Canopy phenology of a dry forest in western Brazil

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(With 2 figures)

Abstract

Dry forests are common, although highly threatened in the Neotropics. Their ecological processes are mostly influenced by rainfall pattern, hence their cycles exhibit contrasting phases. We studied the phenology of canopy trees in a primary dry forest in Western Brazil in the foothills of the Urucum mountain chain, in order to improve our knowledge on the functioning of these poorly-known forests. Leaf shedding started in the early dry season and was massive in the latter part of this period. Most leaf loss occurred in dry hills, while wet valleys remained evergreen. Anemochorich and autochorich species predominated in dry hills, presumably due to their tolerance to dry conditions and enhanced exposition to winds, which favour diaspores removal and dispersal. Conversely, zoochorich species dominated the wet valleys. Flowering was intense in the late dry season, the driest period of the year, while fruiting was massive just after the onset of rains, as well as flushing. Therefore, most flowering was unrelated to wet conditions, although such an abiotic factor, potentially, triggered the major fruiting episode, widely comprised by zoochorich species. Anemochorich and autochorich species flowered and fruited in the course of the long dry season. The contrasting environmental conditions present in the hills and valleys determine the arrangement of a mosaic in which patches of zoochorich and evergreen trees alternate with patches of non zoochorich and highly deciduous species. Consequently, species with such syndromes exhibited marked flowering and fruiting patterns, accordingly to the pronounced seasonality.

Keywords: canopy trees, deciduous forest, seasonality, dispersal syndromes, flowering and fruiting.

Fenologia do dossel em uma mata seca do oeste brasileiro

Resumo

Matas secas neotropicais estão amplamente distribuídas, porém sob elevado risco de desmatamento. Os processos ecológicos nesses ambientes são fortemente influenciados pelo clima, sobretudo o padrão de chuvas, de tal forma que seus ciclos apresentam fases muito contrastantes. Nesse estudo, avaliamos a produção de folhas, flores e frutos em uma mata seca do oeste brasileiro situada no sopé do maciço do Urucum. A perda de folhas teve início no começo da estação seca, mas foi massiva ao final desse período, o mais seco do ano. Espécies decíduas predominaram nas escarpas secas, enquanto as perenifólias foram comuns nos vales úmidos. Nas escarpas, espécies anemo e autocóricas eram muito comuns, potencialmente, por serem mais tolerantes à baixa umidade, bem como favorecidas por ventos mais fortes. Porém, eram raras ou mesmo ausentes nos vales úmidos dominados por espécies zoocóricas. A floração foi intensa, exibindo um pico acentuado ao final da estação seca, seguida de um pronunciado pico de frutificação e produção de folhas com o início das chuvas. Dessa forma, enquanto a floração massiva não foi influenciada pelas chuvas, a frutificação e produção de novas folhas estiveram fortemente relacionadas a esse fator abiótico. As espécies anemo e autocóricas floresceram e frutificaram durante a prolongada estação seca, ao contrário da maioria das zoocóricas. As condições ambientais contrastantes dos vales e escarpas, potencialmente determinam um mosaico em que porções altamente decíduas de mata, com predomínio de espécies anemo e autocóricas, se alternam com outras sempre verdes, dominadas por espécies zoocóricas. Além disso, a forte sazonalidade influencia diferentemente espécies com síndromes de dispersão distintas.

Palavras-chave: dossel, floresta decídua, sazonalidade, floração, frutificação.

1. Introduction

Dry forests are widespread in the neotropics, and as major features exhibit low trees, scarce understory, and pronounced leaf shedding in the course of the dry season (Bullock and Solís-Magallanes, 1990). In such forests, most plant families include one or exceptionally few species (Gentry, 1995), which usually are patchily distributed (Hubbell, 1979). As dry forests occur in highly seasonal areas, flowering and fruiting pattern are mostly influenced by rainfall pattern (van Schaik et al., 1993). Therefore, with respect to the dispersal pattern, there is a propensity for a balanced number of tree species adapted to animal or non animal seed dispersal (Bullock, 1995).

