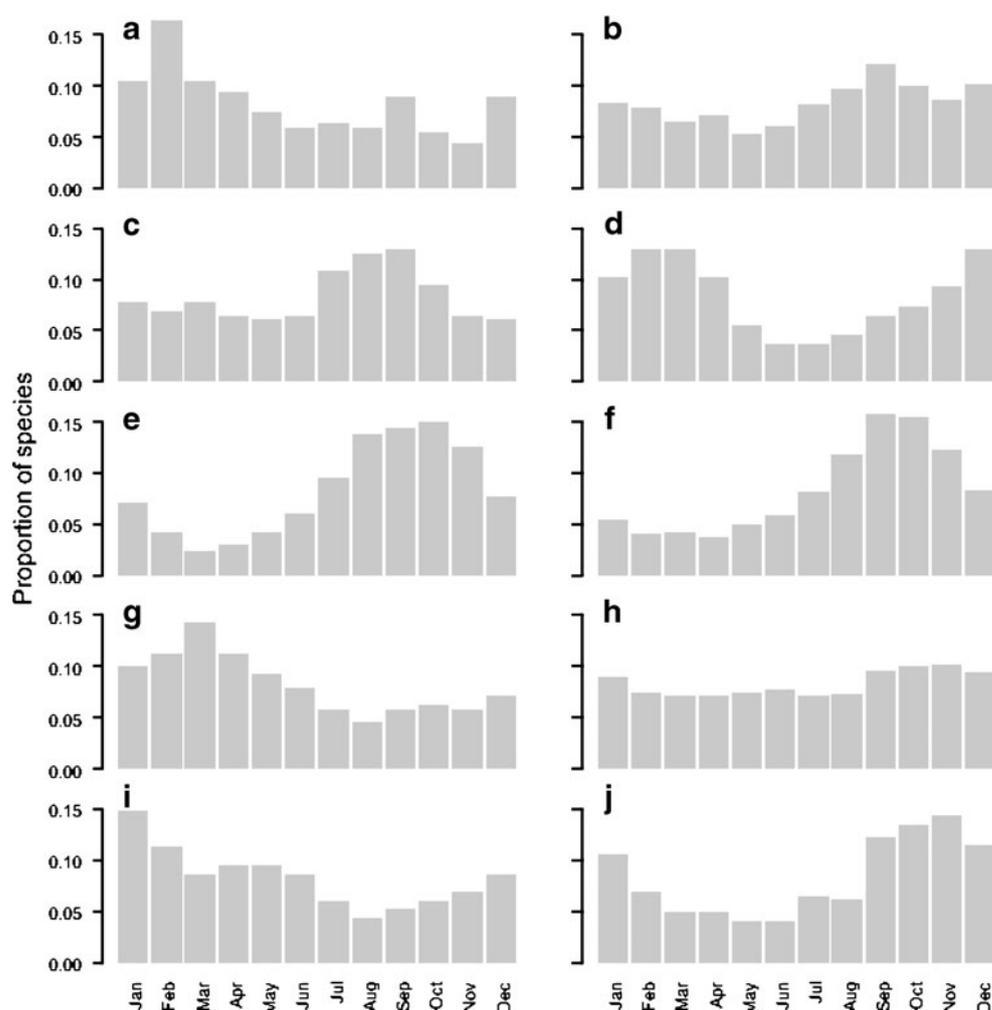
day length as a determinant of peaks in flowering of plant communities in cerrado and riparian forests (Table 3). Thus, sun-related variables may also explain the reproductive peaks in plant communities where species have access to water during most of the year, such as those in riparian forests.

4.3 Comparisons between woody and herbaceous component

We observed in the cerrado sites (1) reproductive peaks of woody species at the end of the dry season—beginning of the wet season and (2) reproductive peaks of herbaceous

Table 2 Rayleigh test of uniformity (Z), mean angles (in degrees) of flowering and fruiting periods and the months that correspond to the average of the reproductive period distributions in cerrado and riparian forest sites in southeastern and central Brazil

Region	Vegetation type	Component	Phenological data	Mean angle	Month	Z	P
Southeastern	Cerrado	Herbaceous	Flowering	52.9	February	0.188	0.001
Southeastern	Cerrado	Herbaceous	Fruiting	73.1	March	0.223	0.001
Southeastern	Cerrado	Woody	Flowering	290.3	October	0.136	0.001
Southeastern	Cerrado	Woody	Fruiting	309.3	November	0.087	0.017
Southeastern	Swamp forest	Herbaceous	Flowering	30	January	0.272	0.001
Southeastern	Swamp forest	Herbaceous	Fruiting	53.9	February	0.194	0.013
Southeastern	Swamp forest	Woody	Flowering	267.8	September	0.369	0.001
Southeastern	Swamp forest	Woody	Fruiting	309.9	November	0.299	0.001
Central	Cerrado	Woody	Flowering	198.7	August	0.131	0.001
Central	Gallery forest	Woody	Flowering	238.8	September	0.389	0.001

Table 3 Correlation test between the number of flowering herbaceous and woody species in cerrado and riparian forests and both monthly rainfall and day length, in southeastern and central Brazil. Significant values of R^2 are in bold (α=0.05)

