

# Phenological patterns of *Ficus citrifolia* (Moraceae) in a seasonal humid-subtropical region in Southern Brazil

Rodrigo Augusto Santinelo Pereira ·  
Efraim Rodrigues · Ayres de Oliveira Menezes Jr

Received: 11 October 2004 / Accepted: 1 May 2006 / Published online: 26 May 2006  
© Springer Science+Business Media B.V. 2006

**Abstract** Year-round flowering is widely reported in fig trees and is necessary for the survival of their short-living, specialized Agaonid pollinators. However, seasonality in both fig and leaf production has been noted in almost all published phenological studies. We have addressed the following questions in the present study: (1) Are reproductive and vegetative phenologies seasonal and, consequently, related to climate? (2) Does *Ficus citrifolia* produce ripe figs year round? (3) Is the fig development related to climate? And, (4) Are reproductive and vegetative phenologies independent? By investigating these questions with a *F. citrifolia* population over a two-year period, at the southern edge of the tropical region in Brazil, we detected phenological seasonality that was significantly correlated with climate. Our findings can be summarized as follows: (1) Trees became deciduous during the cold and dry months; (2) The flowering onset was asynchronous among individuals, but with moderate concentration during the hot and rainy months; (3)

There was a correlation between the onset of flowering and vegetative phenology, with significantly higher crop initiations in individuals with full-leaf canopy; (4) Fig developmental time was longer in cold months; and (5) Ripe fig production occurred year-round and was not correlated with climate. Our results suggest that there are strong selection pressures that maintain the year-round flowering phenology in figs, for we have observed little seasonality in the phenology of such species despite the strong seasonality in the environment.

**Keywords** Climate · Fig phenology · Generalized least squares · Keystone species · Mutualism · Temporal auto-correlation

## Introduction

Year-round flowering is widely reported in fig trees (*Ficus* spp., Moraceae) (Janzen 1979; Weiblen 2002). This phenological pattern is necessary for the survival of their short-living, specialized Agaonid pollinators. The sexual reproduction of the plant depends exclusively upon pollination services carried by Agaonid fig wasps, whilst each Agaonid larva develops within a single galled fig ovule (Galil and Eisikowitch 1968b).

Due to their year-round fruiting phenology, *Ficus* species have been considered keystone

---

R. A. S. Pereira (✉)  
Depto de Biologia, FFCLRP-USP, Ribeirão Preto,  
SP 14040-901, Brazil  
e-mail: raspereira@ffclrp.usp.br

E. Rodrigues · A. de Oliveira Menezes Jr  
Depto de Agronomia, CCA-UEL, C.P. 6001,  
Londrina, PR 86051-970, Brazil

resources for frugivores in tropical forests as well as in other habitats, for they produce fruits when other fruit resources are relatively scarce (Terborgh 1986; Lambert and Marshall 1991; Kinnaid et al. 1996; Kannan and James 1999; Shanahan et al. 2001a; Ragusa-Netto 2002). Moreover, by attracting frugivores, fig trees also help the arrival of seeds that had been born inside the guts of those fruit consumers (Kinnaid et al. 1996; Thornton et al. 1996; Galindo-Gonzalez et al. 2000; Shanahan et al. 2001b; Thornton et al. 2001; Guevara et al. 2004).

Flowering and fruiting in *Ficus* species of the *Americana* section are strongly intra-individually synchronous but asynchronous among individuals (Milton et al. 1982). However, seasonality in both fig and leaf production has been noted in several phenological studies (Milton et al. 1982; Kjellberg et al. 1987; Bronstein 1989; Windsor et al. 1989; Corlett 1993; Damstra et al. 1996; Spencer et al. 1996; Patel 1996, 1997; Harrison et al. 2000; Tweheyo and Lye 2003). Such seasonality is expressed, in variable degrees, by leaf dropping during the dry seasons and the periods of the year with higher proportions of individuals that initiate fig crops (Milton et al. 1982). These published data suggest that phenological seasonality reflects climate seasonality given that many regions, even in low latitudes, show rainfall seasonality, e.g. Panama (Milton et al. 1982; Windsor et al. 1989), India (Patel 1996), and Uganda (Tweheyo and Lye 2003). Additional support for the role that rainfall plays over fig individual phenology comes from non-seasonal environments in Borneo, where severe drought substantially affected phenology (Harrison et al. 2000; Harrison 2001). In contrast, in a non-seasonal environment in Singapore fig species did not show significant synchrony among individuals (Corlett 1984, 1987, 1993). Therefore, phenological patterns that are known to *Ficus* seem to follow those described for other tropical tree species, in which water-related factors appear to be an important proximate cause of seasonal phenology (Frankie et al. 1974; Opler et al. 1980; Borchert 1983; Reich and Borchert 1984; Wright 1996). However, Borchert (1983) suggested that flowering in tropical trees may be internally controlled and affected by environmental factors, and only indirectly