Taking into account the temporal pattern of water availability as the most important factor determining leaf, flower, and fruit production in the dry forests (Bullock, 1995), their effect on canopy trees is expected as more severe, since this vegetation layer is under harsher environmental conditions in relation to the more wet and dark understory (Lowman and Wittman, 1996). Hence, a major consequence on canopy phenology is a contrasting dynamics, which includes wide modifications of forest microclimate, as well as the relationships with primary consumers, whose activities are also markedly seasonal (van Schaik et al., 1993).

In western Brazil, although under an accelerated deforestation process, dry forests are still common, similar to the dry forests present elsewhere in South America (Murphy and Lugo, 1986). These forests remain almost unstudied, except for neighboring areas in Bolivia (Justiniano and Fredericksen, 2000). The ‘Urucum’ is a prominent mountain chain within the ‘Pantanal’ flood plain. In such mountains, dry forests are the major vegetation type from the foothills up to near the top, in which rock fields are present. As phenology studies are a useful tool to improve our knowledge on the functioning of the dry forests, in this study we examined the leaf, flower, and fruit phenology of canopy trees in the foothills of the Urucum mountain chain (Serra Santa Cuz).

2. Methods

2.1. Study site

This study was developed in the foothills of the Urucum mountain chain (Serra Santa Cruz, Municipality of Corumbá, State of Mato Grosso do Sul, 58° 34’ W and 19° 13’ S, elevation 150-200 m). The vegetation in this hilly terrain encompasses a gradient of tall dry forest in the foothills, followed by low dry forest up to the timberline (700-800 m), and rock fields up to the top (approximately 1100 m). In the foothills there is a predominance of iron rich soils, and the undulated topography includes wet valleys interspersed with dry hills. The forest canopy in this tract is 12-15 m tall, but emergent trees may reach 17-18 m. From June to September many tree species drop their leaves (mainly on the hills). The climate exhibits two contrasting seasons (Awa according to Köppen; Soriano 1997), so that 70-80% of the annual rainfall (around 1100 mm) occurs from November to March (wet season). During the wet season, the average temperature is 26 °C, while during the dry season (April to September), on average 19 °C is recorded, and in the coldest months frosts may occur (source: mining company in the Urucum mountain chain [Mineração Corumbaense Reunida S/A, Grupo Rio Tinto Brasil]; (Figure 1).

