Phenology of two *Ficus* species in seasonal semi-deciduous forest in Southern Brazil

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Received: June 2, 2014 – Accepted: October 2, 2014 – Distributed: November 30, 2015 (With 3 figures)

Abstract

We analyzed the phenology of *Ficus adhatodifolia* Schott ex Spreng. (23 fig tree) and *F. eximia* Schott (12 fig tree) for 74 months in a remnant of seasonal semi-deciduous forest (23°27'S and 51°15'W), Southern Brazil and discussed their importance to frugivorous. Leaf drop, leaf flush, syconia production and dispersal were recorded. These phenophases occurred year-round, but seasonal peaks were recorded in both leaf phenophases for *F. eximia* and leaf flushing for *F. adhatodifolia*. Climatic variables analyzed were positively correlated with reproductive phenophases of *F. adhatodifolia* and negatively correlated with the vegetative phenophases of *F. eximia*. In despite of environmental seasonality, little seasonality in the phenology of two species was observed, especially in the reproductive phenology. Both species were important to frugivorous, but *F. adhatodifolia* can play a relevant role in the remnant.

Keywords: Ficus adhatodifolia, F. eximia, figs, food resources, tropical forest.

Fenologia de duas espécies de *Ficus* em floresta estacional semidecidual no sul do Brasil

Resumo

Foi analisada a fenologia de *Ficus adhatodifolia* Schott ex Spreng. (23 indivíduos) e *F. eximia* Schott (12 indivíduos), por 74 meses em um remanescente de floresta estacional semidecidual (23°27'S e 51°15'W, centro de visitantes) no sul do Brasil e discutido sua importância para os frugívoros. Foram registradas as fenofases: queda e brotamento de folhas, produção e dispersão de siconios. Estas fenofases ocorreram ao longo do ano, porém picos sazonais foram registrados em abscisão e brotamento foliares para *F. eximia* e brotamento foliar para *F. adhatodifolia*. As variáveis climáticas analisadas foram positivamente correlacionadas com as fenofases reprodutivas de *F. adhatodifolia* e negativamente correlacionadas com as fenofases vegetativas de *F. eximia*. Apesar da sazonalidade ambiental, foi observada baixa variação sazonal na fenologia das duas espécies, especialmente na fenologia reprodutiva. Ambas as espécies foram consideradas importantes para os frugivoros, porém *F. adhatodifolia* pode desempenhar papel de destaque no fragmento florestal.

Palavras-chave: Ficus adhatodifolia, F. eximia, figueiras, floresta tropical, recurso alimentar.

1. Introduction

Although, the seasons are less evident in the tropics than in the temperate regions, several studies showed seasonality in leaf change and reproductive phenology in the tropics (Reich, 1995; Justiniano and Fredericksen, 2000; Morellato et al., 2000; Shanahan et al., 2001; Bianchini et al., 2006; Singh and Kushwaha, 2006).

A period of lower water availability is characteristic of seasonal forest in the tropics (Gurevitch et al., 2009). Rain seasonality associated with temperature and photoperiod seasonalities, as observed in southern Brazil, can generate a

seasonal phenological pattern in forest species, as observed by Marques et al. (2004) and Bianchini et al. (2006).

Species that produce leaves, flowers or fruits during periods of low resource availability may be considered important food producers for fauna (Terborgh, 1986; Shanahan et al., 2001; Ragusa-Netto, 2006; 2007). Among them, we highlight the fig tree (*Ficus* spp.), that are a remarkable food resource for frugivores, mainly in periods of fruit scarcity, as has been highlighted in several studies in various parts of the world (Terborgh, 1986; Lambert and Marshall, 1991; Shanahan et al., 2001; Ragusa-Netto,

2002, 2007; Tello, 2003). However, another authors found different results in their studies and not confirmed the key role of these species (Gautier-Hion and Michaloud, 1989; Kattan and Valenzuela, 2013).

Ficus species exhibit diverse fruiting phenology patterns (Spencer et al., 1996). Although the leaf change can occur seasonally (Spencer et al., 1996; Zhang et al., 2006; Pereira et al., 2007), the reproductive phenology has been registered as asynchronous at the population level (Eshiamwata et al., 2006; Zhang et al., 2006; Pereira et al., 2007; Ragusa-Netto, 2007), probably due to constraints imposed by the obligate mutualism with pollinating wasps.

In species with broad geographical distribution, as *F. eximia* Schott, would be important to determine whether the phenological pattern is repeated across the area of their occurrence. According to Muhanguzi and Ipulet (2011), an understanding of the figs' phenology and the influencing factors is of significant importance for the biodiversity conservation and appropriate forest management. This is especially important in Seasonal Semi-deciduous Forest in Brazil, once these forests are highly fragmented.

This paper describes the phenology of *Ficus adhatodifolia* Schott ex Spreng. and *F. eximia* Schott in a remnant of seasonal semi-deciduous forest (SSF) in the South limit of tropical zone and the South edge of species distribution ranges. These figs species are among the most abundant *Ficus* species in SSF in Southern Brazil. We aim to contribute in determining the importance of figs in food fauna during periods of lower food resource in SSF. We ask the following questions: (1) what are the patterns of leaf and reproductive phenology of these species? (2) Theses phenological patterns accredit *F. adhatodifolia* and *F. eximia* as important food producers for wildlife? This is the first study conducted in the Southern edge of range for both species and little is known about the basic ecology and life history for these species.

In this study, the species names are in according to Berg and Villavicencio (2004). Also, we adopted the position of these authors that recognizes *F. adhatodifolia* as a good species, although it is very similar to *F. insipida*.