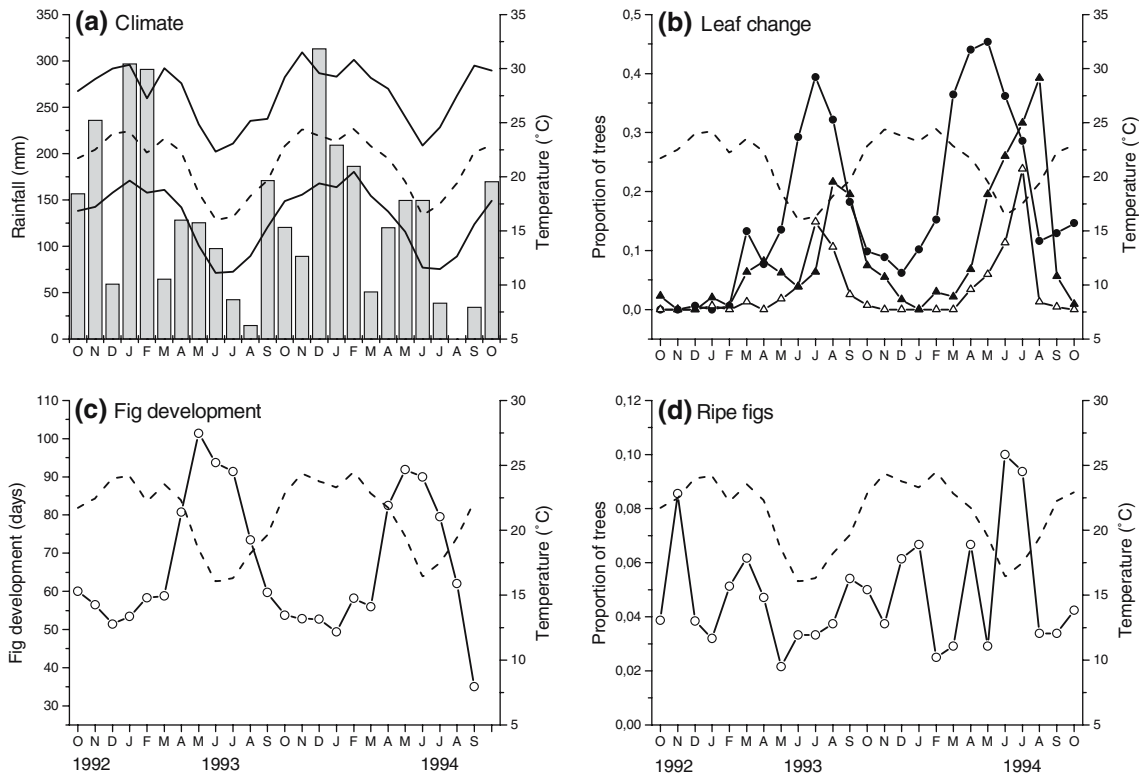
through their effects on seasonal vegetative development.

Studies on the phenology of fig individuals that are found in the surroundings of their distribution edges may reveal selective pressures that drive the year-round phenological pattern of figs and thereby stabilize mutualism with their pollinators. They may also reveal the reasons for so many fig species that are restricted to tropical habitats. By following such idea, we investigated the reproductive and vegetative phenologies of *Ficus citrifolia* at the southern edge of the tropical region. We have addressed the following questions in the present study: under such nearly subtropical climate, (1) Are reproductive and vegetative phenologies seasonal and, consequently, related to climate? (2) Does *F. citrifolia* produce ripe figs year round? (3) Is fig development related to climate? (4) Are reproductive and vegetative phenologies independent?

## Methods

### Study site

The current study was carried out from October, 1992 to October, 1994 at the Londrina State University campus, Londrina, Paraná State (approximately, 23°19' S, 51°12' W). The campus is located at the southern tropical limit (15 km away from the Tropic of Capricorn). It is an approximately 115-ha area, mainly covered with gardens and lawns where several spontaneous and ornamental arboreal species grow. According to Koeppen's Classification system, the climate of the region is Cfa (humid subtropical), characterized by hot summers, non-defined dry seasons and average temperature above 22°C in the warmest month (Corrêa et al. 1982). The lowest monthly average temperature occurs in July (16°C), and the highest in December (24°C). The average annual rainfall rate in the region is 1,615 mm. The rainiest month is January, with more than 200 mm on the average. The driest months are July and August, when total rainfall average rates go down to less than 60 mm. Figure 1a shows climate conditions observed during the study period.



**Fig. 1** Climatic variables (a) during the study period and phenology of *Ficus citrifolia* in Londrina, Paraná State. (b) Proportion of trees shedding (●), flushing (▲) and without leaves (△). (c) Average fig development in days.

(d) Proportion of trees with ripe figs. Dashed lines represent the average temperature and solid lines are minimum and maximum temperature rates

## Study species

*Ficus citrifolia* P. Miller (subgenus *Urostigma*, section *Americana*) is a monoecious tree that normally grows as a hemi-epiphyte on other trees or buildings and frequently develops within disturbed areas (R.A.S. Pereira, personal observation). In Brazil, *F. citrifolia* is pollinated by *Pegoscapus tonduzi* and associated to other 14 non-pollinating Chalcid wasp species (Pereira et al. 2000, referred to as *F. eximia*). *Ficus citrifolia* presents considerable morphological variation and has been given several names in different localities, such as *F. guaranitica* Chodat & Vischer in Brazil (Carauta 1989) and *F. hemsleyana* Standley in Costa Rica (W. Ramírez B., pers. comm.). DeWolf (1960) lists 29 synonyms for *F. citrifolia*. Figs are born in pairs on the leaf axils and reach 2–2.5 cm in diameter when mature.

## Sampling

We monitored individuals of *F. citrifolia* for 25 months, weekly. We firstly observed 35 individuals and gradually included new individuals during the study, until a total amount of 60 monitored individuals was reached (37, 39, 53, and 60 individuals at the end of the 1st, 2nd, 6th and 8th months, respectively). In each sampling, we examined individuals for the presence of figs and leaf phenology. We classified the developmental phases in figs according to the proposal of Galil and Eisikowitch (1968b), which splits the developmental cycle in figs into five phases, namely A to E. We considered phases A and E, the flowering onset and the presence of ripe figs in the analyses, respectively.