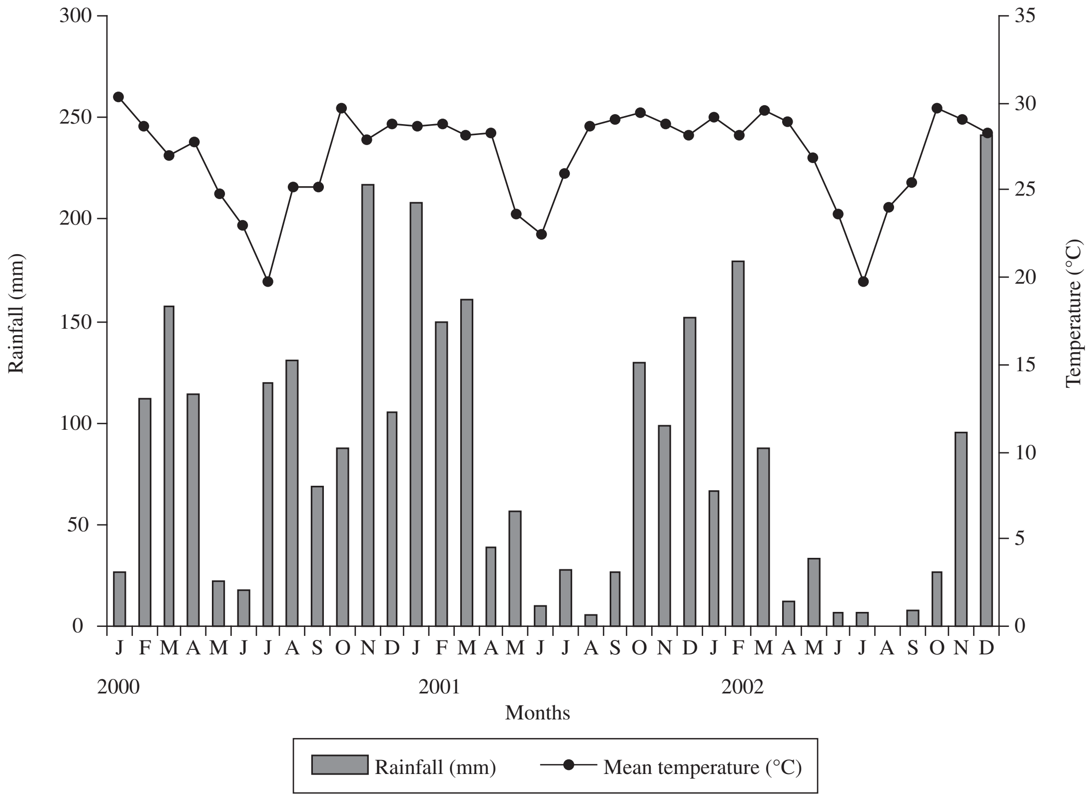
2.2. Fieldwork procedures

To select trees to sample leaf, flower, and fruit production, 18 points were positioned (300 m apart from each other) along a 6 km permanent access trail. Consequently, there were eight points in the hills, and 10 in the valleys. At each point the 15 nearest trees with diameters at breast height (DBH) equal to or greater than 30 cm were numbered with aluminum tags. This criterion was adopted to assure the inclusion of canopy and emergent trees. Also, a tree was selected only if at least 80% of the crown could be observed from the forest floor. Individual crowns were monitored monthly (between day 20 and 25, from September 2000 to February 2002) for the presence of leaves, flowers and fruits, with the aid of 8 x 40 binoculars. The abundance of such organs was ranked on a relative scale ranging from total absence (0) to the full crown capacity (4) of a given phenophase (Fournier, 1974). Thus, for a specific phenophase, the monthly index of resource abundance resulted from the sum of all abundance scores. Tree species were identified by comparison with samples in the herbarium at the Universidade Federal do Mato Grosso do Sul (Corumbá campus) and following Lorenzi (1998). A detailed analysis of dispersal syndromes was beyond the scope of this study since we perform no evaluation on the dispersal process. However, in order to distinguish contrasting diaspores using dispersal syndromes as an organizing tool, we determined the dispersal mode of fruits based on their mesocarp features (shape, texture, color, and size; van der Pijl, 1972). Therefore, we grouped tree species according to dispersal syndromes in order to analyze the relationships between fruit type and phenophase pattern.

3. Results

3.1. Foliar phenology

The 56 tree species from the phenology sample belong to 26 families (Table 1). Most species (30) as well as trees sampled (168, N = 270) produced fleshy fruits, while 102 trees from 26 species produced dry fruits (Table 1). Deciduous species predominated in the foothills (54%), followed by a substantial proportion of species which exhibited partial leaf loss (37%). Only 9% were evergreen species, all of them zoochorich. Leaf shedding started in April, so that in May and June some species (mainly *Eriotheca roseorum* (Cuatrec.) A. Robyns (1963) and *Erythrina dominguezii* Hassl.



