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# Phenology of Tree Species in a Fragment of Atlantic Forest in Pernambuco – Brazil

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## ABSTRACT

A close examination of the phenological behavior of tropical forests is fundamental to our understanding of the ecological processes occurring there, including the period of greatest availability of plant resources for animal pollinators, herbivores, and seed dispersers. This information is especially important in environments that have experienced strong anthropogenic degradation as is the case of the Brazilian Atlantic Forest. The present work sought to identify the phenological behavior (leaf flush, leaf fall, flowering, and fruiting) of 47 arboreal species (133 individuals) occurring in 1800 $m^2$ of ombrophilous forest located in Igarassu/PE, Brazil. These plants were observed every two weeks during the period between September/2002 and August/2003. Spearman's correlation was used to examine the relationships of the phenophases with precipitation, and none of the phenophases were found to be significantly correlated with rainfall. Leaf flush and leaf fall were continuous throughout the year, although there was a tendency for these phenophases to occur during the driest period (Sept. – Dec.) and during the transition from the dry to the rainy season (Jan. – Feb.). A marked seasonality of flowering and fruiting was observed, with flowering occurring principally during the dry period and at the start of the rainy season, while fruiting was most concentrated at the start of the rainy season. The majority of species that flowered initiated the production of flowers during the period with lowest precipitation. All of the species that fruited had zoochory as a dispersal syndrome. These results are similar to those previously reported in the literature, and indicate that the dry period is favorable to flowering and leaf renewal, while the rainy season was most propitious to seed dispersal.

**Keywords:** flowering, fruiting, northeastern Brazil, seasonality, tropical rain forest

## INTRODUCTION

In seeking to understand the processes that determine the structure of plant communities it is necessary to examine many different aspects, including its phenological patterns (Schott 1995). The importance of phenological studies resides in the fact that they allow us to characterize species and communities, to identify their reproductive and vegetative patterns and aid our comprehension of the dynamics and functioning of ecosystems (Lieth 1974; Fournier 1976). Additionally, it is known that the activities of animal pollinators, seed dispersers, and herbivores (Janzen 1967; van Schaik *et al*. 1993; Brody 1997; Sakai 2001), and the fauna involved in decomposition and nutrient recycling directly influence the vegetative and reproductive cycles of plants (Schessl *et al*. 2008).

There is a growing awareness in the scientific community of the necessity of preservation and conservation and of restoring ecosystems that have been strongly degraded (Turner and Corlett 1996), such as the Brazilian Atlantic Forest (MMA 2003). This ecosystem has been greatly reduced over the centuries and currently occupies only approximately 7.6% of its original range (Morellato and Haddad 2000). This situation is graver still in northeastern Brazil, especially in Pernambuco State, where only 4.6% of the area of its original Atlantic Forest remains (Lima 1998), and even this small total area is formed by a large number of small fragments that are isolated within a matrix of sugarcane plantations - as the studies undertaken by Ranta *et al*. (1998) and Trindade *et al*. (this number) have shown. Other studies have demonstrated the biological consequences of fragmentation on these forest remnants, which includes the reduction of genetic diversity within plant populations due to reduced genetic flow between fragments (Young *et al*. 1996), greater mortality of trees and the development of vine and shrub species along the edges of the fragments due to microclimatic changes (Murcia 1995; Báldi 1999), local extinction of species (Woodroffe and Ginsberg 1998), and variations in the production of leaf-litter (Schessl *et al*. 2008). Phenological studies supply useful information about the dynamics and availability of forest resources such as flowers, fruits and seed and, consequently, about the structure of the plant community.

Different authors have observed an elevated biological diversity in humid tropical forests that is likewise expressed in their very complex phenological patterns (Lieth 1974; Fournier 1976; Newstrom *et al*. 1994; Sakai 2001). In spite of the importance of phenological information, few studies have been undertaken within the Atlantic Forest (Morellato 2003). The few works that have been published (principally in the humid and seasonal semideciduous forests of southeastern Brazil) have demonstrated the importance of climatic events on plant phenology (Morellato *et al*. 1989, 1990; Morellato and Leitão-Filho 1990; Morellato 1995; Morellato *et al*. 2000; Talora and Morellato 2000). Relatively few studies have been undertaken in the Atlantic Forest region of northeastern Brazil (e.g. Andrade-Lima 1958; Mori *et al*. 1982).

In general, work undertaken in diverse tropical forest areas of the world have shown that phenological events tend to be seasonal (Janzen 1967; Frankie *et al*. 1974; Fournier 1976; Opler *et al*. 1976; Alencar *et al*. 1979; Borchert 1994) even in humid tropical forests (Alencar *et al*. 1979; Morellato *et al*. 2000; Talora and Morellato 2000; Huete *et al*.

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2006). In the forests of southeastern Brazil, for example, a close relationship has been demonstrated between plant phenology and temperature, precipitation, and photoperiod in both humid (Morellato *et al*. 2000; Talora and Morellato 2000) and seasonal semideciduous forests (Morellato *et al*. 1989, 1990; Morellato and Leitão-Filho 1990; Morellato 1995). Mori *et al*. (1982) reported that the phenological events of arboreal species in a hygrophilous forest in southern Bahia State tend to occur in the spring, and are related to increases in both the photoperiod and the temperature; although the authors noted that there were always some species in phenological activity throughout year.