We estimated leaf phenology per individual with the use of a six-point scoring procedure as follows: 0—no leaves, 1—canopy with > 0 and < 50% of

flushing leaves, 2—canopy with  $\geq 50$  and  $< 100\%$  of flushing leaves, 3—full canopy (100%), 4—canopy with  $\geq 50$  and  $< 100\%$  of shedding leaves, and 5—canopy with  $> 0$  and  $< 50\%$  of shedding leaves.

Although weekly surveys were important to measure phenology more accurately (some fig phases and leaf changes last less than one week), we grouped data monthly. Monthly intervals seemed to fit biological interpretations better and were more appropriate for statistical analyses for observations were less auto-correlated than in weekly data (see below for auto-correlation considerations). Then, at the populational level, monthly phenological patterns were represented by (1) proportions of individuals shedding (sum of classes 4 and 5) or flushing (sum of classes 1 and 2) leaves, (2) proportions of individuals initiating crops or with ripe fruits, and by (3) the average fig development. In a given month, fig development was estimated with the average of the time for fig development, in days, of the crops initiated in that certain month. This variable represents the duration of the fruiting episode that should be expected for one individual as it initiates a crop in that month.

#### Meteorological data

Instituto Agronômico do Paraná (IAPAR), located five kilometers away from the study site, provided us with meteorological records. Series consisted of month means of daily average, minimum, and maximum temperatures ( $^{\circ}\text{C}$ ); rainfall (mm); and soil water storage (%) estimated from a sequential water balance. Water balance was calculated with the BHseq V6.3, 2002 software (Rolim et al. 1998) by making use of Thornthwaite's and Mather's method (1955) and assuming soil water capacity at 125 mm. To ensure that the water balance did start with water storage at 100% of the soil water capacity, we initiated calculations 8 months before beginning to sample, in March 1992, which was a particularly rainy month ( $\sim 360$  mm).

#### Data analysis

We used simple regressions to verify whether phenological (dependent) variables were

explained with climatic (independent) variables. Since fig individuals should take some time to respond to some climatic conditions, we computed a series of delayed climatic variables up to 60 days at 15-day intervals. Thus, we took climatic variables corresponding to the monthly averages that occurred 15, 30, 45 and 60 days before each sampling date. Dependent variables analyzed were: proportion of individuals (1) shedding leaves, (2) flushing leaves, (3) initiating crops (flowering onset), (4) with ripe figs, and, in addition, (5) fig development. Independent variables were monthly means of: average, minimum and maximum temperatures ( $^{\circ}\text{C}$ ), rainfall (mm) and soil water storage (%). For leaf changes and flowering onset, we also analyzed the series of delayed independent variables to examine their predictors.

Data structured in time series, like those analyzed in this study, are auto-correlated in general. Such auto-correlation breaks the assumption of serial independence required for most classical inference tests (Pyper and Peterman 1998). Therefore, we used generalized least squares (GLS) models with auto-correlated errors (Venables and Ripley 1999). All statistical analyses were performed with the S-Plus 6.1<sup>®</sup> Insightful Co. statistical package.

We initially fit simple regressions to see if residuals showed significant auto-correlation. Simple regression residuals were examined with correlograms, and the auto-correlation function (ACF) and partial ACF plots (Rasmussen et al. 1993) were used to detect the presence of significant auto-correlation and its form. Subsequently, analyses were redone with the use of GLS models and incorporation of the auto-correlation error structure. In all analyses, autoregressive models (AR) of orders 1 or 2 were appropriate to represent residual auto-correlations.

As analyses that involved the proportions of individuals initiating crops and those with ripe figs did not present significant auto-correlations in the residuals, we initially used generalized linear models assuming binomially distributed errors (Venables and Ripley 1999). However, the ratio from the residual deviance to the residual degrees of freedom was around 0.3, showing considerable under-dispersion and suggesting that the assumption of binomial errors was not appropriate

(Crawley 1993). Therefore, we analyzed these data with simple regressions. In all analyses, residuals showed no obvious patterns, and plots of ranked residuals against standard normal deviations were close to straight lines, thus supporting the assumption of normal errors. For proportion data, we tested the arcsine-square-root transformation, as suggested by Zar (1996), but as it weakened residual distributions, we carried out final analyses without data transformation.

For the 36 individuals that we observed during the whole period (25 months), we used Kuiper's test (Zar 1996) to assess whether the distribution of the flowering onset was uniform throughout the year. In addition to these individuals, we checked, with Pearson's correlation, to see if the sizes of fig individuals, expressed by their diameter at breast height (DBH), were correlated with the number of crops initiated during the study period. To obtain the DBH rate in individuals that bore more than one trunk at breast height, we summed the cross-sectional areas of all the trunks and back-calculated their diameter.

We fit log-linear models to data, assumed a Poisson error and used the log-link function (Venables and Ripley 1999) to verify if the percentage of flowering onset in each of the six

vegetative scores was not different from the average value of 3.5% (considering that the flowering onset had occurred with the same proportion in all vegetative phases). We tested the statistical significance of each vegetative score by comparing the change in deviance caused by its removal from the full model to a  $\chi^2$  distribution, with one degree of freedom.

## Results

### Leaf change

*Ficus citrifolia* was deciduous, with a higher proportion of individuals shedding leaves during the cold months (Fig. 1b). Some individual trees also shed leaves in other periods of the year. The temporal leaf change sequence was characterized by leaf shedding until all leaves had fallen off and a new flush started (Fig. 1b). However, leaf flushing sometimes overlapped leaf shedding.