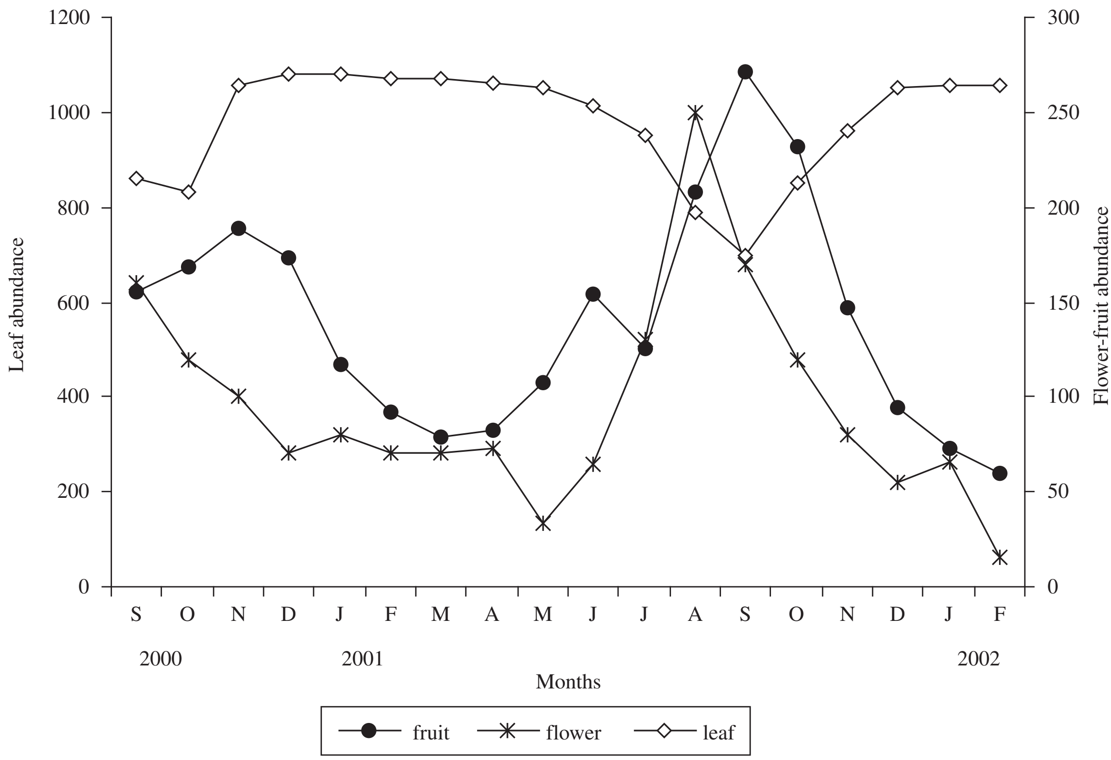


Figure 1. Climate (data from January 2000 to December 2002), and the general patterns of leaf, flower, and fruit abundance (N = 270 trees) in the Urucum foothills.

Table 1. Abundance (N = 270 trees), and fruit type of the tree species (N = 56) in the dry forest in the foothills of the Urucum mountain chain.

