Reproductive phenology of an herbaceous-subshrub layer of a Savannah (Campo Sujo) in the Cerrado Biosphere Reserve I, Brazil

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(With 3 figures)

Abstract

The objective of this study was to analyse the phenological events in the herbaceous and subshrub layer in relation to rainfall and the dispersion syndromes of the species at a Campo Sujo community in the Água Limpa Farm (FAL), Brasília-DF. Campo Sujo is a *grassland* Savannah with a few scattered shrubs and small trees. The climate is Aw by Köppen classification with a mean annual precipitation of 1500 mm. Herbaceus species with three to ten individuals were monitored totalling 519 individuals of 61 species. The individuals were observed quarterly from October 1999 to February 2001. An accidental fire happened in the area two months before the beginning of this study and stimulated flowering and fruiting of the studied species. Flowering at the community level was distributed all over the study period with a concentration of flowering species in the rainy season. The pattern of fruiting was similar to the flowering, with most species maturing their diaspore from the middle to the end of the rainy season. The correlation between anemochoric species producing mature fruits and precipitation was significant and inverse. Anemochoric and autochoric species are dominant at the herbaceous-subshrub layer of the Campo Sujo and they determine the phenological pattern of the community.

Keywords: phenology, dispersion syndromes, anemochoric, herbaceous layer, Cerrado.

Fenologia reprodutiva da camada herbácea e subarbustiva de savana (Campo Sujo) na Reserva da Biosfera do Cerrado I, Brasil

Resumo

O objetivo deste estudo foi analisar os eventos fenológicos na camada herbácea subarbustiva em relação à precipitação e às síndromes de dispersão das espécies em uma comunidade de Campo Sujo na Fazenda Água Limpa (FAL), Brasília-DF. O Campo Sujo é uma savana predominantemente herbácea com poucos arbustos e pequenas árvores. O clima da região é do tipo Aw, segundo a classificação de Köppen, com uma precipitação média anual de 1500 mm. Foram selecionadas as espécies que possuíam de 3 a 10 indivíduos, resultando em 61 espécies e 519 indivíduos amostrados. Os indivíduos foram observados quinzenalmente de outubro de 1999 a fevereiro de 2001. O fogo ocorrido na área dois meses antes do início do estudo estimulou a floração e a frutificação das espécies amostradas. A floração na comunidade apresentou-se distribuída por todo o período estudado com concentração de espécies florescendo na estação chuvosa. A produção de frutos foi similar, com a maioria das espécies amadurecendo seus diásporos do meio para o final da estação chuvosa. A correlação entre as espécies anemocóricas produzindo frutos maduros e a precipitação foi significativa e inversa. As espécies anemocóricas e autocóricas são dominantes na camada herbácea subarbustiva de Campo Sujo e determinam o padrão fenológico da comunidade.

Palavras-chave: fenologia, síndromes de dispersão, anemocórico, camada herbácea, Cerrado.

1. Introduction

The Cerrado Biome ocuppied, originally, 23% of Brazil's land area (Ratter et al., 1997) covering the Brazilian Central Plateaux and presenting a wide physiognomic range, from grassland to tall woodlands where most physiognomies fit the definition of tropical Savannah (Sarmiento, 1983).

Campo Sujo is a physiognomy of the Brazilian Savannah (Cerrado) characterized by a continuous herbaceous layer dominated by grasses with some broadleaf herbs and sub-shrubs and few scattered shrubs and trees, the woody layer covering less than 10% (Eiten, 1972, 1979, 1993; Ribeiro and Walter, 1998).

The herbaceous sub-shrub layer is an important component of all physiognomies of Cerrado from Grasslands (Campo Limpo) to Woodlands (Cerrado *sensu stricto* and Cerradão). It is the layer richest in species (Felfili et al., 1994; Mendonça et al., 1998), with over 90 million ha used as natural pasture (Haridasan et al., 1996) but there have been few studies of the community structure (Goldsmith, 1974; Mantovani and Martins, 1993; Felfili et al., 1994; Meirelles et al., 2002). The most phenological studies of the herbaceous subshrub layer of the Cerrado were carried out at outlying sites, in the southern São Paulo State (Batalha et al., 1997; Batalha and Mantovani, 2000), only Batalha and Martins (2004) analysed the reproductive phenological patterns of the plant species at a core Cerrado site at the community level. The turnover of species of different life-forms over the year and their phenological patterns still need to be studied.