The proportion of individuals shedding leaves was negatively correlated with the current monthly average temperature (Table 1), whereas leaf flushing was better correlated with the monthly average temperature within 15- and 45-

**Table 1** Results of generalized least squares (leaf shedding and leaf flushing) and ordinary least squares (flowering onset) regressions that explain the effect of monthly climatic variables on the phenology of *Ficus citrifolia* trees

Effect	Average temperature			Water storage			Rainfall		
	Stand. coef.	<i>t</i>	<i>P</i>	Stand. coef.	<i>t</i>	<i>P</i>	Stand. coef.	<i>t</i>	<i>P</i>
<i>Leaf shed</i>									
No delay	-0.37†	-2.1	0.046	-0.11‡	-1.8	0.083	-0.16†	-1.6	0.115
Delay 15	-0.34†	-2.0	0.058	-0.15‡	-1.6	0.112	-0.07†	-0.8	0.419
Delay 30	-0.22‡	-1.2	0.255	0.03‡	0.4	0.669	0.03†	0.3	0.752
Delay 45	0.08‡	0.4	0.678	0.04‡	0.5	0.636	-0.01†	-0.1	0.958
Delay 60	0.12‡	0.6	0.549	0.05‡	0.7	0.466	0.04‡	0.6	0.569
<i>Leaf flush</i>									
No delay	-0.49†	-2.4	0.027	-0.04†	-0.3	0.762	-0.16†	-1.1	0.293
Delay 15	-0.55†	-2.9	0.009	0.23†	1.4	0.184	-0.03†	-0.2	0.817
Delay 30	-0.53†	-2.7	0.014	0.15†	1.0	0.322	-0.14†	-1.0	0.348
Delay 45	-0.67†	-3.5	0.002	0.07†	0.5	0.645	-0.03†	-0.2	0.821
Delay 60	-0.49†	-2.2	0.037	0.12†	0.9	0.364	-0.10†	0.7	0.506
<i>Onset of flowering</i>									
No delay	0.41	2.2	0.042	-0.20	-1.0	0.328	0.01	0.03	0.974
Delay 15	0.42	2.2	0.039	-0.61	-3.6	0.002	-0.26	-1.3	0.210
Delay 30	0.35	1.8	0.084	-0.52	-2.9	0.009	-0.18	-0.9	0.387
Delay 45	0.29	1.4	0.161	-0.23	-1.1	0.268	-0.01	-0.04	0.966
Delay 60	0.20	1.0	0.347	-0.04	-0.2	0.849	<0.01	-0.01	0.994

N = 25 months. We used autoregressive models of order 1 (†) or order 2 (‡) for error structure

day time lags (Table 1). These high correlations with the delayed average temperatures probably reflect the temporal sequence of leaf shedding and flushing. Leaf change was not significantly correlated with soil water storage and rainfall (Table 1).

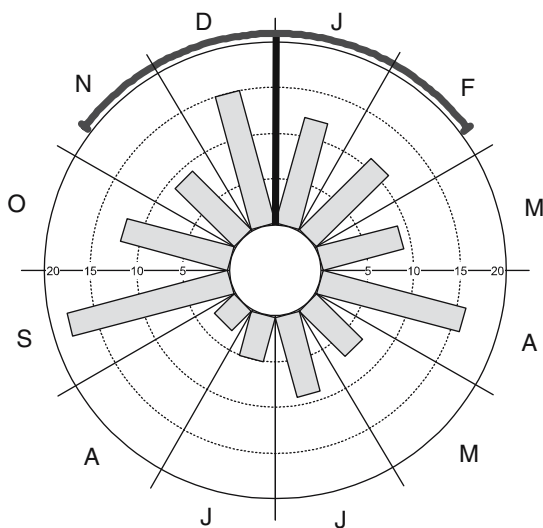
### Flowering onset

*Ficus citrifolia* was asynchronous in flowering onset and initiated fig crops throughout the year (Fig. 2). Among individuals that were observed in the whole period (25 months), some individuals initiated up to three fig crops per year, with a mean  $\pm$  SD of  $1.8 \pm 0.6$  crops year<sup>-1</sup> (N = 36 individuals). The number of crops that these individuals initiated showed a marginally significant positive correlation with their sizes, expressed in DBH (Pearson's correlation:  $r=0.329$ ,  $P=0.066$ , N = 32 individuals). At the populational level, flowering onset did not occur randomly over the year (Kuiper's test:  $V=2.61$ ,  $P < 0.01$ ), with moderate concentration during the hot and rainy months (Fig. 2). The average flowering onset angle for the 25-month period was  $0.22^\circ$  (early January) and its C.I.<sub>95%</sub> corresponded to November–February (Fig. 2). However, two flowering peaks occurred and these corresponded

to renewed rainfall periods after droughts (April in both years and September, 1993—Figs. 1a and 2).

The proportion of flowering individuals was positively correlated with the monthly average temperature (Table 1), but the highest correlation value was observed for the monthly average temperature with a 15-day time lag (Table 1). Flowering onset was negatively correlated with the soil water storage with 15- and 30-day time lags (Table 1), suggesting that a higher proportion of individuals initiated crops after a dry period. Besides the observed correlations with water storage, rainfall was not significantly correlated with the proportion of crop-initiating individuals (Table 1). The rainfall raw value does not seem to be a good predictor as it probably does not accurately reflect the amount of available water to plants in the soil.