Plant taxa	N	Fruit type
ANACARDIACEAE		
Astronium fraxinifolium	14	Anemoch.
Myracrodruon urundeuva	6	Anemoch.
Spondias lutea	8	Zoochorich
ANNONACEAE		
Annona montana	2	Zoochorich
APOCYNACEAE		
Aspidosperma cylindrocarpon	1	Anemoch.
Aspidosperma subincanum	13	Anemoch.
ARALIACEAE		
Schefflera morototoni	5	Zoochorich
ARECACEAE		
Acrocomia aculeata	4	Zoochorich
Attalea phalerata	7	Zoochorich
BIGNONIACEAE		
Jacaranda cuspidifolia	1	Anemoch.
Tabebuia impetiginosa	6	Anemoch.
Tabebuia roseo-alba	2	Anemoch.
BOMBACACEAE		
Ceiba boliviana	1	Anemoch.
Eriotheca roseorum	7	Anemoch.
Pseudobombax longiflorum	1	Anemoch.
BURSERACEAE		
Protium heptaphyllum	43	Zoochorich
CECROPIACEAE		
Cecropia pachystachya	1	Zoochorich
COMBRETACEAE		
Combretum leprosum	1	Anemoch.
Terminalia argentea	3	Anemoch.
FLACOURTIACEAE		
Casearia gossypiosperma	3	Zoochorich
HIPPOCRATEACEAE		
Salacia elliptica	3	Zoochorich
LAURACEAE		
Nectandra cissiflora	1	Zoochorich
LEGUMINOSAE		
Acacia tenuifolia	1	Autoch.
Acosmium cardenasii	1	Autoch.
Albizia niopoides	2	Autoch.
Anadenanthera colubrina	10	Autoch.
Caesalpinia pluviosa	4	Autoch.
Guibourtia hymenaefolia	1	Zoochorich
Dipteryx alata	8	Zoochorich
Enterolobium contortisiliquum	1	Autoch.
Erythrina dominguezii	4	Autoch.
Hymenaea courbaril	4	Autoch.
Inga vera	1	Zoochorich
Lonchocarpus pluvialis	3	Autoch.
Peltophorum dubium	4	Autoch.
Pterogyne nitens	1	Anemoch.
MELIACEAE		
Cedrela fissilis	1	Anemoch.
Guarea guidonia	24	Zoochorich
Trichilia catigua	9	Zoochorich
Trichilia elegans	2	Zoochorich
MORACEAE		
Ficus calyptroceras	1	Zoochorich
Ficus gardneriana	1	Zoochorich
Ficus gommelleira	2	Zoochorich
Ficus insipida	1	Zoochorich
Maclura tinctoria	1	Zoochorich
MYRTACEAE		
Eugenia sp.	1	Zoochorich
NYCTAGINACEAE		
Guapira areolata	3	Zoochorich
OPILIACEAE		
Agonandra brasiliensis	3	Zoochorich
RHAMNACEAE		
Rhamnidium elaeocarpum	1	Zoochorich
RUBIACEAE		
Coussarea hydrangaeifolia	5	Zoochorich
RUTACEAE		
Zanthoxyllum chiloperone	2	Zoochorich
SAPOTACEAE		
Pouteria torta	20	Zoochorich
SAPINDACEAE		
Dilodendron bipinnatum	3	Zoochorich
STERCULIACEAE		
Sterculia striata	1	Zoochorich
TILIACEAE		
Apeiba tibourbou	2	Anemoch.
Luehea grandiflora	4	Autoch.

(1922)) were completely leafless. As the dry season progressed leaf loss enhanced dramatically up to the late dry season, when rainfall was usually minimal (Figures 1, 2). Anemochorich and Autochorich species comprised the bulk of deciduous trees, since almost all of them drop their leaves massively, mainly from the middle to the end of the dry season. Common species such as *Astronium fraxinifolium* Schott (1827), *Tabebuia impetiginosa* (Mart. ex DC.) Standl. (1936), *Myracrodruon urundeuva* Allem. (1862), and *Anadenanthera colubrina* (Vell.) Brenan (1955), became completely leafless, while *Aspidosperma subincanum*

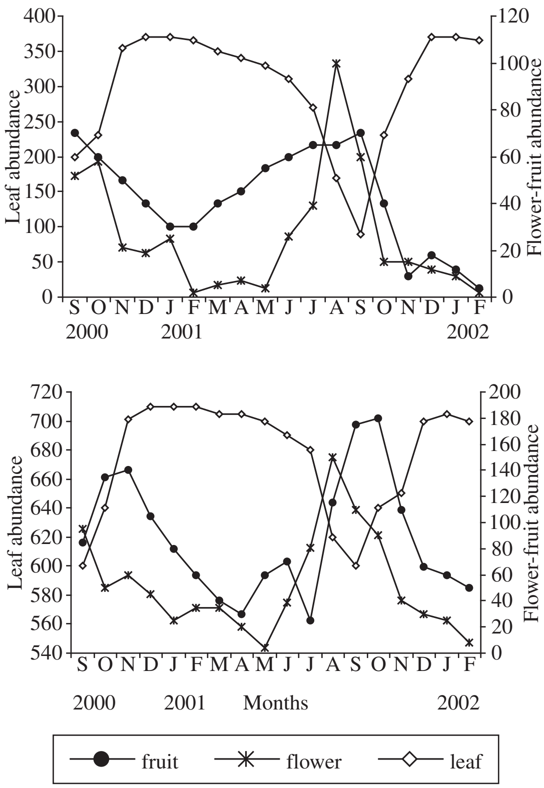


Figure 2. The abundance of leaves, flowers and fruits from anemochorich-autochorich (above), as well as from zoochorich trees (below). (Due to the similar phenology pattern the data from anemochorich and autochorich trees were grouped).