2. Methods

This study was developed in Mata dos Godoy State Park (MGSP) (23°27'S and 51°15'W – visitors center) located in Londrina Municipality, Paraná State, Southern Brazil. The MGSP has 680 ha and is under Köppen's Cfa climate - humid subtropical mesothermal (Bianchini et al., 2003). The average annual temperature is 21.3°C, with registered temperatures up to 40°C in summer and frosts in winter, as occurred in 2000. The average annual rainfall is 1,567 mm. Rainfall in summer is about two times higher than in winter (Bianchini et al., 2001). The dry and cold considered period goes from April to September (autumn and winter) and warm and wet period from October to March (spring and summer). Although, precipitation is low only in July and August (Figure 1).

The MGSP presents good preservation conditions, nevertheless it is surrounded by an agricultural matrix.

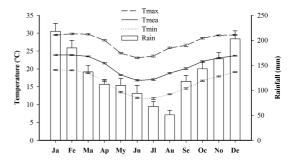


Figure 1. The means monthly rainfall (bars) and temperature (line) for Londrina Municipality, Paraná State, Southern Brazil. Rainfall and Temperature averages are from 1976 to 2012 (records granted by the Instituto Agronômico do Paraná). Errors bars indicate standard errors.

The forest canopy is between 12 m and 16 m, with emergent trees reaching 35 m in height.

Ficus adhatodifolia (subgenus Pharmacosycea) shows close affinities to F. insipida (Berg and Villavicencio, 2004). The species is a monoecious tree, freestanding, light-demanding and can become large emergent trees (Carauta and Diaz, 2002). In Brazil, the species occurs in both wet (Amazonian and Atlantic Forests) as dry (Cerrado and Caatinga regions) tropical forests (Romaniuc-Neto et al., 2010). Their figs are axillary (or in pairs), green and can reach 5 cm in diameter (Carauta and Diaz, 2002; Berg and Villavicencio, 2004). In the MGSP, Ficus adhatodifolia showed a density of six individuals per hectare (Soares-Silva and Barroso, 1992).

Ficus eximia (subgenus Urostigma) is big monoecious tree and can present hemi-epiphytic habit (Carauta and Diaz, 2002). It is an endemic Brazilian species and occurs in Amazon, Cerrado and Atlantic Brazilian's biomes (Romaniuc-Neto et al., 2010). Its syconia are axillary, light green and can reach 1-1.5 cm in diameter. They are sessile or subsessile and have prominent ostiole. The syconia cluster at the terminal portion of the branches (Carauta and Diaz, 2002). In the MGSP, the species showed a density of about three individuals per ha (field observations).

We monitored 23 and 12 figs tree of *F. adhatodifolia* and *F. eximia*, respectively, along two trails in the MGSP northern part. The sampled area was about 4 ha. Phenology monitoring was conducted monthly, with the aid of binoculars, from April 1999 to December 2003 and from April 2005 to September 2006, totaling 74 months of observations. Because no observations were made during the interval between two sampling dates (usually 30 d), it was assumed that in a fig tree a particular phenophase began before, or continued beyond, the date of the first/last record. So, phenological phases durations were calculated from 15 days before the date on which the event was recorded for the first time to 15 days after the date on which the event was recorded for the last time, according to Singh and Kushwaha (2006).

Leaf drop (by observing the presence of leaves on the ground and/or the presence of gaps in the canopy), leaf flush (presence of stipules on the floor and/or young leaves on the branches), syconia production and syconia dispersal were recorded. The syconia represent both flower and fruit production and we can not recognize these stages externally. So, we registered the syconia production when we observed the emergence of syconia in a given individual and we recorded syconia dispersal when we observed any evidence of it (presence of softened syconia on the ground, change in syconia color, crop reduction or animal movement).

At each census, the phenophases were quantified, as a proportion of the crown, using a 0-3 scale (0 – absent phenophase, 1 – up to 30% of the crown presents phenophase, 2 – from 30% to 60% of the crown presents phenophase, 3 – more than 60% of the crown presents phenophase) (Bianchini et al., 2006).

Data are presented as mean intensity of production and average percentage of individuals displaying the phenophase in each month of study. The intensity was determined by adding the scores of each individual at each sampling date.

To evaluate whether the phenophase were seasonal, we using the ORIANA software for circular data analyses (Kovach, 1994). The mean angle or mean date is the time of the year around which the dates of a given phenophase occurred. The Rayleigh test (z) determines the significance of the mean angle. There is a significant mean angle or mean direction and consequently, there is some seasonality. The vector r has no units and may vary from 0 (when phenological activity is distributed uniformly throughout the year) to 1 (when phenological activity is concentrated around one single date or time of the year).

We used linear correlation analysis to assess whether the phenophases were correlated with climatic variables. For this analysis, in each month, phenological data (dependent variables) were correlated with monthly precipitation, with the monthly average temperature and monthly photoperiod (independent variables). We also considered the climatic variables corresponding to the monthly averages that occurred on prior month (30-days time lags). In general, data structured in time series, like those analyzed in this study, are auto-correlated. Therefore, we used generalized least squares (GLS) models with auto-correlated errors. The autoregressive models were selected using Akaike information criterion. More details are available in Pereira et al. (2007). In these analyses, the occurrence of phenophase in an individual was considered only the first time it was recorded. These statistical analyses were performed with the R software (R Development Core Team, 2005).

We also recorded animals species that fed on *F. adhatodifolia* and *F. eximia* between September 2005 and July 2006, during the phenological observations (about 24 h by species).