Crop initiation depended on vegetative phenology ( $G$ -test:  $G_5=20.4$ ,  $P=0.001$ ). Fig individuals with a full canopy (score 3) initiated significantly more crops than the expected mean value of 3.5% if flowering onset did not depend on vegetative phenology. On the other hand, individuals at the beginning of leaf shedding (score 4) or producing new leaves (scores 1 and 2) initiated significantly fewer crops. Crop initiation developed by trees at the end of leaf shedding or without leaves (scores 0 and 5) was not significantly different from the expected value (Fig. 3).



**Fig. 2** Number of *Ficus citrifolia* trees mo<sup>-1</sup> initiating crops. N = 36 trees monitored over 25 months. Bold bars represent the mean angle for flowering onset and its 95% confidence interval (C.I.<sub>95%</sub>)

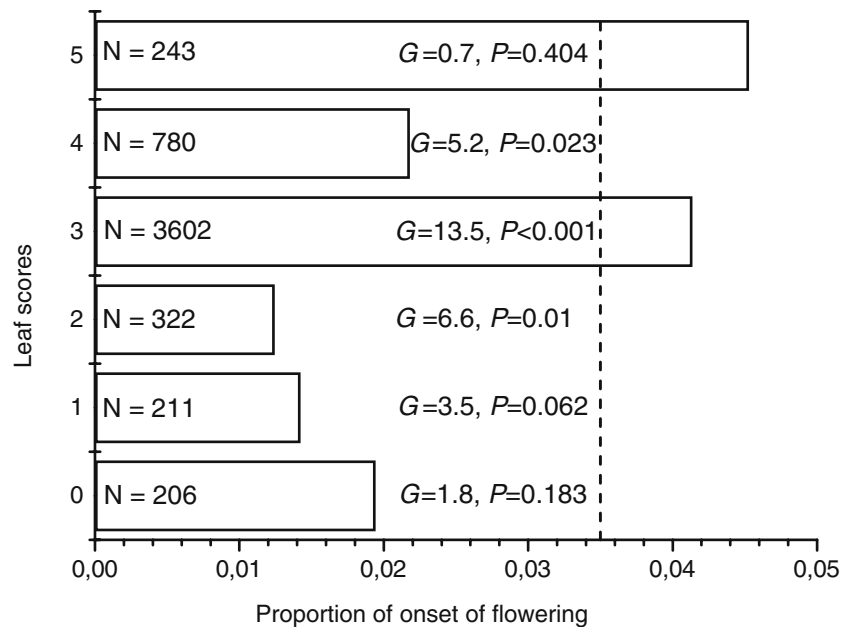
### Fig development

Throughout the 2-year round study, the mean fig development varied from 35 day in warm months to 101 day in cold months (Fig. 1c) and was significantly negatively correlated with temperature (GLS models with AR1: minimum temperature,  $b = -0.68$ ,  $t_1 = -3.4$ ,  $P=0.003$ ; average temperature,  $b = -0.69$ ,  $t_1 = -4.1$ ,  $P=0.001$ ; maximum temperature,  $b = -0.66$ ,  $t_1 = -4.4$ ,  $P < 0.001$ ).

### Ripe fruits

We observed fig individuals with ripe fruits throughout the year, with a mean  $\pm$  SD of  $2.6 \pm 2.1$  individuals week<sup>-1</sup>. The percentage of individuals with ripe fruits month<sup>-1</sup> varied from 2.2 to 10.0%

**Fig. 3** Crop initiation proportion of each leaf score (see “Methods” for phenology scores). The vertical dashed line represents the average observed value of 3.5% of flowering onset, irrespective of leaf phenology. We assessed statistical significance using log-linear models (see “Methods”)



(Fig. 1d). The proportion of individuals with ripe fruits was not significantly correlated with any of the studied climatic variables: average temperature ( $P=0.641$ ), minimum temperature ( $P=0.689$ ), maximum temperature ( $P=0.545$ ), water storage ( $P=0.239$ ) or rainfall ( $P=0.331$ ).

## Discussion

### Phenological seasonality

*Ficus citrifolia* has shown a clear deciduous pattern, followed by a flushing of new leaves associated with the climatic seasonality observed at the study site. Such synchronized leaf shedding is commonly observed in *Ficus* species during dry seasons in seasonal habitats (Windsor et al. 1989; Milton 1991; Damstra et al. 1996; Spencer et al. 1996; Patel 1997; Tweheyo and Lye 2003). Other tropical trees and treelets are also deciduous during dry periods (Opler et al. 1980; Wolf 1994; Morellato et al. 2000), and their water status and drought sensitivity probably determine leaf exchanges (Reich and Borchert 1984; Wright 1996). Milton (1991) noted that hemi-epiphytic fig species (subgenus *Urostigma*) were deciduous in the driest months in Panama, whereas free-standing species (subgenus *Pharmacosycea*) were ever-

green. Such variation in leaf dynamics may possibly reflect adaptations to different water deficits experienced by hemi-epiphytic and free-standing species, for leaf changes in *Urostigma* species are more conspicuous in epiphytic than terrestrial-phase individuals (Putz et al. 1995). In a relatively non-seasonal region in Borneo, Harrison et al. (2000) and Harrison (2001) reported a sudden increase in the deciduousness of fig species that was associated with severe drought linked to the El Niño event of 1997–1998, thus suggesting that major rainfall oscillations may substantially affect phenology.