Several studies with tropical species indicate that their phenology is determined by a series of factors such as rainfall regime, solar irradiance and temperature (Alvin, 1967; Frankie et al., 1976; Monastério and Sarmiento, 1976; Sarmiento, 1983; Sarmiento and Monastério, 1983; Reich and Borchert, 1984; Rathcke and Lacey, 1985; Silva, 1987; van Schaik et al., 1993; Seghieri et al., 1995); pollinators, syndromes of dispersion and seed germination (Janzen, 1967; Frankie et al., 1974; Rathke and Lacey, 1985).

The phenological patterns of individual species and also of groups of congeneric species has been related to the distinct seasonality of the Cerrado, with wet summers and dry winters (Barros and Caldas, 1980; Ribeiro et al., 1982; Gottsberger, 1986; Batalha et al., 1997) as well as the phenological patterns of communities (Mantovani and Martins, 1988; Oliveira, 1994; Oliveira and Moreira, 1992; Gouveia and Felfili, 1998; Batalha and Mantovani, 2000; Batalha and Martins, 2004).

According to Borchert (1999), a prolonged dry period in a seasonal tropical climate is the main climatic determinant of the foliar phenology. According to Sarmiento (1984) the phenology of the herbaceous tropical Savannah grasses is determined by the seasonality of those ecosystems. The drought affects the phenology of the plants of the herbaceous-subshrub layer that have superficial root systems (Mantovani and Martins, 1988; Batalha et al., 1997; Batalha and Mantovani, 2000; Batalha and Martins, 2004). Those authors found a strong reduction in flowering during the dry season, especially from June to August and a peak of species flowering during the rainy season, from January to April.

Resources partioning for growth of vegetative and reproductive structures can also influence the life cycle of a species in a plant community. The understanding of the life-forms of the herbaceous-subshrub layer and their phenology depends on the knowledge of the temporal and spatial distribution of the species in the community and their relationship with environmental factors. We assume that rainfall is the main determinant of the phenology of herbaceous and subshrub species in a Campo Sujo.

This study evaluates the influence of rainfall on the vegetative (leaf production) and reproductive (flowering and fruiting) of the herbaceous-subshrub layer of a Campo Sujo community. We also look at the phenological patterns by life-form and dispersion syndrome.

2. Materials and Methods

This study was conducted from October 1999 to February 2001 at the Água Limpa Farm (FAL), (15° 56' to 15° 59' S and 47° 55' to 47° 58' WGr.), the experimental station of the University of Brasília and the nuclear area of the Cerrado Biosphere Reserve. The Campo Sujo area studied is located near to the gallery forest of the Taquara stream and suffered an occasional burning in the first week of August 1999, two months before the beginning of this study.

The climate is Aw, according to Köppen's classification and characterized by a rainy season from October to April and a dry season from May to September. The highest monthly average temperature is 28.5 °C and the minimum average is 12.0 °C. The mean annual precipitation in the studied period was 1500 mm registered by the IBGE climatological station.

For this study only species with three to ten individuals found at the transects set up for phytosociological studies were selected. To avoid monitoring ramets of a same individual, each individual selected for this study had to be at least three meters distant from each other. For the phytosociological studies an area of 400 x 400 m of Campo Sujo was divided in four portions of 200 x 200 m. At each portion one transection off at 40 m was randomly located in the direction perpendicular to the border of the Taquara stream gallery forest. The method of line intersection (see Canfield, 1941, 1950) was used to sample the floristic composition and the linear coverage of the species. This method consists of projecting transections over the vegetation and recording the projection of each species over it.

A total of 519 individuals of 61 species in 23 families were monitored at quarterly intervals from October 1999 to February 2001. The phenological phase was recorded on a four point scale: 1) floral buds; 2) open fowers; 3) new fruit and 4) mature fruits. The observations were qualitative, i.e. only presence and ausence of the phenological phase was registred. The species were classified, according to their dispersal syndromes (Pijl, 1972), into anemo, auto or zoochoric, when they were dispersed by wind, explosion or gravity and animals, respectively.

Spearman rank correlation between each phenological event and rainfall was calculated for the community (Sokal and Rohlf, 1981). The phenological variables used for the analyses were number of individuals and number of species presenting the event.