3. Results

For both species, we did not observe the temporal order of phenological events. In some observations, syconia production could occur simultaneously with leaf shed and leaf flush on the same individual.

In *F. adhatodifolia* population, the leaf shedding occurred throughout the year, but higher values occurred in March and August (Figure 2a). Each individual may

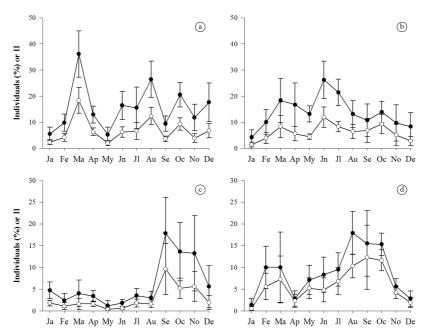


Figure 2. Leaf fall (a, b) and leaf flushing (c, d) in *Ficus adhatodifolia* (a, c) and *F. eximia* (b, d) trees in the Mata dos Godoy State Park, Londrina Municipality, Paraná State, Southern Brazil. The values are based on 74 months of observations. Solid circles = % of individuals; leaked circles = II (intensity index). Errors bars indicate standard errors.

shows more than one major event per year, and in each event, they lose only part of their crown leaves. We rarely observed individuals with completely defoliated crowns and these records were made in September 2000, November 2001 and October 2005 (12%, 4% and 4% of individuals, respectively). On average, these individuals remained leafless for 25 days (\pm 16). This phenophase was aseasonal (Table 1) and did not correlate with the climatic variables analyzed in the same month of phenological observation (Table 2). However, it was positively correlated with total precipitation within 30-days time lags (Table 2).

In *F. eximia*, the leaf shedding occurred throughout the year, with higher values from March to October and peak in June (Figure 2b). We observed about four times more individuals without leaves from June to September (about 12% of individuals) than in the other months of the year (about 3%). Tree leafless occurred once a year and, on average, the individuals remained leafless for 31 days (\pm 17). There was no difference when comparing the warm and wet period (October-March) (28 ± 16) and

the cold and dry period (April to September) (32 ± 17) . This phenophase showed weakly seasonal (Table 1) and negatively correlated with all climatic variables in the same month of phenological observation and with average temperature and photoperiod of the prior month to sampling (Table 3). In the period from May to August 2006 rained only 98 mm and, during this period, 67% of individuals had their crown without leaves, which was not observed in other years.

The occurrence of frost in July 2000, caused severe leaf shedding in all individuals. This phenophase extending until October to *F. adhatodifolia* and until September to *F. eximia*. For the last species, leaf shed occurred again in April 2001.

In *F. adhatodifolia*, leaf flushing occurred year-round with higher percentages from September to November (Figure 2c). This phenophase was seasonal (Table 1), but did not correlate with climatic variables analyzed (Table 2).

Leaf flushing also occurred thoughtout year in *F. eximia* with higher percentages from August to October (Figure 2d).

Table 1. Results of circular statistic analyses testing for the occurrence of seasonality on phenological phases in *Ficus adhatodifolia* (FA) and *F. eximia* (FE) at the Mata dos Godoy State Park, Londrina Municipality, Paraná State, Southern Brazil.

	Leaf shed	Leaf flush	Fig production	Fig dispersal
FA				
Observations (n)	187	75	156	157
Mean group	May	October	February	February
Circular standard deviation	145.1°	68.7°	108.4°	115.2°
Length of mean vector (r)	0.04	0.49	0.17	0.13
Rayleigh test uniformity (P)	0.74	< 0.01	< 0.05	0.06
FE	Leaf shed	Leaf flush	Fig production	Fig dispersal
Observations (n)	133	107	88	82
Mean group	June	August	August	September
Circular standard deviation	98.7°	91.3°	115.1°	99.6°
Length of mean vector (r)	0.23	0.28	0.13	0.22
Rayleigh test uniformity (P)	< 0.01	< 0.01	0.21	0.02

Table 2. Results of generalized least squares regressions that explain the effect of monthly rainfall, mean monthly temperature and photoperiod on the phenology of *Ficus adhatodifolia* at the Mata dos Godoy State Park, Londrina municipality, Paraná State, Southern Brazil. PM – prior month of phenological observations; SC – Standard coefficient; SM – same month of phenological observations.

	Rainfall		Te	Temp			Photo	oto	
	SC	t	P	SC	t	P	SC	t	P
Leaf shed									
SM#	-0.03	-0.31	0.75	0.01	0.03	0.98	-0.03	-0.50	0.62
PM#	0.21	2.44	0.017	-0.08	-1.03	0.30	-0.01	-0.05	0.96
Leaf flush									
SM§	0.03	0.33	0.74	0.12	0.96	0.34	0.01	1.42	0.16
PM£	0.06	0.53	0.59	-0.12	-0.66	0.51	-0.07	-0.57	0.57
Fig produc.									
SM§	0.36	3.80	< 0.01	0.35	4.41	< 0.01	0.23	2.49	0.02
PM§	0.46	5.05	< 0.01	0.39	5.55	< 0.01	0.35	4.76	< 0.01
Fig dispers.									
SM§	0.20	1.98	0.05	0.252	2.56	< 0.01	0.132	1.26	0.210
PM§	0.34	3.52	< 0.01	0.283	3.52	< 0.01	0.252	3.19	< 0.01

Note: we used autoregressive models of order 1 (£), 3 (\S) or 4 (#) for error structure. Bold numbers indicate significant regressions (P<0.05).

This phenophase was weakly seasonal (Table 1) and negatively correlated with the average temperature and photoperiod of the prior month to sampling (Table 3).