In the light of this reported variability and the reduced amount of data available in the literature about phenological patterns of the arboreal species in the Atlantic Forest of northeastern Brazil, the present work was designed to describe the phenology of the species of the canopy and sub-canopy layers in a fragment of humid forest in Pernambuco State, Brazil receiving less than 100 mm per month of rainfall during four months of the year.

## MATERIALS AND METHODS

### Study site

The present study was undertaken in a 306 ha forest fragment locally known as the "São José" or "Piedade" forest, located in the municipality of Igarassu, Pernambuco State (7° 49′ 12.66″ to 7° 50′ 55.43″ S, 35° 00′ 35.92″ to 34° 59′ 21.29″ W; average altitude 72 m) (see Trindade *et al*., this number), located about 50 km north of the state capital, Recife. The wooded area is a fragment of dense lowland ombrophilous forest (IBGE 1992) with little evidence of anthropogenic disturbance (Santos *et al*. 2001) that has been converted into the Usina São José Ecological Reserve (FIDEM 1987). Most of the canopy trees are between 18 and 20 m tall, with some emergents reaching 25 m. The woody sub-canopy is characterized by many young individuals of canopy and emergent species, as well as many species of the families Myrtaceae and Rubiaceae; the herbaceous understory has populations of shade-tolerant Marantaceae, Heliconiaceae and Poaceae. There are few vascular or non-vascular epiphytes.

Information concerning the temperature and precipitation in the reserve was obtained from a meteorological station located approximately 1.5 km from the study area. The regional climate is type As' (Köppen classification) hot and humid, with an average annual rainfall of 1687 mm. The driest period (less than 100 mm of rainfall per month) extends from September to December, while the rainy season lasts from January to August (**Fig. 1**). During the study period, this climatic pattern varied slightly, with well above average rainfall occurring in January, while only 67 mm of rainfall was recorded for April (which is historically a month with high precipitation rates). In spite of this variation in the rainfall pattern, the month of April was considered humid, as high precipitation rates were registered in the previous months and there was much accumulated water in the soil (for more a detailed consideration of the local climate, refer to Schessl *et al*. 2008).

During the study period, approximately 90% of the average annual rainfall occurred between January and August, very close to the historical average of 85% (Schessl *et al.* 2008). During the short dry season (September to December) the average monthly