Region	Vegetation type	Component	Rainfall			Day length		
			R^2	t	P	R^2	t	P
Southeastern	Cerrado	Herbaceous	0.25	1.82	0.10	0.06	0.82	0.43
Southeastern	Cerrado	Woody	0.06	0.78	0.45	**0.31**	2.19	0.05
Southeastern	Swamp forest	Herbaceous	**0.73**	5.26	0.01	**0.45**	2.87	0.02
Southeastern	Swamp forest	Woody	0.03	0.55	0.59	0.23	1.75	0.11
Central	Cerrado	Woody	0.2	−1.60	0.14	0.07	−0.87	0.41
Central	Gallery forest	Woody	0.07	−0.91	0.38	0.01	0.21	0.84

species at the end of the wet season, as in other studies (Batalha and Mantovani 2000; Batalha and Martins 2004). Thus, the climatic seasonality provides a potential axis of niche separation by phenology for the herbaceous and woody plants in cerrado (Scholes and Archer 1997). It has been argued that this phenological separation is due to the differential moisture availability for woody and herbaceous species (Batalha and Martins 2004; Sarmiento and Monasterio 1983). Whereas the woody component is predominantly deep rooted and can reach soil layers where water is available (Oliveira et al. 2005), the herbaceous component depends on the rainy season, when the species gradually develop their shoots and reproductive structures (Sarmiento and Monasterio 1983). However, the phenological pattern that we observed in riparian forests does not support this expectation. The reproductive peaks were similar to those observed in cerrado sites, even though riparian forest soils do not experience extensive water shortage (Naiman and Décamps 1997). Again, annual variation in sun-related environmental factors may explain the observed patterns in both riparian forest and cerrado sites (Morellato et al. 2000; Borchert et al. 2005).

We did not observe a flowering pattern among species of the same component in both cerrado and riparian forests, even when considering the components under the same regional climate. In a seasonal tropical forest, differences of microhabitat, such as water and light conditions, are related to distinct patterns of flowering and fruiting at the same regional climate (Thies and Kalko 2004). Future studies should investigate the influence of microclimatic variables over the reproductive events in cerrado and riparian forests. However, in southeastern sites, the flowering peaks in the riparian forest occurred before those in the cerrado, reinforcing that the plants in riparian forest are independent from the first rains to flowering, especially the herbaceous species with shallow roots (Sarmiento and Monasterio 1983).

4.4 Fruiting peaks

The fruiting peaks were similar in cerrado and riparian forest. The peaks of fruiting in the wet season suggest an overall ecological strategy of plants in both vegetation types to improve the germination success, by dispersing fruits and releasing seeds during wetter soil conditions. Thus, germination success seems to be the ultimate cause of fruiting synchronization, but the onset of the wet season is the proximate cue. Oliveira (2008) has observed that cerrado species with distinct fruiting periods synchronise the seed germination and seedling establishment to the beginning of the rainy season. In this case, species that release their seeds at the end of the wet season or during the dry season keep them dormant until the beginning of the next rainy season (Oliveira 2008). This adjustment maximises the survival of the seedling that has the entire rainy season to grow. Accordingly, the water shortage in the dry season seems to be a stronger selective force for synchronisation of germination than for synchronization of fruiting. In riparian forests, however, the water shortage may be not a selective force and the adjustment of the germination is not predicted.

4.5 Phylogenetic signal

The phylogenetic signal in reproductive events has been found in several tropical plant communities (Boulter et al. 2006; Kochmer and Handel 1986; Staggemeier et al. 2010; Wright and Calderon 1995). Phylogenetic signals seem to be a characteristic of plant traits related to environmental tolerances, such as light, soil moisture and pH (Prinzing et al. 2001). These traits are associated with habitat requirements and consequently they define the 'β niche' of the species, referring to the scale at which β-diversity is determined (Silvertown et al. 2006). However, absence of phylogenetic signal in traits that determine within-habitat α-diversity (α niche) may also be common (Silvertown et al. 2006), because α niches define the species interactions within a community and therefore are expected to be different for species to coexist (Silvertown et al. 2006). Nevertheless, evidence of overdispersion of reproductive periods that would indicate a mechanism of coexistence is generally little (Boulter et al. 2006). Thus, our results supported the idea that the evolution of reproductive periods may be indeed random in relation

to species phylogeny. In seasonal forests, flowering patterns of taxonomically related species are also not different from random (Stevenson et al. 2009). Thus, even if there is a phylogenetic signal in reproductive periods of tropical communities (Boulter et al. 2006; Staggemeier et al. 2010; Wright and Calderon 1995), it may have a lower importance in plant communities under marked seasonal variation.

Recently, Staggemeier et al. (2010) demonstrated the shared influence of environment and phylogeny on the reproductive events of Myraceae species, i.e. closely related plants flowered under similar climatic conditions. However, we did not find any evidence of phylogenetic conservatism of flowering and fruiting time in cerrado and riparian forest. Although the combined effect of environment and phylogeny is predicted to be present in other plant families (Staggemeier et al. 2010), at the community level, this effect may be hard to detect. The mixture of different phenological strategies in plant communities in cerrado (Monasterio and Sarmiento 1976; Sarmiento and Monasterio 1983) may hide the phylogenetic constrains present at smaller taxonomic scales.

5 Conclusions

The riparian forests showed peaks of flowering and fruiting similar to cerrado, in spite of the small seasonality in soil moisture availability. These peaks were partially explained by day length and rainfall. Therefore, sun-related factors may be the main cues for the phenology of species in both cerrado and riparin forest, as well as in other vegetation types (Morellato et al. 2000; Borchert et al. 2005). Nevertheless, the reproductive periods of plants under seasonal climatic variation may not be under phylogenetic constraints, as observed in nonseasonal plant communities (Wright and Calderon 1995) and in restricted taxonomic groups (Staggemeier et al. 2010). Climatic factors seem to be more important than phylogenetic history in determining the reproductive periods of plants in savannas and riparian forests. Further studies should search for phylogenetic constraints in phenological events and for correlations between climatic variables and reproductive periods in other vegetation types under seasonal climatic variation (for example, in grasslands) to corroborate our generalisation.

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