The general periodic fruiting pattern exhibited by *F. adhatodifolia* varied among years, but the syconia production occurred year-round (intrapopulation asynchrony). The species experienced continuous population-level fruiting

as at least one of their individuals was in fruit throughout the monitoring period. The higher percentages of syconia production were observed in January and February (Figure 3a). Each reproductive event took 44 ± 26) days, being longer in the cold and dry period (53 ± 30) than in the warm and wet period (37 ± 20) . Most individuals had a great crop annually, with an average interval of 283 ± 199) days.

Table 3. Results of generalized least squares regressions that explain the effect of monthly rainfall, mean monthly temperature and photoperiod on the phenology of *Ficus eximia* at the Mata dos Godoy State Park, Londrina Municipality, Paraná State, Southern Brazil. PM – prior month of phenological observations; SC – Standard coefficient; SM – same month of phenological observations.

	Rainfall	Temp				Photo			
	SC	t	P	SC	t	P	SC	t	P
Leaf shed									
SM#	-0.30	-3.14	< 0.01	-0.24	-0.01	< 0.01	-0.30	-3.87	< 0.01
PM#	-0.11	-1.05	0.30	-0.27	-2.80	< 0.01	-0.21	-2.36	0.02
Leaf flush									
SM§	0.06	0.51	0.61	-0.18	-1.73	0.087	-0.17	-1.55	0.13
PM#	-0.01	-0.01	0.99	-0.32	-3.34	< 0.01	-0.29	-3.15	< 0.01
Fig produc.									
SM§	-0.12	-1.31	0.20	-0.09	-0.99	0.32	-0.06	-0.58	0.56
PM§	-0.08	-0.86	0.39	-0.17	-1.88	0.06	-0.11	-1.15	0.25
Fig dispers.									
SM#	0.06	0.53	0.60	-0.04	0.30	0.67	-0.01	-0.09	0.93
PM§	-0.15	-1.32	0.19	-0.19	-1.91	0.06	-0.16	-1.58	0.12

Note: we used autoregressive models of order 3 (§) or order 4 (#) for error structure. Bold numbers indicate significant regressions (P<0.05).

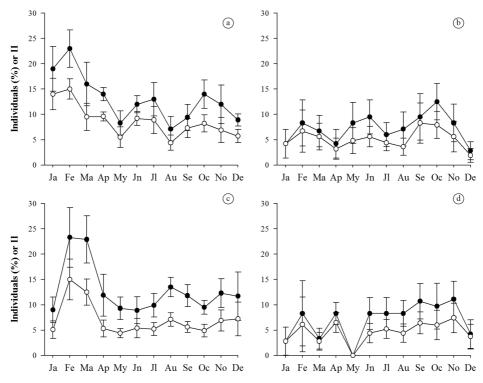


Figure 3. Syconia production (a, b) and dispersal (c, d) in *Ficus adhatodifolia* (a, c) and *F. eximia* (b, d) trees in the Mata dos Godoy State Park, Londrina Municipality, Paraná State, Southern Brazil. The values are based on 74 months of observations. Solid circles = % of individuals; leaked circles = II (intensity index). Errors bars indicate standard errors.

	Municipality, Paraná State, Southern Brazil, from Septemb	\ /	a dos Godoy State
	Species	FA	FE
Mammals	Cebus apella (Linnaeus, 1758)	X	X

Table 4. Species observed eating syconia of Figus adhatodifolia (FA) and Figus eximia (FF) in the Mata dos Godov State

	Species	FA	FE
Mammals	Cebus apella (Linnaeus, 1758)	X	X
	Dasyprocta azarae Lichtenstein, 1823	X	
Birds	Pachyramphus validus (Lichtenstein, 1823)	X	
	Dacnis cayana (Linnaeus, 1766)		X
	Baryphtengus ruficapillus (Vieillot, 1818)	X	
	Aratinga auricapillus (Kuhl, 1820)	X	X
	Pionus maximiliani (Kuhl, 1820)	X	X
	Pyrrhura frontalis (Vieillot, 1817)	X	X
	Ramphastos dicolorus Linnaeus, 1766	X	
	Selenidera maculirostris (Lichtenstein, 1823)	X	X
	Euphonia chlorotica (Linnaeus, 1766)	X	

This phenophase was aseasonal (Table 1) and positively correlated with all climatic variables analyzed of the same and prior month to sampling (Table 2).

In F. eximia, the syconia production occurred year-round without characterizing a period of increased production (Figure 3b). We did not observe the syconia production in 28 of the 74 months evaluated. Among 12 individuals monitored, only five (38%) fruiting more than once per year for at least one year studied. The average interval between two great crops was 292 (\pm 131) days. In average, this phenophase lasted 38 (\pm 25) days, being slightly longer in cold and dry period (44 \pm 28) than in the warm and wet period (32 \pm 21). It was as easonal (Table 1) and did not correlate with climatic variables analyzed (Table 3).

In F. adhatodifolia, syconia dispersal occurred around year, but higher values occurred in February and March (Figure 3c). This phenophase was aseasonal (Table 1) and positively correlated with average temperature of the sampling month and with all climatic variables of the previous month (Table 2).

In *F. eximia*, we observed syconia dispersal (Figure 3d) in all months, except May. This phenophase was weakly seasonal (Table 1) and did not correlate with all climatic variables analyzed (Table 3).