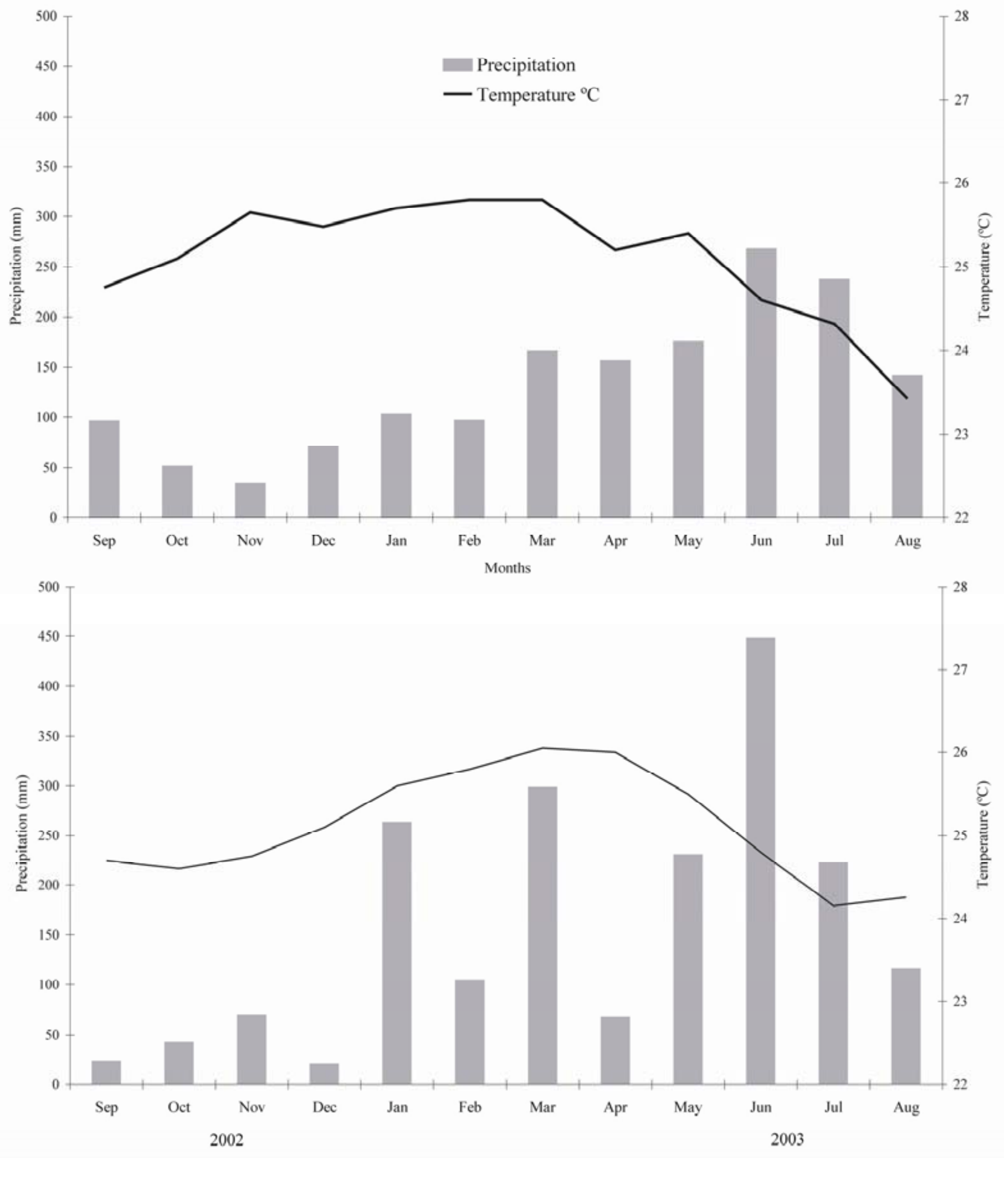

**Fig. 1** (**A**) Average monthly precipitation and temperature during the period between 1998 and 2003 and (**B**) monthly precipitation during the period between September, 2002 and August, 2003. São José Forest, Igarassu/PE, Brazil. (Source: rain gauge at the São José Sugar Mill).

precipitation was less than 100 mm. The average annual temperature was 25°C. March was the warmest month and August the coldest, with temperatures of 25.7 and 23.6°C, respectively. The average annual evapotranspiration is 1639 mm (Schessl *et al*. 2008).

## Data collection

Phenological observations were made every two weeks during the period from September/2002 to August/2003 on 133 individuals (with a trunk circumference at breast height greater than or equal to 15 cm) present in a sampling area of 1800 m$^2$ of forest. These individuals were distributed among 47 species belonging to 26 plant families (**Table 1**). Specimens of all of the species examined were deposited in the Professor Vasconcelos Sobrinho Herbarium (PEUFR) at the Federal Rural University of Pernambuco (UFRPE).

Phenological information collected included the presence or absence of: leaf flush, leaf fall, flowering, and fruiting (Machado *et al*. 1997). An individual was considered to be in the phenophase of leaf flush when it exhibited small, shiny, light-green to yellow or red leaves; to be in the phenophase of leaf fall when its leaves were dry or their color changed (to dark green-red, or orange), and/or when there were empty spaces in the crown or branches without leaves (Morellato *et al*. 1989); to be in the flowering phase when their flowers were open and/or closed; and to be fruiting when there was any production of fruits, without specifying their degree of maturity. A species was considered to be in a given phenophase when at least one individual expressed that phenophase.

The results are presented in the form of tables and graphs. Additionally, the Fournier intensity percentage was calculated (Fournier 1974) for the community, indicating the intensity of the occurrence of a given phenological event as a percentage. This factor is calculated using data collected in a semi-quantitative manner on a scale varying from 0 to 4, where “0” indicates the absence of a given phenophase; “1” indicates the intensity of a phenological event with from 1 to 25% of the individuals in the study population participating, “2” with from 26 to 50% participating, “3” with from 51 to 75%, and “4” with from 76 to 100% of the individuals demonstrating the same phase.

Spearman’s correlation ($r_s$) was utilized (Zar 1996) to establish the monthly relationships between the phenological behavior of a given species and precipitation. Dispersal syndromes were classified according to the criteria described by van der Pijl (1982).

## RESULTS

### Vegetative phenophases

All of the analyzed phenophases were continuous (*sensu* Newstrom *et al*. 1994) throughout the year, although there were periods in which any given phenophase was more accentuated. Leaf flush, for example, demonstrated a slight tendency to be more intense during the dry season (Sept. – Dec.) and during the transition from the dry to the rainy season. Leaf fall demonstrated a similar pattern, although the amplitude changes of this phenophase were larger (**Fig. 1, Fig. 2A, Table 1**). In spite of this apparent tendency towards seasonality, no significant correlation of leaf flush or leaf fall with precipitation was established (leaf flush rs = -0.508; p = 0.09; leaf fall: rs = -0.433; p = 0.16).

In is important to note that during the entire year there were always some species demonstrating leaf flush. Approximately 43% of the species budded leaves (at low