3. Results

A total of 45% of the Campo Sujo species monitored in this study were anemochoric, 40% autochoric and 15% zoochoric (Table 1, Figure. 1).

Table 1. Species by dispersion syndromes in a herbaceous and Sub-Shrub species Savannah (Campo Sujo) Community in Água Limpa Farm at the Cerrado Biosphere Reserve, Federal District, Brazil. (N = number of individuals monitored in this study).

Species	N	Dispersion Syndromes
Andropogon leucostachyus Kunth.	10	Anemochoric
Andropogon selloanus (Hack.) Hack.	4	Anemochoric
Arthropogon villosus Nees	10	Anemochoric
Aspilia foliacea (Spreng.) Baker	10	Anemochoric
Axonopus brasiliensis (Spreng.) Kuhlm.	10	Anemochoric
Axonopus marginatus (Trin.) Chase	10	Anemochoric
Baccharis humilis Sch. Bip. ex Baker	10	Anemochoric
Borreria poaya (A. St.-Hil.) DC.	3	Zoochoric
Bulbostylis paradoxa (Spreng.) Lindm.	4	Anemochoric
Byrsonima rigida A. Juss.	10	Zoochoric
Calea cuneifolia DC.	3	Anemochoric
Calea gardneriana Baker	7	Anemochoric
Calea platylepis Sch. Bip. ex Baker	4	Anemochoric
Campomanesia xanthocarpa O. Berg.	10	Zoochoric
Campomanesia pubescens (DC.) O. Berg	10	Zoochoric
Casearia sylvestris Sw.	9	Autochoric
Chamaecrista pohliana (Benth.) H.S. Irwin and Barneby	10	Autochoric
Chresta sphaerocephala DC.	7	Anemocoric
Clitoria guianensis (Aubl.) Benth.	10	Autochoric
Croton antisyphiliticus Mart.	10	Autochoric
Croton campestris (A. St.-Hil.) Müll. Arg.	10	Autochoric
Croton goyazensis Mart.	10	Autocoric
Cuphea linarioides Cham. and Schltdl.	10	Autochoric
Cuphea spermacoce A. St.-Hil.	10	Autochoric
Dalechampia caperonioides Baill.	8	Autocoric
Echinolaena inflexa (Poir.) Chase	10	Autochoric
Elionurus muticus (Spreng.) Kuntze	10	Anemochoric
Eringium juncifolium (Urb.) Mathias and Constance	9	Autocoric
Eriope complicata Mart. ex Benth.	10	Autochoric
Eriope crassipes Benth.	10	Autochoric
Erythroxylum deciduum A. St.-Hil.	10	Autochoric
Eugenia cristaensis O. Berg.	10	Zoochoric
Eugenia myrcianthes Nied.	10	Zoochoric
Evolvulus lagopodioides Meisn.	10	Anemochoric
Galactia grewiifolia DC.	10	Autocoric
Habenaria nasuta Rchb. F. and Warm.	3	Anemochoric
Hyptis lanuginosa Glaziou ex Epling.	10	Autochoric
Hyptis nudicaulis Benth.	6	Autocoric
Ipomoea campestris Meisn.	10	Autochoric
Ipomoea procurrens Meisn.	10	Autochoric
Leptocoryphium lanatum (Kunth) Nees	10	Anemochoric
Mimosa nuda Benth.	6	Autochoric
Mimosa setosa Benth.	10	Autochoric
Myrcia linearifolia Cambess.	5	Zoochoric
Myrciaria herbacea O. Berg.	10	Zoocoric
Ouratea floribunda (A. St.-Hil.) Engl.	4	Autochoric
Paepalanthus speciosus Gardner	10	Anemochoric

Table 1. Continued...

Species	N	Dispersion Syndromes
Palicourea coriacea (Cham.) K. Schum.	10	Autochoric
Paspalum stellatum Humb. and Bonpl. In Flüeggé	10	Anemochoric
Peixotoa goyana C.E. Anderson	9	Autochoric
Piriqueta sidifolia Urb.	7	Autochoric
Polygala sp.	3	Autochoric
Rhynchospora consanguinea Boeck.	10	Anemochoric
Riencourtia oblongifolia Gardner	10	Anemochoric
Ruellia dissitifolia (Nees) Hiern	10	Autochoric
Simaba suffruticosa Engl.	10	Zoochoric
Smilax goyazana A. DC.	10	Zoochoric
Vernonia bardanoides Less.	10	Anemochoric
Vernonia megapotamica Spreng.	4	Anemochoric
Viguiera robusta Gardner	10	Anemochoric
Xyris schizachne Mart.	4	Anemochoric