We observed two mammals and eight birds species eating the syconia of F. adhatodifolia (Table 4). The syconia were eaten in all months by araçari-poca (Selenidera maculirostris (Lichtenstein, 1823)) and a great number was consumed at each visit. In addition to observations of capuchin monkey (Cebus apella (Linnaeus, 1758)) feeding on figs, we observed syconia with teeth mark on the forest floor, in all months, indicantig the importance of F. adhatodifolia in feeding this monkey species. One mammals and five birds species eating the syconia of F. eximia were observed (Table 4). During field observations, we verified that F. eximia syconia were removed preferably at night, possibly nocturnal mammals, especially bats (syconia observed beneath the fig trees had teeth marks of these animals).

4. Discussion

In both species, the phenofases did not occur sequentially in the time, a fact already observed in other species of *Ficus* (Windsor et al., 1989; Milton, 1991) and both populations exhibited great variability within and among years in the periods of phenophase occurrence, in particular the syconia production. Furthermore, the vegetative and reproductive phenologies differed between species.

Ficus adhatodifolia may be considered an evergreen species whereas F. eximia a deciduous species because some individuals exhibit leafless crowns in certain periods of the year. Milton (1991) recorded similar results to F. insipida and to some subgenus Urostigma species (F. obtusifolia Kunth, F. costaricana (Liebm.) Miq.). Ficus citrifolia (subgenus Urostigma) was also considered deciduous (Pereira et al., 2007) in the same region of this study. These variation in leaf dynamics may possibly reflect different adaptations to water deficits in hemi-epiphytic and freestanding species. The results suggested that the climatic variables could act as triggers for this phenophase in F. eximia.

Although leaf flushing occurred throughout year in F. adhatodifolia, it was more abundant in the beginning wet period, but in F. insipida, Milton (1991) observed a tendency to concentrate flushing into the drier portion of the year in Barro Colorado, Panama. In F. adhatodifolia, leaf flushing peak did not occur temporally associated with leaf shed peak, which suggests that the fall of old leaves is not the stimulus for leaf flushing. As this phenophase did not correlate with any climatic variable analyzed, other factors could be the stimulus for this phenophase.

In MGSP, F. eximia showed higher leaf flushing in the dry and wet periods transition, unlike what was reported for subgenus Urostigma species in Panama that peaked leaf flushing in dry season (Windsor et al., 1989; Milton, 1991). Usually the F. eximia individuals in MGSP lose leaves during the dry season, remain leafless for some time and then flush. The increase of temperature and photoperiod could be the stimulus for this phenophase. It is possible that the fall of old leaves (less efficient physiologically) also

contribute to the expansion of vegetative buds (Borchert, 2000). Milton (1991) observed that *F. costaricana* and *F. obtusifolia* tended to produce quantities of new leaves only when old leaf crops were dropped.

The new leaves production in the dry season can serve as a food source for wildlife. In another forest fragment in the same region, during the dry season (lower supply of fruit), increased consumption of *F. eximia* young leaves by *Alouatta clamitans* (Cabrera, 1940) (Santos et al., 2013).

Milton (1991) observed that the average time interval between figs crop in F. insipida was higher than that observed to F. adhatodifolia in this study, and this time interval was smaller for larger individuals. In addition, fig trees tended to shift their order in terms of the timing of phenological events across years, in this study. Figs generally experience relatively short fruiting intervals (Lambert and Marshall, 1991; Zhang et al., 2006), heavy fruit production and most often, asynchronous fruiting patterns (Coates-Estrada and Estrada, 1986; Zhang et al., 2006). These findings suggest that climatic variables are not directly involved with syconia initiation and possibly it is under endogenous control, as suggested by Borchert (1983, 2000). Perhaps, the accumulation of resources will be required to cause a large figs crops, as suggested by Milton et al. (1982). The greater accumulation of resources during warm and wet period could promote the syconia production. This phenological pattern is in agreement with the observations of higher fruit production in some tropical forest in the period of maximum irradiance (Van Schaik et al., 1993).

In spite of this phenophase occur throughout the year, we observed periods of higher syconia production in F. adhatodifolia, as previously reported in other studies on Ficus (Milton et al., 1982; Windsor et al., 1989; Lambert and Marshall, 1991; Spencer et al., 1996; Ragusa-Netto, 2002; Pereira et al., 2007). The population asynchrony would be required for maintenance of the pollinating wasps population (Smith and Bronstein, 1996) while periods of increased production could be related to best time for dispersal and/or seed germination (Milton et al., 1982). In MGSP, the time of greatest forest-wide zoochorous fruit availability occurs in November-February (Perina, 2011). The major syconia dispersal in F. adhatodifolia occurs soon after the period of maximum zoochorous fruit abundance in the forest and thus is consistent with a seed dispersal hypothesis. However, the efficient distribution of very small seeds, which presumably require large light gaps for successful establishment (Milton, 1991), should be considered.

In MGSP, the probability of finding *F. adhatodifolia* individuals producing syconia at any time of the year is great, so the species could be considered as a reliable resource producer, according to Peres (2000). In contrast, *F. insipida* presented two syconia production peaks in Barro Colorado, one peak at the time of scarcity zoochorous fruits (dry period) and, therefore, the species was considered a key resource for frugivores in Barro Colorado (Milton et al., 1982).

Ficus eximia showed syconia production around the year, similar to other *Urostigma* species studied by Windsor et al. (1989) in Panama. This fact and the absence of correlation with climatic variables suggest that other factors or processes could be involved with this phenophase. Borchert (1983) suggested that flowering in tropical trees may be primarily under endogenous control.

In addition to the species observed feeding on *F. adhatodifolia* syconia (Table 4), six species of bats (Muller and Reis, 1992) and three terrestrial mammals species (W. J. Rocha, personal observations) use the species as a resource food.