Mart. (1891), and *Hymenaea courbaril* L. (1753) exhibited partial leaf shedding (Figure 2). Among zoochorich species, pronounced leaf loss occurred in species such as *Spondias lutea L. (1762), Dilodendron bipinnatum* Radlk. (1878), and in the genus *Ficus,* while *Protium heptaphyllum* March. (1873), *Guarea guidonia* (L.) Sleumer (1956), and *Pouteria torta* Radlk. (1882) were evergreen (Figure 2). Trees massively produced new leaves from October to December after the first heavy rainfall (Figures 1, 2).

3.2. Flowering phenology

Flower production fluctuated substantially during the year, however every month at least some species produced flowers. Flower production declined abruptly during rains, while it was massive in the late dry season (Figures 1, 2). From April to July up to 10 species flowered, whereas up to 22 species did so from August to October. Anemochorich and Autochorich species flowered mainly from the early to the middle of the dry season (39%, N = 26). Among them *Anadenanthera colubrina, Erythrina dominguezii,* and *Astronium fraxinifolium* produced a very large flower crop every year. Only 19% (N = 29) of zoochorich species flowered in the same period. Zoochorich species produced flowers predominantly from the middle to the late dry season comprising the pronounced flowering peak in August-September (Figure 2). Such a peak arose mainly from flowering of *Protium heptaphyllum*, and *Guarea guidonia*. Other zoochorich species important for the flowering pattern were *Pouteria torta,* and *Spondias lutea*.

3.3. Fuiting phenology

Fruit production was also seasonal with two evident peaks (Figures 1, 2). A minor peak was recorded in the middle of the dry season, whereas a very pronounced fruiting peak occurred in the transition from the dry to the wet season (Figures 1, 2). The first peak arose mostly from fruiting in *Anadenanthera colubrina, Cedrela fissilis* Vell. (1829), *Caesalpinia pluviosa* DC. (1825), and *Dipteryx alata* Vogel (1837). In this period 17 species fruited, of which only 47% produced fleshy fruits. On the other hand, the major peak of fruit production resulted from fruiting of abundant species such as *Protium heptaphyllum, Guarea guidonia, Pouteria torta,* and *Spondias lutea*. This fruiting peak included up to 20 species, most of which (70%) bore fleshy fruits. If only species with fleshy fruits are considered, *Protium heptaphyllum* was particularly important, since it comprised 43% of the fruiting peak in October 2001 (Figure 2).

4. Discussion

4.1. Foliar phenology

During the dry season, although most species at least partially shed their leaves, a semi-deciduous pattern was evident as a result of the large number of evergreen trees. Moreover, even considering that the evaluation of species distribution was beyond the scope of this study, pronounced leaf shedding was clear in the dry hills while evergreen species dominated in the wet valleys. Apparently, in the valleys, soil layer is deeper while the water table is shallower. During the rains, small streams commonly emerged from several points in the valleys. By contrast, exposed rocks were common in the dry hills, and streams occurred in no place during rains. Therefore, wet conditions potentially favored the prolonged lifespan of leaves from trees under a less pronounced water deficit (Borchert, 1994).

In anemochorich and autochorich species, leaf loss started in the early dry season, mainly in those species which flowered in the middle of this period while leafless (e.g. Bignoniaceae and Bombacaceae). Other species which contributed to the major flowering peak became leafless during the driest months, when they flower. These species remain leafless up to the windiest months (August and September) when they bore fruits. As mentioned above, deciduous trees were prominent in the dry hills, in which potentially soil moisture storage was comparatively reduced and wind flow was stronger, favoring diaspore dispersal.