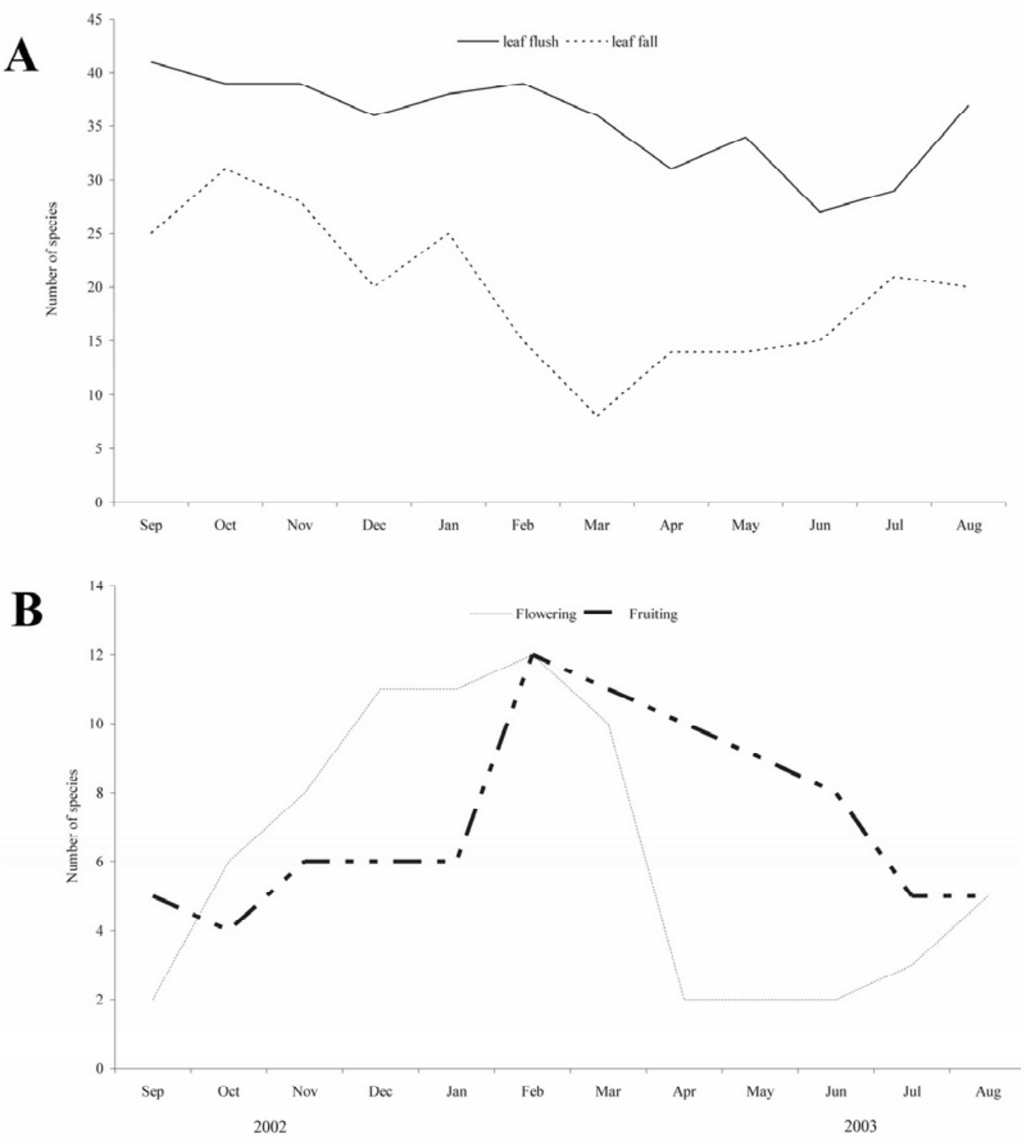

**Fig. 2** Number of species demonstrating leaf flush and leaf fall (**A**) and flowering and fruiting (**B**) during the period between September, 2002 and August, 2003. São José Forest, Igarassu/PE, Brazil..

**Table 1** List of the arboreal families/species and their periods of leaf flush and leaf fall during the period between September/2002 and August/2003 at the São José Forest, Igarassu/PE, Brazil. NI – number of individuals.