We found significant correlation between leaf shedding and monthly temperature, but neither between leaf shedding and soil water storage nor rainfall. Nevertheless, we did not reject the role that water availability plays over *F. citrifolia* deciduousness. By comparing diagrams in Fig. 1 (a and b), proportion peaks of individuals without leaves visibly matched with dry periods in both years. Moreover, we found near significant correlation between leaf shedding and soil water storage. As we used indirect measures for water availability, our interpretation is that the measured rainfall rate and the estimated water storage probably did not accurately reflect the actual water status of the monitored individuals.

Individuals of *F. citrifolia* have shown a sub-annual pattern of flowering onset and, at the populational level, flowering occurred year-round. These two features suggest that individuals were interspersing fig crop-initiating times throughout the year. As fig mutualistic pollinators have a short lifetime (up to 2 days) (Kjellberg et al. 1988; Figueiredo and Sazima 1997), inter-individual flowering asynchrony is essential for the reproduction of the pollinating fig wasps and, consequently, for the success of the fig–fig wasp mutualism (Weiblen 2002). However, our results pointed out moderate seasonality in crop initiations that was significantly correlated with climatic seasonality. It is important to stress that Londrina is located at the southern tropical edge, has a humid subtropical climate (Corrêa et al. 1982) and presents temperature and rainfall seasonality. We observed larger proportions of individuals initiating crops during hot and rainy months (Nov.–Feb., see  $CI_{95\%}$  in Fig. 2). Such observation supports the pattern reported for *F. variegata* in Australia (Spencer et al. 1996) and for *Ficus* spp. in Uganda (Tweheyo and Lye 2003), but not with those of many other fig species that concentrated their phenological activities during moderately dry seasons (Milton et al. 1982; Windsor et al. 1989; Milton 1991; Damstra et al. 1996; Patel 1996, 1997). However, these phenological patterns are consistent with the observations that leaf and fruit productions in some tropical forests coincide with the peak of solar irradiance (Wright and van Schaik 1994; Talora and Morellato 2000; Morellato et al. 2000).

The increase in *F. citrifolia* crop initiation during the wet season was probably associated with the accumulation of reproductive reserves during the rainy months. The occurrence of two flowering peaks, corresponding to renewed rainfall periods after droughts, supports this postulate. Moreover, larger *F. citrifolia* individuals (in DBH) tended to produce more fig crops, as also reported by Milton et al. (1982). These results are in agreement with the suggestion of Borchert (1983) that flower initiation in tropical trees may go off mainly under endogenous control and is indirectly affected by environmental factors through their effects on seasonal vegetative development, as discussed below.

### Flowering onset vs. leaf change

Our results point out that flowering onset and vegetative phenology are dependent events. The significantly higher crop initiations in full-leaf canopy individuals, but not with senescent or flushing leaves, suggests that flowering onset in *F. citrifolia* is linked to the branch maturation status. *Ficus citrifolia* produces figs in the leaf axils at the terminal (and younger) portion of the branches. Then, the annual cycle of vegetative development, which is associated with the environmental seasonality, seems to constrain flowering onset. Harrison et al. (2000) observed a correlation between leaf flushing and crop initiation in *F. fulva*, that also produces its figs at branch tips, but these two phenological events were uncorrelated in other cauliflorous species.

### Fig developmental time

The variance found in fig developmental time was a conspicuous pattern observed in our analyses. Crops in cold months took almost three times as long to develop as crops in warm months did, and the mean fig development per month presented a strong negatively significant correlation with temperature.

Bronstein (1989) postulated that the ability figs have to develop more slowly in cold seasons should be a mechanism that might allow mutualism to persist in seasonal environments as delaying permitted wasps to emerge at a better time so that they could locate a receptive fig. Her postulate is based on evidence that fig maturation appears to be under wasp control (Galil et al. 1973) and developmental rates of some insects are temperature-dependent (Wolda 1988). Kjellberg et al. (1987) reported that male figs (*F. carica*) visited by wasps in late spring (May) ripened in summer (July), while figs visited in late summer (August) produced adult wasps in the next spring. Empirical studies on monoecious species, however, are required to check if temporal plasticity increases the success of the pollinating fig wasps in seasonal habitats; moreover, the incorporation of developmental time variance in simulation studies (such as in Kjellberg and Maurice 1989 and Bronstein et al. 1990) deserves attention.



## Availability of ripe fruits

*Ficus citrifolia* produced ripe figs year-round, independent of climatic seasonality. This fig species is probably important as a food resource for frugivorous animals that dwell within the university campus. Diets of frugivorous bats at the Londrina State University campus were composed mainly of figs (I. P. Lima, unpublished data). Thus, the year-round production of ripe figs observed in the present study is consistent with other reports that consider *Ficus* species as key-stone resources for frugivorous animals, as they produce fruits when other fruit resources are relatively scarce (Terborgh 1986; Lambert and Marshall 1991; Kinnaird et al. 1996; Kannan and James 1999; Shanahan et al. 2001a; Ragusa-Netto 2002). Such phenological pattern suggests that this fig species could potentially be used in restoration projects on degraded land, given that frugivores may track fig production over large distances and, potentially, disperse seeds of a mix of other rain-forest trees species (Kinnaird et al. 1996; Thornton et al. 1996; Galindo-Gonzalez et al. 2000; Shanahan et al. 2001b; Thornton et al. 2001; Guevara et al. 2004).