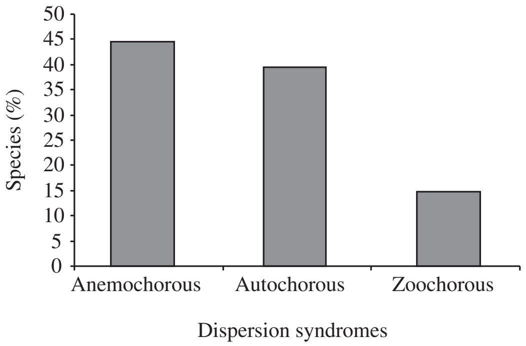

Figure 1. Species by dispersion syndromes in the herbaceous-subshrub layer in a Savannah (Campo Sujo) Community in Água Limpa Farm at the Cerrado Biosphere Reserve, Federal District, Brazil.

3.1. Correlation of phenology and rainfall

Spearman rank correlation was significant ($p < 0.05$) for the relationship between rainfall and the phenological events, flowering and fruiting, for anemochoric species (Table 2). The correlation was also significant for species fruiting for autochoric and zoochoric species (Table 2). The correlation between anemocoric species with mature fruits and precipitation was significant and inverse. The correlation between precipitation and buds production was significant and positive for anemochoric species and inverse for zoochoric species.

3.2. Flowering

The emission of floral buds and openning flowers in the Campo Sujo was distributed throughout the year. Anemochoric species presented a peak of flower production at the middle of the rainy season, 31% of the species produced floral buds in January 2000 (Figure 2a) and 28.4% produced opening flowers in February (Figure 2b). In February 2000, the first rainy season after the burning, the opening flowers reached 28.4% while in the same period in the following year, when no burning was registered, this event was three times lower suggesting that the flowering of Anemochoric species was favoured by fire (Figure 2b).

For autochoric species, flowering was better distributed during the year, with peaks both in the rainy and in the dry season, but with higher rates in the latter, reaching 25% of the flower bud production at the end of September (Figure 2a) and 25% of new flowers in December 1999 (Figure 2b).

Zoochoric species reproduction was more related to the end of the dry season, flower buds appeared at the end of the rainy season, during the dry season and at the beginning of the rains when the flowering peaks also happened (Figure 2a). However, a peak of flowering also happened during the rainy season (Figure 2b).

3.3. Fruiting

Fruiting occurred throughout the year with a concentration of new fruits in the rainy season. Zoochoric species presented most new fruits in that period, 33% from November 1999 to February 2000 (Figure 3a). Fruit production was reduced for anemochoric, zoochoric and autochoric species in the dry season (Figure 3a), but most mature fruits were found for anemochoric species at this time (37%) (Figure 3b). Several anemochoric species such as *Evolvulus lagopodioides, Paepalanthus speciosus, Riencourtia oblongifolia, Vernonia bardanoides, Vernonia megapotamica* and *Xyris schizachne* matured their fruits in this period with the dispersion happening at the beginning of the rains.

For autochoric species mature fruits peaked in January and March 2000, 52.1 and 50% respectively (Figure 3b). However, the rates of mature fruits remained high during the dry season, reaching 24.5% in July and 16% in September.

Table 2. Spearman rank correlation of precipitation and reproductive phenology phases (buds, new and mature flowers, new and mature fruits), for the total of species in a Savannah (Campo Sujo) Community in Água Limpa Farm at the Cerrado Biosphere Reserve, Federal District, Brazil.