| Families / Species | NI | Leaf flush | Leaf fall |
|---|---|---|---|
| **Anacardiaceae** | | | |
| *Tapirira guianensis* Aubl. | 13 | whole year | Sep-Jan/Mar-May/Jul-Aug |
| *Thyrsodium spruceanum* Benth. | 3 | Sep-Oct/ Jan-Jun | Sep/Nov-Jan/Jun |
| **Apocynaceae** | | | |
| *Aspidosperma discolor* A.DC. | 4 | whole year | Nov/Jan |
| *Himatanthus phagedaenicus* (Mart.) Woodson | 3 | Sep-Apr/Aug | Oct-Jan/May/Aug |
| *Tabernaemontana salzmannii* A. DC. | 3 | Sep-Mar/Jun-Aug | Not recorded |
| **Araliaceae** | | | |
| *Schefflera morototoni* (Aubl.) Maguire, Steyerm. & Frodin | 3 | Oct-Jul | Oct/Feb/May-Aug |
| **Arecaceae** | | | |
| *Bactris ferruginea* Burret. | 1 | Dec-Aug | whole year |
| **Bombacaceae** | | | |
| *Eriotheca crenulaticalyx* A.Robyns | 2 | Sep-Oct/Aug | Oct/Jul |
| **Boraginaceae** | | | |
| *Cordia superba* Cham. | 1 | Sep-Nov/Apr-May/Jul-Aug | Jan/Apr-Aug |
| **Burseraceae** | | | |
| *Protium giganteum* Engl. | 12 | Sep-Dec/Feb-Aug | Sep-May/Jul-Aug |
| *Protium heptaphyllum* (Aubl.) Marchand | 3 | Sep-Jan/Mar | Oct-Nov/Jun-Aug |
| *Tetragastris* cf. *catuaba* Soares da Cunha | 1 | Sep-Oct/Feb | Sep-Oct/Jan |
| **Caesalpiniaceae** | | | |
| *Hymenaea rubriflora Ducke* | 2 | whole year | whole year |
| *Sclerolobium densiflorum* Benth. | 3 | whole year | whole year |
| **Cecropiaceae** | | | |
| *Cecropia pachystachya* Trec. | 1 | whole year | whole year |
| **Celastraceae** | | | |
| *Maytenus* cf. *distichophylla* Mart. | 4 | whole year | Oct/Jan/Apr/Jul |
| **Clusiaceae** | | | |
| Clusiaceae A | 1 | Oct-Dec/Aug | Sep/Nov |
| *Tovomita brevistaminea* Engl. | 1 | whole year | Not recorded |
| **Erythroxylaceae** | | | |
| *Erythroxylum squamatum* Sw. | 1 | Sep-Apr | Sep-Jan |
| **Euphorbiaceae** | | | |
| *Pogonophora schomburgkiana* Miers ex Benth. | 5 | whole year | Not recorded |
| **Lauraceae** | | | |
| *Ocotea gardneri* (Meissn.) Mez | 2 | Sep-Mar | Nov/Jan-Feb/Apr-May/Jul-Aug |
| *Ocotea glomerata* (Ness) Mez | 3 | Sep-May/Aug | Sep-Feb |
| *Ocotea limae* Vattimo | 4 | Sep-May/Aug | Sep-Feb/Jun-Aug |
| **Lecythidaceae** | | | |
| *Eschweilera ovata* (Cambess.) Miers | 3 | Nov-May/Aug | Sep/Dec |
| **Meliaceae** | | | |
| *Trichilia lepidota* Mart. | 1 | Oct-Mar/Jul-Aug | Not recorded |
| **Mimosaceae** | | | |
| *Hymenolobium janeirense* Kuhlm. | 1 | Feb/Jul-Aug | Dec-Jan |
| *Inga capitata* Desv. | 1 | Sep-Nov/May/Aug | Oct/Apr-Aug |
| *Inga* sp.2 | 6 | Sep-May | Sep-Feb/May-Aug |
| *Parkia pendula* (Willd.) Benth. ex Walp. | 9 | Sep-Mar/May-Aug | Sep-Dec/Apr-Jun |
| **Moraceae** | | | |
| *Brosimum guianense* (Aubl.) Huber | 3 | whole year | Sep-Oct/Mar |
| *Helicostylis tomentosa* (Poepp. & Endl.) Rusby | 6 | whole year | whole year |
| **Myrtaceae** | | | |
| *Myrcia fallax* (Rich.) DC. | 1 | whole year | Sep-Oct/Aug |
| *Myrcia sylvatica* (G. Meyer) DC. | 2 | whole year | Nov |
| **Nyctaginaceae** | | | |
| *Guapira laxa* (Netto) Furlan | 1 | whole year | Not recorded |
| *Guapira opposita* (Vell.) Reitz | 3 | whole year | Sep-Dec |
| **Piperaceae** | | | |
| *Piper arboreum* Aubl. | 1 | Sep-Jun/Aug | Sep-Oct/Jan |
| **Polygonaceae** | | | |
| *Coccoloba* sp. | 1 | Sep-Oct/Jun | Nov-Jan |
| **Rubiaceae** | | | |
| *Coussarea* sp. | 1 | Sep-Nov/Jan-Jul | Oct-Feb |
| **Sapotaceae** | | | |
| *Chrysophyllum* cf. *flexuosum* Mart. | 1 | Sep-Nov/Jun-Aug | Feb |
| *Pouteria bangii* (Rusby) T.D. Penn. | 7 | whole year | Sep-Apr/Jul-Aug |
| *Pouteria peduncularis* (Mart. & Eichl. ex Miq.) Baehni | 1 | Sep-Mar/Aug | Sep-Mar/Jun-Jul |
| *Pradosia* cf. *glycyphloea* (Casar.) Liais | 1 | Sep-May/Jul-Aug | Oct-Nov |
| Sapotaceae A | 2 | whole year | Sep-Nov |
| Sapotaceae B | 2 | whole year | Sep-Nov/Apr-May/Jul-Aug |
| **Tiliaceae** | | | |
| *Apeiba tibourbou* Aubl. | 2 | Sep-Mar/Jul | Sep-Nov |