Among zoochorich species leaf shedding was conspicuous in species present in the dry hills, such as *Spondias lutea, Dilodendron bippinnatum,* and *Ficus calyptroceras.* Conversely, the most common species, *Protium heptaphyllum, Guarea guidonia,* and *Pouteria torta,* maintained most of their leaves and were very common in the wet valleys, where they exhibit a contrasting pattern in relation to the bare trees in the hills. Therefore, during the dry season this vegetation was arranged as a mosaic in which patches of deciduous trees alternate with evergreen ones, potentially, according to water soil storage (Borchert, 1994; Reich, 1995). The influence of this factor on the life span of leaves was also suggested in the case of some common species which occurred both in hills and valleys (e.g. *Protium heptaphyllum,* and *Spondias lutea*). In such species leaf shedding was conspicuously more pronounced on hills in comparison with valleys. As mentioned above, typically, leaf shedding started earlier and was severe on dry hills.

4.2. Flowering and fruiting phenology

In Neotropical dry forests, massive flowering usually occurs between the late dry and the early wet season, followed closely by fruit production (Frankie et al., 1974; Bullock and Solis-Magallanes, 1990). As in such forests, tree species may be represented by many individuals, much of the flowering pattern results from their synchronous flower production (Bullock, 1995). This potentially was the case in the Urucum foothills, since the species which comprised most of the flowering peaks, besides being common, fruited during early rains. It is widely accepted that trees time flowering synchronously in order to attract pollinators to enhance pollen flow and/or avoid substantial flower loss to nectar robbers (van Schaik et al., 1993). On the other hand, species with reduced water storage, at dry sites, flower with the first rains, so that rehydration is the major cause for flowering, instead of other environmental cues (Borchert, 1994). The pronounced flowering peaks recorded in this study mostly resulted from flower production of abundant zoochorich species (*Protium heptaphyllum, Pouteria torta,* and *Guarea guidonia*), commonly present in the wet valleys. Therefore, much of the major flowering episodes potentially resulted from the adaptations of tree species to their pollen vectors, since the pronounced flowering peak occurred in August and September, the driest month (Figure 1).

In the Urucum foothills, apparently fleshy fruits predominated among canopy trees, a trend found in other Neotropical forests as well (Fenner, 1985; Bullock, 1995). The marked fruiting peak of species with fleshy fruits were potentially conformed to rainfall seasonality, since in the dry forests massive fruit production is usually triggered with the onset of the rains (Frankie et al., 1974; Bullock and Solis-Magallanes, 1990; van Schaik et al., 1993; Funch et al., 2002). Although in the Urucum foothills forest species with fleshy fruits were more common, fruiting was markedly seasonal, so that plentiful fleshy fruit availability was restricted to a few months from the early to the middle of the wet season. Only some species represented by few individuals bore fleshy fruits during the prolonged dry season. Not surprisingly, most of them fruited asynchronously (palms and figs). A substantial fleshy fruit production after the early rains is presumably related to the short period with wet conditions, in forests often subjected to a severe dry season. Then, both seed germination and seedling establishment usually take place in the beginning of the wet season to avoid unfavorable conditions and consequently a higher risk of mortality during the late wet season (van Schaik et al., 1993). Seedlings from many species that fruited during the early wet season, especially those from the abundant *Protium heptaphyllum*, formed a carpet in some places of the forest floor in the middle of the wet season (pers. obs.).

The wind-dispersed species, on the other hand, bore fruits mainly from the middle to the late dry season, during the windy months. The absence of their leaves favors wind circulation through the bare crowns, which potentially is enhanced at the more exposed hills dominated by such species. Leaf absence and dry conditions also favors seed dispersal in several autochorich species (Bullock and Solis-Magallanes, 1990; van Schaik et. al. 1993; Bullock, 1995). In addition, besides often being present in the dry hills, the emergent trees (mainly anemochorich), also produced fruits during the windiest months when the propensity for efficient seed dispersal is higher (van Schaik et al., 1993). Hence, to conclude, the Urucum foothills forest is arranged as a mosaic of deciduous and evergreen patches in which predominated non-zoochorich and zoochorich trees, respectively. Such areas exhibit a contrasting temporal phenological pattern in response to both rainfall and soil moisture.

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