Our results have shown that there was little reproductive seasonality in *F. citrifolia* despite the strong environmental seasonality. This suggests that there are strong selection pressures that maintain the year-round flowering phenology in figs. Year-round flowering has been described as essential to allow mutualistic wasps to survive continuously (Ramírez 1974). However, there is no selective pressure on individual figs to maintain the wasp population, as fig wasps and fig trees have conflicting evolutionary interests (Anstett et al. 1997). As other Moraceae species show intra-specific asynchrony with fruit production, Milton (1991) presented an alternative interpretation, suggesting that such asynchrony in Moraceae—and *Ficus* particularly—could have evolved as a response from selective pressures related to the efficient distribution of unusually tiny seeds, which presumably require large light gaps for successful establishment. However, the selective pressures involved in the evolution of such phenological pattern have not been investigated (Anstett et al. 1997).

In this current study, we presented a phenological pattern that, to some extent, seems to be linked to seasonal variations in the environment. However, one should analyze *Ficus* species phenologies that have wide latitudinal distributions and compare their patterns so that such relationship could be better understood. In Kenya (2°08' S), *F. sycomorus* presented a year-round flowering pattern (Galil and Eisikowitch 1968b), whereas in Namibia (23°34' S), fewer blossoming individuals were observed during winter (Wharton et al. 1980). In contrast, in the severe Israeli (32°05' N) winter, *F. sycomorus* individuals were nearly dormant and figs were hardly ever initiated when temperatures went down below zero (Galil and Eisikowitch 1968a). Thus, widely distributed *F. citrifolia* seems to be a very suitable species to carry out such wide-range and standardized study on the relationship between climate and *Ficus* phenology and its effect on the fig–fig wasp mutualism.

**Acknowledgements** We thank Finn Kjellberg, George Weiblen, Maria T. Z. Toniato, Marco A. Batalha, Rhett Harrison and one anonymous referee for the critical review of the manuscript, Glauco S. Rolim for meteorological advice, Maria M. Justi for field assistance and Fernando Santiago dos Santos for the English review. This project was supported by Capes (Programa Especial de Teinamento, PET/Capes).

## References

- Anstett MC, Hossaert-McKey M, Kjellberg F (1997) Figs and fig pollinators: evolutionary conflicts in a co-evolved mutualism. *Trends Ecol Evol* 12:94–99
- Borchert R (1983) Phenology and control of flowering in tropical trees. *Biotropica* 15:81–89
- Bronstein JL (1989) A mutualism at the edge of its range. *Experientia* 45:622–639
- Bronstein JL, Gouyon PH, Gliddon C, Kjellberg F, Michaloud G (1990) The ecological consequences of flowering asynchrony in monoecious figs: a simulation study. *Ecology* 71:2145–2156
- Corlett RT (1984) The phenology of *Ficus benjamina* and *Ficus microcarpa* in Singapore. *J Singapore Natl Acad Sci* 13:30–31
- Corlett RT (1987) The phenology of *Ficus fistulosa* in Singapore. *Biotropica* 19:122–124
- Corlett RT (1993) Sexual dimorphism in the reproductive phenology of *Ficus grossularioides* Burm. f. in Singapore. *Malayan Nat J* 46:149–155
- Corrêa AR, Godoy H, Bernardes LRM (1982) Características climáticas de Londrina. IAPAR, Curitiba