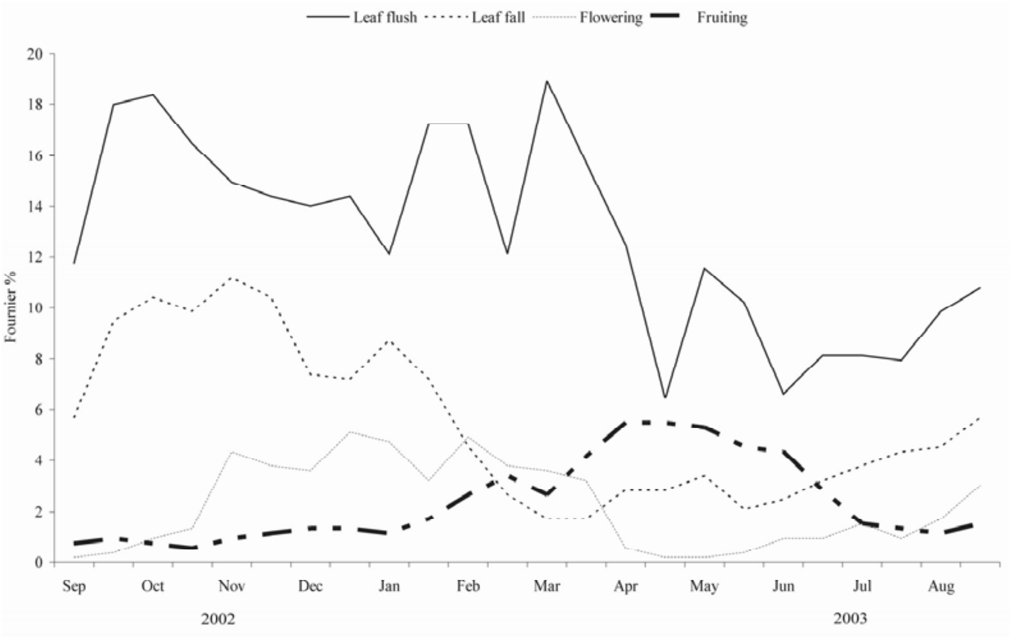

**Fig. 3 Fournier intensity percentage of the phenophases of leaf flush, leaf fall, flowering, and fruiting of 133 individual trees observed during the period between September, 2002 and August, 2003.** São José Forest, Igarassu/PE, Brazil.

intensity) during the entire year. All of the species demonstrated leaf flush during the dry season (Sept. – Dec.). During the wettest and coldest period of the year the number of species demonstrating leaf flush diminished, with July being the month with the smallest number of trees changing leaves (27 species, or approximately 60%) (**Fig. 2A**).

The period of the year with the largest number of species demonstrating leaf fall occurred between September and January, at the transition from the dry to the rainy season. During this period, approximately 85% of the species demonstrated leaf fall. The maximum peak of leaf fall occurred in October, when 67% of the species were in this phenophase. Starting in the January there was a decrease in leaf fall, with March showing the smallest number of species (approximately 20%) (**Fig. 2A**). Starting in July, there was a gradual increase in the number of species demonstrating this phenophase.

According to the Fournier intensity percentage, which measures the intensity of a given phenological event, leaf flush was greater within the community during the period from September to March, with peaks of intensity in September and October (18%) at the start of the dry period, and in February and March (17 to 20%) at the transition of the dry season to the start of the rainy season (**Fig. 3**). From April until August leaf flush intensity diminished considerably, reaching 6% in April and June. The Fournier intensity percentage indicated that there was intense leaf fall activity just at the start of the dry period, with a peak in November (11%). After this month, the intensity of leaf fall diminished gradually as the rainy season approached, with the lowest intensity being observed in March (less than 2%). At the end of the rainy season (August) the intensity of leaf fall began to increase again (**Fig. 3**). In general, the Fournier intensity percentage indicated that leaf flush and leaf fall activity occurred at low intensities throughout the entire year, as maximum values never passed 20%.

## Reproductive phenophases

The occurrence of reproductive events was greater during the transition from the dry to the rainy season (**Fig. 1, Fig. 2B**), although these phenophases demonstrated no significant correlations with precipitation (flowering: rs = -0.071; p = 0.82; fruiting: rs = 0.376. p = 0.22). **Table 2** presents a list of the species that flowered or produced fruits, and shows the occurrence and duration of these phenophases during the year.

Flowering was distinctly more intense during the period of decreased precipitation (September to February), when 86% of the species that flowered (n = 21 species) initiated flower production (**Fig. 1, Fig. 2B; Table 2**) - in spite of fact that there was no statistical correlation with precipitation. From October onward there was a gradual increase in

**Table 2** Species that flowered and/or fruited during the period between September/2002 and August/2003, ordered according to the initiation of flowering and indicating the time of year in which these phenophases occurred. São José Forest, Igarassu/PE, Brazil. "X" = flowering; "+" = fruiting.

| Species | S | O | N | D | J | F | M | A | M | J | J | A |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Cordia superba* | X | X | X | X | X | X | | | | | | |
| | | | + | + | | + | | | | | | |
| *Tapirira guianensis* | | X | X | X | X | X | X | | | | | |
| | | | | | | | + | + | + | + | + | + |
| *Pouteria bangii* | | X | X | | | | X | X | X | X | X | X |
| | + | + | + | + | + | + | + | | | | | |
| *Schefflera morototoni* | | X | X | | | | X | X | X | X | X | |
| | + | + | + | + | + | + | + | | | | + | + |
| *Sclerolobium* | | X | | | | | | | | | | |
| *densiflorum* | | | + | | | | | | | | | |
| *Tovomita brevistaminea* | | | X | X | X | X | X | | | | | |
| *Cecropia pachystachya* | | | X | X | X | X | | | | | | |
| | | | | | | + | + | | | | | |
| Clusiaceae A | | | X | X | | | | | | | | X |
| *Pogonophora* | | | | X | X | X | X | X | | | | |
| *schomburgkiana* | | | | | | | + | + | + | + | + | |
| *Guapira opposita* | | | | X | X | X | | | | | | |
| | | | | | + | + | | | | | | |
| *Guapira laxa* | | | | X | X | | | | | | | |
| *Thyrsodium spruceanum* | | | | X | X | | | | | | | |
| | | | | | | + | | | | | | |
| *Parkia pendula* | | | | X | | | | | | | | X |
| | + | | | + | | | | | | | | |
| *Himathanthus* | | | | | X | X | X | | | | | |
| *phagedaenicus* | | | | | | | | | | + | + | + |
| *Maytenus* cf. | | | | | X | X | X | | | | | |
| *distichophylla* | | | | | | | | | | + | + | + |
| *Helicostylis tomentosa* | | | | | X | X | | | | | | |
| | | | | | | + | + | + | + | + | | |
| *Brosimum guianense* | | | | | | X | X | | | | | |
| | | | | | | + | + | + | + | | | |
| *Coussarea* sp. | | | | | | X | X | | | | | |
| *Protium giganteum* | | | | | | | X | | | | | |
| *Ocotea gardneri* | | | | | | | X | | | | | |
| | | | | | | | + | + | + | + | | |
| *Inga capitata* | | | | | | | | | | | | X |
| | | | + | + | + | + | + | + | + | + | + | + |
| *Inga* sp.2 | | | | | + | + | | | | | | |