Phenology phases	Anemochoric	Autochoric	Zoochoric
Buds	0.45 (p = 0.01)*	–0.12 (p = 0.50)	–0.40 (p = 0.02)*
New flowers	0.35 (p = 0.05)	0.31 (p = 0.08)	0.13 (p = 0.46)
Mature flowers	0.38 (p = 0.03)*	0.23 (p = 0.20)	–0.06 (p = 0.72)
New fruits	0.10 (p = 0.57)	0.49 (p = 0.007)*	0.69 (p = 0.0001)*
Mature fruits	–0.55 (p = 0.002)*	0.006 (p = 0.97)	–0.27 (p = 0.14)

* $p < 0.05$

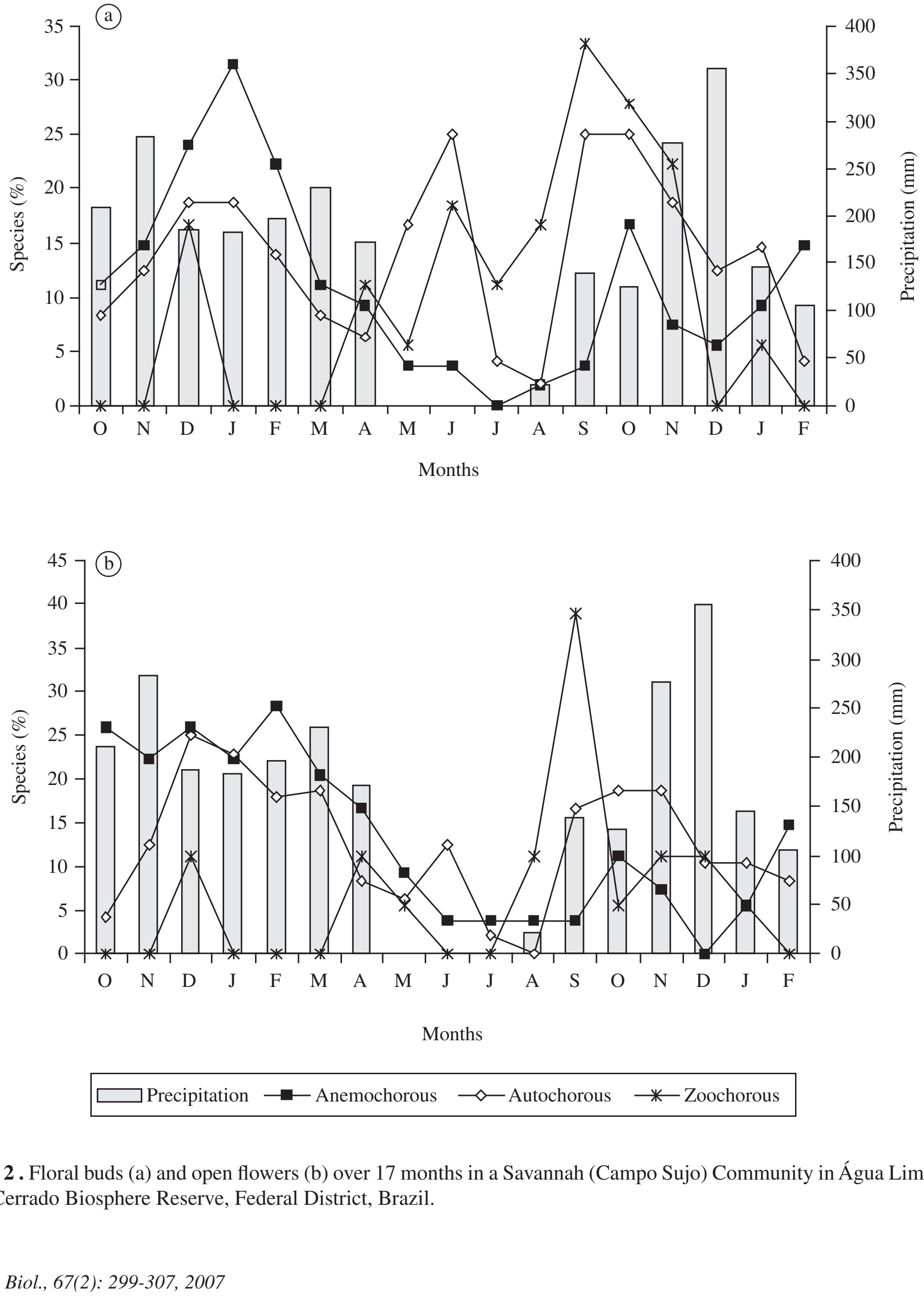

Figure 2 . Floral buds (a) and open flowers (b) over 17 months in a Savannah (Campo Sujo) Community in Água Limpa Farm at the Cerrado Biosphere Reserve, Federal District, Brazil.