The inclusion of a species as a essential resources producer to wildlife depends on the species density, the amount of the resource produced by the individual and the population, the demand for it by the animals, the availability throughout the year and the period of peak resource production (Gautier-Hion and Michaloud, 1989; Lambert and Marshall, 1991; Peres, 2000; Shanahan et al., 2001). The results analyses showed the importance of F. adhatodifolia in providing resources for frugivores of MGSP. First, the species is a reliable producer for presenting continuous syconia production throughout the year (Peres, 2000). Second, the lower availability of zoochorous fruit during the dry season in the Londrina region (Novaes, 2006) suggests a period of resources scarcity. As F. adhatodifolia presents a syconia production during this period, the species provides resources for frugivores in this period of reduced food supply. Field observations and literature data on the use of F. adhatodifolia in feeding animal species in MGSP (Muller and Reis, 1992) reinforce this idea. Third, the density of species in the study area (about six individuals.ha-1) and the large size of the individuals (crown developed) could ensure large syconia production which could feed the associated frugivorous. Gautier-Hion and Michaloud (1989) did not consider Ficus spp. as an important resource for wildlife, but the average density of all 20 species of figs in the study area was only 1.5 individuals.ha⁻¹.

Several species of bats are found in MGSP (Muller and Reis, 1992) that consume *F. eximia* syconia, like *Artibeus jamaicensis* Leach, 1821 (Sekiama and Rocha, 2006). *Brotogeris tirica* (Gmelin, 1788) (Green Parakeet) and *Cebus apella* (capuchin monkey) that occurring in the MGSP are also described in the literature as a consumer of *F. eximia* syconia (Shanahan et al., 2001).

The *F. eximia* syconia can be considered a reliable resource because they are produced throughout the year (Peres, 2000), the individual production is high (tree reaching 30 m in height and spreading crowns) and density of about three individuals per ha (field observations). Nevertheless, analysis of the results suggests that *F. eximia* may have redundant role in feeding the frugivorous fauna in MGSP, during warm and wet period. In this period occur the peak of zoochorous fruit production in the region (Novaes, 2006) and, according to Peres (2000), a resource can be completely replaceable if it is produced during the peak production of other resources. However, in other forest

remnant in the region, the selectivity of brown howler monkey (*Alouatta clamitans*) was mainly directed to species capable of providing fruits along the year, prioritizing these species even when other fruit sources are available (Santos et al., 2013). Three *Ficus* species (*F. adhatodifolia*, *F. eximia* and *F. citrifolia*) were among the species selected by *A. clamitans*.

In conclusion, both species showed aseasonal or weakly seasonal phenological patterns. *Ficus adhatodifolia* can be considered a relevant species in the food resources production for wildlife of the MGSP. In addition, this species can be used in reforestation, conservation and management of impacted ecosystems by being important food resource (Carauta and Diaz, 2002) and have the potential to attract frugivores (Cavalheiro et al., 2002), which could increase rain of propagules and introduce new species in such areas (Galindo-González et al., 2000; Guevara et al., 2004). According to Eshiamwata et al. (2006), planting *Ficus* spp. trees could be an important management tool to sustain the diversity of frugivorous.

Ficus eximia may not have the same importance in feeding the local wildlife. However, when it is considered the reproductive phenology of both species and F. citrifolia in the same fragment forest (J.M. Emmerick, unpublished data), we observed a complementarity in the syconia production. So there will be large supply of ripe syconia in each month, indicating the importance of Ficus species in the maintenance of frugivorous fauna in seasonal semi-deciduous forest.

Acknowledgements

We are grateful to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Biology Pos-Graduation Program of Universidade Estadual de Londrina, Setor de Agrometeorologia of Instituto Agronômico do Paraná for providing the climate data and Instituto Ambiental do Paraná for permission to work at MGSP.

References

BERG, C.C. and VILLAVICENCIO, X., 2004. Taxonomic studies on *Ficus* (Moraceae) in the West Indies, extra-Amazonian Brazil, and Bolívia. *Ilicifolia*, vol. 5, pp. 1-173.

BIANCHINI, E., PIMENTA, J.A. and SANTOS, F.A.M., 2001. Spatial and temporal variation in the canopy cover in a tropical semi-deciduous forest. *Brazilian Archives of Biology and Technology*, vol. 3, pp. 269-276.

BIANCHINI, E., POPOLO, R.S., DIAS, M.C. and PIMENTA, J.A., 2003. Diversidade e estrutura de espécies arbóreas em área alagável do município de Londrina, Sul do Brasil. *Acta Botanica Brasilica*, vol. 17, no. 3, pp. 405-419. http://dx.doi.org/10.1590/S0102-33062003000300008.

BIANCHINI, E., PIMENTA, J.A. and SANTOS, F.A.M., 2006. Fenologia de *Chrysophyllum gonocarpum* (Mart. & Eichler) Eng. (Sapotaceae) em floresta semidecídua do Sul do Brasil. *Brazilian Journal of Botany*, vol. 29, no. 4, pp. 595-602. http://dx.doi.org/10.1590/S0100-84042006000400009.

BORCHERT, R., 1983. Phenology and control of flowering in tropical trees. *Biotropica*, vol. 15, no. 2, pp. 81-89. http://dx.doi. org/10.2307/2387949.

BORCHERT, R., 2000. Organismic and environmental controls of bud growth in tropical trees. In: J.D.VIÉMONT and J.CRABBÉ, eds. *Dormancy in plants: from whole plant behavior to cellular control. Wallingford*: CAB international, pp. 87-107.