the number of species flowering, reaching a maximum in February with 12 species in activity, indicating that there was an interspecific synchrony in the community. There was an abrupt decrease in flowering after this month, reaching a minimum in April with only two species in flower (**Table 2**). The number of species in flower remained low during the entire rainy season.

As the number of species flowering increased, so did the number of species fruiting, with both peaks coinciding in February (12 species each). Of the 17 species observed fruiting, 13 (76%) initiated the production of fruits in the dry or transitional season (**Table 2**). As can be seen in **Fig. 2B**, the number of species demonstrating fruiting doubled from January to February, and after March (now during the rainy season) there was a gradual decrease in the number of species in this phenophase reaching the lowest number in July, with only five species. As such, it can be seen that many fruits were produced for dispersal during the rainy season. During the period from September to January and from July to August the number of species fruiting varied little (between four and six) (**Fig. 2B**). All of the plants that fruited (36% of the species studied) were classified as zoochoric (**Table 2**).

The Fournier intensity percentage demonstrated that both flowering and fruiting had low values during the year (< 6%), although they did vary between the dry and the rainy season. The percentage of plants flowering was greater in the dry and transitional seasons, with values varying between 4 and 5%. The production of flowers was very low during the rainy period, reaching values near zero in the months of April and May. At the end of the rainy season in August the production of flowers began to increase.

In contrast to flowering, the greatest percentage of fruit production occurred in the first half of the rainy season, specifically during the months of April and May, reaching values near 6%. In the second half of the rainy season, the production of fruits was as low as that recorded for the dry season, with values below 2%.

## DISCUSSION

### Regulation of leaf flush and leaf fall

The vegetation studied maintained an ever-green appearance during the entire year. This observation is supported by the absence of correlation between precipitation and leaf fall or leaf flush and a continuous production and loss of leaves. However, in spite of the fact that this and other humid forests in Brazil demonstrate continuous phenophases, there is a noted tendency to seasonality. This may be explained by the close relationships of the phenophases with variations in the temperature and photoperiod (Mori *et al.* 1982; Morellato *et al.* 2000; Talora and Morellato 2000) or the intensity of solar radiation (Wright and van Schaik 1994; Barone 1998).

The fact that leaf flush activity and intensity are greater in the dry and transitional seasons than in the rainy season indicates that precipitation is not a limiting or inducing factor for leaf flush in the studied forest. According to Borchert (1994) and Holbrook *et al.* (1995), the continuity of leaf growth even in the dry season is possible due to the availability of water in the deeper soil levels. Another factor that may be inducing a large production of leaves during the dry season is the high solar radiation levels that occur during this time of the year (Wright and van Schaik 1994; Barone 1998). These authors noted that the cloud cover during the rainy season significantly diminished the quantity of solar radiation reaching the plants, thus diminishing their photosynthetic activity and the production of new leaves. Thus the dry season, the period of maximum solar radiation, would be a more favorable epoch for plants to initiate leaf production. At least one study in the Amazon forest supports this theory (Huete *et al.* 2006).

In the humid forests of the southeastern Brazil, as in the studied forest, there was greater leaf flush activity during the period with the longest photoperiod and the highest temperatures (although in the southeastern humid forests this is the wet season, while in the study area it is the driest time of the year). If precipitation had a strong effect on leaf flush in the "São José" forest it might be expected that the greatest leaf production would occur in the wettest period (Fall-Winter), however, leaf flush was observed to occur at the driest time of the year (Spring-Summer) with the longest photoperiod. This suggests that other variables must be influencing leaf flush (and not precipitation directly). In spite of the fact that the photoperiod variation in the study area is only about an hour (Lammi 2005), it does appear to be a variable that should be more closely investigated in relation to the induction of leaf flushing (see Mori *et al.* 1982). Some studies have emphasized the effects of photoperiod on plant phenology (Leopold 1951; van Schaik *et al.* 1993; Wright and van Schaik 1994), while others have already proven a direct link to leaf flush in tropical forests, even in regions very close to the equator where the photoperiodic variation is less than 30 minutes (Borchert and Rivera 2001; Rivera *et al.* 2002; Elliot *et al.* 2006). Bulhão and Figueiredo (2002) pointed out that plants from tropical or equatorial regions are sensitive to small variations in the photoperiod and that photoperiod effects on inducing leaf flush and flowering should be more closely investigated.