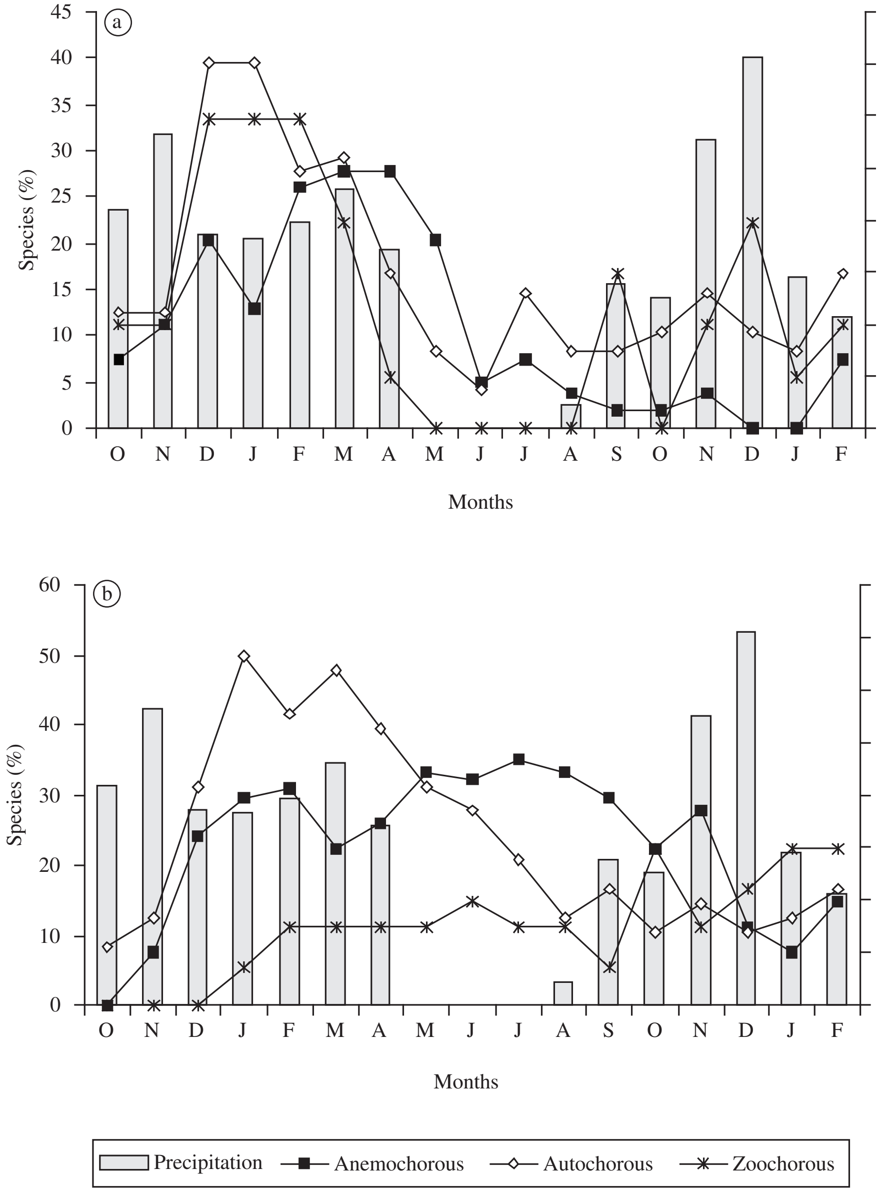

Figure 3. Production of new fruits (a) and mature fruits (b) during 17 months in a Savannah (Campo Sujo) Community in Água Limpa Farm at the Cerrado Biosphere Reserve, Federal District, Brazil.

After the fire, the percentage of autochoric species fruiting was the highest, reaching 40% of the production of new fruits in December 1999 while in 2001, when no burning was registered in the area, it reached only 12% in the same period (Figure 3a) suggesting that the fire stimulated the fruiting. The same happened to anemochoric species but the differences were wider with 20% of the species producing new fruits in December 1999 but none in 2000.

From June 2000 to January 2001 the number of species producing new fruits suffered a drastic reduction compared to the previous nine months when fire seems to have stimulated fruit production (Figure 3a).

4. Discussion

Anemochoric and autochoric species dominate the herbaceous subshrub layer of the Campo Sujo in Água Limpa Farm and determine the phenological pattern of the community. Wind dispersion has been generally associated to open vegetation types (Howe and Smallwood, 1982) such as Campo Sujo, whereas in a denser physiognomy of Cerrado (a Savannah woodland) a more even distribution between the three dispersion syndromes has been found (Batalha et al., 1997).