CARAUTA, J.P.P. and DIAZ, B.E., 2002. *Figueiras no Brasil*. Rio de Janeiro: Editora da UFRJ.

CAVALHEIRO, A.L., TOREZAN, J.M.D. and FADELLI, L., 2002. Recuperação de áreas degradadas: procurando por diversidade e funcionamento dos ecossistemas. In: M.E.MEDRI, E.BIANCHINI, O.A.SHIBATTA and J.A.PIMENTA, eds. *A bacia do rio Tibagi*. Londrina: Moacyr E. Medri. pp. 213-224.

COATES-ESTRADA, R. and ESTRADA, A., 1986. Fruiting and frugivores at a strangler fig in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology*, vol. 2, no. 04, pp. 349-357. http://dx.doi.org/10.1017/S0266467400000985.

ESHIAMWATA, G.W., BERENS, D.G., BLEHER, B., DEAN, W.R.J. and BÖHNING-GAESE, K., 2006. Bird assemblages in isolated *Ficus* trees in Kenyan farmland. *Journal of Tropical Ecology*, vol. 22, no. 06, pp. 723-726. http://dx.doi.org/10.1017/S0266467406003646.

GALINDO-GONZÁLEZ, J., GUEVARA, S. and SOSA, V.J., 2000. Bat- and bird-generated seed rains at isolate tree in pastures in a tropical rainforest. *Conservation Biology*, vol. 14, no. 6, pp. 1693-1703. http://dx.doi.org/10.1046/j.1523-1739.2000.99072.x.

GAUTIER-HION, A. and MICHALOUD, G., 1989. Are figs always keystone resources for tropical frugivorous vertebrates? A test in Gabon. *Ecology*, vol. 70, no. 6, pp. 1826-1833. http://dx.doi.org/10.2307/1938115.

GUEVARA, S., LABORDE, J. and SÁNCHEZ RIOS, G., 2004. Rain forest regeneration beneath the canopy of fig trees isolated in pastures of Los Tuxtlas, Mexico. *Biotropica*, vol. 36, pp. 99-108.

GUREVITCH, J., SCHEINER, S.M. and FOX, G.A., 2009. *Ecologia vegetal*. Porto Alegre: Artmed.

JUSTINIANO, M.J. and FREDERICKSEN, T.S., 2000. Phenology of tree species in Bolivian dry forests. *Biotropica*, vol. 32, pp. 276-281.

KATTAN, G.H. and VALENZUELA, L.A., 2013. Phenology, abundance and consumers of figs (*Ficus* spp.) in a tropical cloud forest: evaluation of a potential keystone resource. *Journal of Tropical Ecology*, vol. 29, no. 05, pp. 401-407. http://dx.doi.org/10.1017/S0266467413000461.

KOVACH, W.L., 1994. *Oriana for Windows, version 1.3*. Pentraeth: Kovach Computer Service.

LAMBERT, F.R. and MARSHALL, A.G., 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *Journal of Ecology*, vol. 79, no. 3, pp. 793-809. http://dx.doi.org/10.2307/2260668.

MARQUES, M.C.M., ROPER, J.J. and SALVALAGGIO, A.P.B., 2004. Phenological patterns among plant life-forms in a subtropical forest in southern Brazil. *Plant Ecology*, vol. 173, no. 2, pp. 203-213. http://dx.doi.org/10.1023/B:VEGE.0000029325.85031.90.

MILTON, K., 1991. Leaf change and fruit production in six neotropical Moraceae species. *Journal of Ecology*, vol. 79, no. 1, pp. 1-26. http://dx.doi.org/10.2307/2260781.

MILTON, K., WINDSOR, D.M., MORRISON, D.M. and ESTRIBI, M.A., 1982. Fruiting phenologies of two neotropical *Ficus* species. *Ecology*, vol. 63, no. 3, pp. 752-762. http://dx.doi.org/10.2307/1936796.

MORELLATO, L.P.C., TALORA, D.C., TAKAHASI, A., BENCKE, C.C., ROMERA, E.C. and ZIPPARRO, V.B., 2000. Phenology of Atlantic Rain Forest trees: a comparative study. *Biotropica*, vol. 32, no. 4b, pp. 811-823. http://dx.doi.org/10.1111/j.1744-7429.2000. tb00620.x.

MUHANGUZI, H.D. and IPULET, P., 2011. Fruiting phenology of fig trees in Kalinzu Forest, Uganda. *African Journal of Ecology*, vol. 50, no. 1, pp. 90-101. http://dx.doi.org/10.1111/j.1365-2028.2011.01301.x.

MULLER, M.F. and REIS, N.R., 1992. Partição de recursos alimentares entre quatro espécies de morcegos frugívoros (Chiroptera, Phyllostomidae). *Revista Brasileira de Zoologia*, vol. 9, no. 3-4, pp. 345-355. http://dx.doi.org/10.1590/S0101-81751992000200022.

NOVAES, T.G., 2006. Fenologia reprodutiva de espécies arbóreas da região de Londrina, PR. Londrina: Universidade Estadual de Londrina. 56 p. Masters Dissertation in Biological Sciences.

PEREIRA, R.A.S., RODRIGUES, E. and MENEZES-JUNIOR, A.O., 2007. Phenological patterns of *Ficus citrifolia* (Moraceae) in a seasonal humid-subtropical region in Southern Brazil. *Plant Ecology*, vol. 188, no. 2, pp. 265-275. http://dx.doi.org/10.1007/s11258-006-9161-0.