It is interesting to note that it is exactly during the period of greatest activity of leaf fall that there is also the greatest production of leaves. In examining the relationships between these events, Reich and Borchert (1984) observed that the loss of leaves might function as an inducing factor for leaf flush, as when a plant loses its leaves there is a reduction in water loss due to evapotranspiration, allowing the individual to re-hydrate and sprout new leaves.

Among the diverse factors that could be associated with leaf fall the most commented in the literature is water stress, for when the dry season begins, the plants that suffer a certain degree of water deficiency begin to lose their leaves (Frankie *et al.* 1974; Machado *et al.* 1997). Considering also that as the leaves become older they have a diminished capacity to control the opening or closing of the stomata, Reich (1995) argued that it would compensate a plant to lose its old leaves and grow new ones with greater stomatal control and greater photosynthetic capacity.

### Regulation of flowering and fruiting

Although flowering did not demonstrate any significant correlation with the climatic variables examined, it did tend to occur during the dry and the transitional seasons, suggesting that climate does play some kind of influence on this seasonal phenophase (*sensu* Frankie *et al.* 1974). This same type of behavior was noted in other tropical forests (Janzen 1967; Frankie *et al.* 1974; Fournier 1976; Alencar *et al.* 1979; Rathcke and Lacey 1985; Morellato *et al.* 1989; van Schaik *et al.* 1993; Locatelli and Machado 2004). According to Talora and Morellato (2000), pollination must have a fundamental role in the regulation of flowering times in plants. Janzen (1967) noted that flowering during the period of least precipitation would accrue certain advantages to plants as a dry climate favors pollinator insect activity while heavy rain, on the other hand, could damage the inflorescences or individual flowers, and dilute nectar.

In addition, a number of workers have hypothesized that flowering may be associated with increases in the photoperiod and environmental temperature (Frankie *et al.* 1974; Fournier 1976; Mori *et al.* 1982; Morellato *et al.* 2000; Borchert and Rivera 2001), the increase in humidity associated with the transition from the dry to the rainy season (Morellato *et al.* 1989), the sporadic rains that occur at this time (Opler *et al.* 1976), and the greater availability of nutrients in the soil (Morellato 1992). This latter author noted that the first rains and the higher temperatures at the end of the dry season accelerate the decomposition of the accumulated leaf litter – which would make more nutrients available to the many tree species that are entering into the period of greatest reproductive activity. A similar pattern was observed in the present study area, where the period of greatest leaf fall and production of leaf litter (Schessl *et al.* 2008) occurred precisely during the dry season – the period just before the flowering peak.

The continuous fruiting pattern observed in the "São José" forest is commonly observed in humid tropical forests (Morellato *et al.* 2000; Talora and Morellato 2000) although, different from the forests in southeastern Brazil (Morellato *et al.* 2000), the "São José" forest demonstrated greater fruit production at the transition of the dry to the rainy season and at the start of the rainy season. This result is similar to that reported by Medeiros *et al.* (2007) in a coastal forest in southern Pernambuco State. According to Griz and Machado (2001), the start of the rainy season presents the best conditions for the germination and growth of seedlings. Fournier and Salas (1966) observed that fruiting during this period gives the seedlings the entire humid season to develop their root system before the start of the next dry season.

All of the species that were observed fruiting (36% of the trees that were accompanied) were zoochoric. It is possible that this represents the general pattern for the arboreal community as a whole, as numerous researchers have confirmed the predominance of zoochory in northeastern humid forests (Griz and Machado 1998; Silva and Tabarelli 2000; Tabarelli and Peres 2002) as well as in southeastern Brazil (Morellato 1995; Talora and Morellato 2000). Different authors have observed that the more humid the region, the greater will be the number of zoochoric species – which tend to fruit in the rainy season when there is greater activity of disperser animals (Janzen 1967; Frankie *et al.* 1974; Alencar *et al.* 1979; Gottsberger and Silberbauer-Gottsberger 1983; Morellato *et al.* 1989).

Silva and Tabarelli (2000) reported that 70% of the arboreal species in the Atlantic Forest of northeastern Brazil are dispersed by vertebrates, and suggest that the humid forests of the region must have a wide spectrum of dispersers of seeds. These are principally birds, as noted by Farias *et al.* (2007) who undertook a survey at the São José Forest and noted the presence of 184 bird species, among which were many frugivorous species, but they also registered the absence of some species of birds that had previously been cited in the literature for that same region. This apparent loss of dispersers could represent a serious threat to the self-sustainability of the highly fragmented Atlantic Forest in northeastern Brazil. It is possible that some plant species could remain restricted to only a certain forest fragment due to a deficiency of seed dispersers, leading to their local extinction. Additionally, another important problem related to seed dispersal is the as yet unknown capacity of birds to cross the sterile and uniform matrix of sugarcane (Silva and Tabarelli 2000; Farias *et al.* 2007).

In general, the examined assemblage demonstrated a tendency to seasonality, although no direct correlation of the phenophases with precipitation was observed. As such, it will be important to undertake more studies in the Atlantic Forest of the Northeast of Brazil to analyze the influence of variables such as photoperiod and solar radiation in order to more fully understand the phenological patterns of this region.

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