- Crawley MJ (1993) GLIM for ecologists. Blackwell Scientific, Oxford
- Damstra KSJ, Richardson S, Reeler B (1996) Synchronized fruiting between trees of *Ficus thonningii* in seasonally dry habitats. *J Biogeogr* 23:495–500
- DeWolf GP (1960) *Ficus* (Tourn.) L. *Ann Miss Bot Garden* 47:146–165
- Figueiredo RA, Sazima M (1997) Phenology and pollination ecology of three Brazilian fig species (Moraceae). *Bot Acta* 110:73–78
- Frankie GW, Baker HG, Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J Ecol* 62:881–913
- Galil J, Eisikowitch D (1968a) Flowering cycles and fruit types of *Ficus sycomorus* in Israel. *New Phytol* 67:745–758
- Galil J, Eisikowitch D (1968b) On the pollination ecology of *Ficus sycomorus* in east Africa. *Ecology* 49:259–269
- Galil J, Zeroni M, Bar-Shalom D (1973) Carbon dioxide and ethylene effects in the coordination between the pollinator *Blastophaga quadraticeps* and the syconium in *Ficus religiosa*. *New Phytol* 72:1113–1127
- Galindo-Gonzalez J, Guevara S, Sosa VJ (2000) Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conserv Biol* 14:1693–1703
- Guevara S, Laborde J, Sánchez-Rios G (2004) Rain forest regeneration beneath the canopy of fig trees isolated in pastures of Los Tuxtlas, Mexico. *Biotropica* 36:99–108
- Harrison RD (2001) Drought and the consequences of El Niño in Borneo: a case study of figs. *Popul Ecol* 43:63–75
- Harrison RD, Yamamura N, Inoue T (2000) Phenology of a common roadside fig in Sarawak. *Ecol Res* 15:47–61
- Janzen DH (1979) How to be a fig. *Annu Rev Ecol Syst* 10:13–51
- Kannan R, James DA (1999) Fruiting phenology and the conservation of the Great Pied Hornbill (*Buceros bicornis*) in the Western Ghats of southern India. *Biotropica* 31:167–177
- Kinnaird MF, O'Brien TG, Suryadi S (1996) Population fluctuation in Sulawesi Red-Knobbed Hornbills: tracking figs in space and time. *The Auk* 113:431–440
- Kjellberg F, Maurice S (1989) Seasonality in the reproductive phenology of *Ficus*: its evolution and consequences. *Experientia* 45:653–660
- Kjellberg F, Doumesche B, Bronstein JL (1988) Longevity of a fig wasp (*Blastophaga psenes*). *Proceed Konink Nederl Akad Wet Ser C Biol Med Sci* 91:117–122
- Kjellberg F, Gouyon PH, Ibrahim M, Raymond M, Valdeyron G (1987) The stability of the symbiosis between dioecious figs and their pollinators: a study of *Ficus carica* L. and *Blastophaga psenes* L. *Evolution* 41:693–704
- Lambert FR, Marshall AG (1991) Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rain forest. *J Ecol* 79:793–809
- Milton K (1991) Leaf change and fruit production in six neotropical Moraceae species. *J Ecol* 79:1–26
- Milton K, Windsor DM, Morrison DW, Estribi MA (1982) Fruiting phenologies of two neotropical *Ficus* species. *Ecology* 63:752–762
- Morellato LPC, Talora DC, Takahasi A, Bencke CC, Romera EC, Zipparro VB (2000) Phenology of Atlantic rain forest trees: a comparative study. *Biotropica* 32:811–823
- Opler PA, Frankie GW, Baker HG (1980) Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *J Ecol* 68:167–188
- Patel A (1996) Variation in a mutualism: phenology and the maintenance of gynodioecy in two Indian fig species. *J Ecol* 84:667–680
- Patel A (1997) Phenological patterns of *Ficus* in relation to other forest trees in southern India. *J Trop Ecol* 13:681–695
- Pereira RAS, Semir J, Menezes AO (2000) Pollination and other biotic interactions in figs of *Ficus eximia* Schott (Moraceae). *Braz J Bot* 23:217–224
- Putz FE, Romano GB, Holbrook NM (1995) Comparative phenology of epiphytic and tree-phase strangler figs in a Venezuelan palm savanna. *Biotropica* 27:183–189
- Pyper BJ, Peterman RM (1998) Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can J Fish Aquat Sci* 55:2127–2140
- Ragusa-Netto J (2002) Fruiting phenology and consumption by birds in *Ficus calyptroceras* (Miq.) Miq. (Moraceae). *Braz J Biol* 62:339–346
- Ramírez BW (1974) Coevolution of *Ficus* and Agaonidae. *Ann Miss Bot Garden* 61:770–780
- Rasmussen PW, Heisey DM, Nordheim EV, Frost TM (1993) Time-series intervention analysis: unreplicated large-scale experiments. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments. Chapman & Hall, New York, pp 138–158
- Reich PB, Borchert R (1984) Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *J Ecol* 72:61–74
- Rolim GS, Sentelhas PC, Barbieri V (1998) Planilhas no ambiente EXCEL<sup>TM</sup> para os cálculos de balanços hídricos: normal, sequencial, de cultura e de produtividade real e potencial. *Rev Bras Agrometeorol* 6:133–137
- Shanahan M, Compton SG, So S, Corlett R (2001a) Fig-eating by vertebrate frugivores: a global review. *Biol Rev* 76:529–572
- Shanahan M, Harrison RD, Yamamura N, Boen W, Thornton IWB (2001b) Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. V. Colonization by figs (*Ficus* spp.), their dispersers and pollinators. *J Biogeogr* 28:1365–1377
- Spencer H, Weiblen GD, Flick B (1996) Phenology of *Ficus variegata* in a seasonal wet tropical forest at Cape Tribulation, Australia. *J Biogeogr* 23:467–475
- Talora DC, Morellato PC (2000) Fenologia de espécies arbóreas em floresta de planície litorânea do sudeste do Brasil. *Braz J Bot* 23:13–26

- Terborgh J (1986) Keystone plant resources in the tropical forest. In: Saulé ME (ed) Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, pp 330–344
- Thorntwaite CW, Mather JR (1955) The water balance. Laboratory of Climatology, New Jersey
- Thornton IWB, Compton SG, Wilson CN (1996) The role of animals in the colonization of the Krakatau Islands by fig trees (*Ficus* species). *J Biogeogr* 23:577–592
- Thornton IWB, Cook S, Edwards JS, Harrison RD, Schipper C, Shanahan M, Singadan R, Yamuna R (2001) Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VII. Overview and discussion. *J Biogeogr* 28:1389–1408
- Tweheyo M, Lye KA (2003) Phenology of figs in Budongo forest Uganda and its importance for the chimpanzee diet. *Afr J Ecol* 41:306–316
- Venables WN, Ripley BD (1999) Modern applied statistics with S-PLUS. Springer-Verlag, New York
- Weiblen GD (2002) How to be a fig wasp. *Annu Rev Entomol* 47:299–330
- Wharton RA, Tilson JW, Tilson RL (1980) Asynchrony in a wild population of *Ficus sycomorus*. *S Afr J Sci* 76:478–480
- Windsor DM, Morrison DW, Estribi MA, De Leon B (1989) Phenology of fruit and leaf production by “strangler” figs on Barro Colorado Island, Panama. *Experientia* 45:647–653
- Wolda H (1988) Insect seasonality: why? *Annu Rev Ecol Syst* 19:1–18
- Wolf JHD (1994) Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio* 112:15–28
- Wright SJ (1996) Phenological responses to seasonality in tropical forest plants. In: Mulkey SS, Chazdon RL, Smith AP (eds) Tropical forest plant ecophysiology. Kluwer Academic Publishers, Boston, pp 440–460
- Wright SJ, van Shaik CP (1994) Light and the phenology of tropical trees. *Am Nat* 143:192–199
- Zar JH (1996) Biostatistical analysis. Prentice Hall, Upper Saddle River