PERES, C.A., 2000. Identifying keystone resources in tropical forests: the case of gums from *Parkia* pods. *Journal of Tropical Ecology*, vol. 16, no. 2, pp. 287-317. http://dx.doi.org/10.1017/S0266467400001413.

PERINA, B.B., 2011. Fenologia de espécies arbóreas de uma floresta estacional semidecidual do sul do Brasil. Londrina: Universidade Estadual de Londrina. 63 p. Masters Dissertation in Biological Sciences.

R DEVELOPMENT CORE TEAM, 2005. R: A language and environment for statistical computing [software]. Vienna: R Foundation for Statistical Computing.

RAGUSA-NETTO, J., 2002. Fruiting phenology and consumption by birds in *Ficus calyptroceras* (Miq.) Miq. (Moraceae). *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 62, no. 2, pp. 339-346. http://dx.doi.org/10.1590/S1519-69842002000200018. PMid:12489406.

RAGUSA-NETTO, J., 2006. Abundance and frugivory of the toco toucan (*Ramphastos toco*) in a gallery forest in Brazil's southern Pantanal. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 66, no. 1A, pp. 133-142. http://dx.doi.org/10.1590/S1519-69842006000100017. PMid:16680316.

RAGUSA-NETTO, J., 2007. Feeding ecology of the Greencheeked parakeet (*Pyrrhura molinae*) in dry forests in western Brazil. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 67, no. 2, pp. 243-249. http://dx.doi.org/10.1590/S1519-69842007000200009. PMid:17876434.

REICH, P.B., 1995. Phenology of tropical forests: patterns, causes, and consequences. *Canadian Journal of Botany*, vol. 73, no. 2, pp. 164-174. http://dx.doi.org/10.1139/b95-020.

ROMANIUC-NETO, S., CARAUTA, J.P.P., VIANNA-FILHO, M.D.M., PEREIRA, R.A.S., RIBEIRO, J.E.L.S., MACHADO, A.F.P., SANTOS, A., PELISSARI, G. and PEDERNEIRAS, L.C., 2010 [viewed 21 May 2014]. *Lista de espécies da flora do Brasil: Moraceae* [online]. Rio de Janeiro: Jardim Botânico do Rio de Janeiro. Available from: http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB10161.

SANTOS, G.A.S.D., BIANCHINI, E. and REIS, N.R., 2013. Seasonal variation of consumption of the species used as fruit source by brown howler monkeys (*Alouatta clamitans*) in southern Brazil. *Biota Neotropica*, vol. 13, no. 3, pp. 148-153. http://dx.doi.org/10.1590/S1676-06032013000300019.

SEKIAMA, M.L. and ROCHA, V.J., 2006. Morcegos no Parque Estadual Mata dos Godoy. In: J.M.D.TOREZAN, ed. *Ecologia do Parque Estadual Mata dos Godoy*. Londrina: Itedes. pp. 152-155.

SHANAHAN, M., SO, S., GOMPTON, S.G. and CORLETT, R., 2001. Fig eating by vertebrate frugivores: a global review. *Biological Reviews of the Cambridge Philosophical Society*, vol. 76, no. 4, pp. 529-572. http://dx.doi.org/10.1017/S1464793101005760. PMid:11762492.

SINGH, K.P. and KUSHWAHA, C.P., 2006. Diversity of flowering and fruiting phenology of trees in a tropical deciduous forest in India. *Annals of Botany*, vol. 97, no. 2, pp. 265-276. http://dx.doi.org/10.1093/aob/mcj028. PMid:16357055.

SMITH, C.M. and BRONSTEIN, J.L., 1996. Site variation in reproductive synchrony in three neotropical figs. *Journal of Biogeography*, vol. 23, no. 4, pp. 477-486. http://dx.doi.org/10.1111/j.1365-2699.1996.tb00009.x.

SOARES-SILVA, L.H. and BARROSO, G.M., 1992. Fitossociologia do estrato arbóreo da porção norte do Parque Estadual Mata dos Godoy, Londrina – PR, Brasil. In: *Anais 8º Congresso SBSP*, 1992; São Paulo. São Paulo: SBSP, p. 101-112.

SPENCER, H., WEIBLEN, G. and FLICK, B., 1996. Phenology of *Ficus variegata* in a seasonal wet tropical forest at Cape Tribulation, Australia. *Journal of Biogeography*, vol. 23, no. 4, pp. 467-475. http://dx.doi.org/10.1111/j.1365-2699.1996.tb00008.x.

TELLO, J.G., 2003. Frugivores at a fruiting *Ficus* in south-eastern Peru. *Journal of Tropical Ecology*, vol. 19, pp. 717-721.

TERBORGH, J., 1986. Keystone plant resources in the tropical forest. In: M.E.SOULÉ, ed. *Conservation biology: the science of scarcity and diversity*. Sunderland: Sinauer, pp. 330-344.

VAN SCHAIK, C.P., TERBORGH, J.W. and WRIGHT, S.P., 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, vol. 24, no. 1, pp. 353-377. http://dx.doi.org/10.1146/annurev.es.24.110193.002033.

WINDSOR, D.M., MORRISON, D.W., ESTRIBI, M.A. and DE LEON, B., 1989. Phenology of fruit and leaf production by "strangler" figs on Barro Colorado Island, Panamá. *Experientia*, vol. 45, no. 7, pp. 647-653. http://dx.doi.org/10.1007/BF01975681.

ZHANG, G., SONG, Q. and YANG, D., 2006. Phenology of *Ficus racemosa* in Xishuangbanna, Southwest China. *Biotropica*, vol. 38, no. 3, pp. 334-341. http://dx.doi.org/10.1111/j.1744-7429.2006.00150.x.