A more even distribution of the reproductive events in the herbaceous-subshrub community in this Campo Sujo compared to that found in the Cerrado *sensu stricto* (Savanna woodland) (Gouveia and Felfili, 1998) may be a reflection of the available humidity found in the soil where seasonality plays a more important role in the *Cerrado* s.s. formation since the watertable is deeper.

Several authors (Barbosa, 1997; Batalha et al., 1997; Mantovani and Martins, 1988; Batalha and Mantovani, 2000; Batalha and Martins, 2004) studying herbaceous-subshrub Campo Sujo and Cerrado communities, also found that the flowering was distributed throughout the year with a higher production of flowers during the rainy season.

The peak of flowering for woody species common between Campo Sujo and Cerrado occurs at the end of the dry/beginning of the rainy season. Gouveia and Felfili (1998) found that while most species flowered at the end of the dry season, most individuals flowered during the rainy season when the most abundant species in a Cerrado *sensu stricto* flowered.

Fire stimulated flowering especially for some species of Gramineae such as *Andropogon leucostachyus, A. selloanus, Arthropogon villosus, Axonopus marginatus, Leptocoryphium lanatum and Paspalum stellatum* and a *Cyperaceae Bulbostylis paradoxa.* Canales et al. (1994) observed that protection from fire reduces the fertility of *Andropogon brevifolius* in Venezuelan Savannahs reinforcing the idea that fire stimulates reproduction of some species. Other studies in Campo Sujo sites periodically burned also showed that fire stimulates the production of flowers and fruits (César, 1980; Silva et al., 1996). According to Coutinho (1982), burning promotes the dehiscense of fruits and seed dispersion of some herbs and subshrubs and could favour the germination of some species. Miranda and Klink (1996) found an increase in sexual reproduction of *Echinolaena inflexa* (Poaceae) after burning. Felfili et al. (1999) found a reduction in fruiting of *Stryphnodendron adstringens* up to two years after an occasional burning in a five-year phenological study, indicating that the trend may be the opposite for woody species.

A higher number of species was found producing new fruits during the rainy season. The number of individuals presenting mature fruits was higher in the dry season, when their diaspores can de dispersed more efficiently, in a similar pattern to that found by Batalha and Martins (2004) for a herbaceous layer and by Gouveia and Felfili (1998) and Felfili et al. (1999) for a woody community suggesting that both layers present a similar strategy of dispersing most of their seeds at the end of the dry season therefore taking advantage of receiving all the oncoming rains for their early stages of development.

Anemochoric species like *Casearia sylvestris, Ouratea floribunda* and *Piriqueta sidifolia* produced fruits during the dry season. Several autochoric species also matured their fruits during the dry season such as *Dalechampia caperonioides, Echinolaena inflexa, Hyptis nudicaulis, Mimosa lanuginosa, M. nuda* and *M. setosa.* This pattern agrees with that found by Batalha et al. (1997) studying the shrub-arboreal community. According to them, that community presents a different pattern of fruiting according to the dispersion syndrome of the species. From May to July, most anemochoric and autochoric species produce fruits while the zoochoric produces most fruits in October at the beginning of the rains. Souza (1993), studying seed-rain in shrub-arboreal communities near Brasília, and Batalha and Mantovani (2000) and Batalha and Martins (2004) studying the herbaceous layer of a Cerrado in São Paulo and Goiás, respectively, found a similar pattern. Arboreal species show different fruiting patterns for anemochoric and zoochoric plants, the first group produces fruits at the end of the dry season while the latter during the rainy season (Mantovani and Martins, 1988; Oliveira, 1998; Batalha and Martins, 2004).

The highest percentages of flowering and fruiting at the beginning of this study are probably more related to a regrowth post-fire, than to the beginning of the rains. Burning increases the nutrient cycling, has a pruning effect, promotes high regeneration capacity, and a boom in flowering for fire-dependent species and helps the dispersion of seeds (Coutinho, 1977, 1982; César, 1980; Rosa, 1990).

In addition to the adaptations presented by the life forms of the herbaceous subshrub layer, other mechanisms probably are needed to start the phenological events, such as seed dormency as found for woody species by Wetzel (1997). The distribution of reproductive events was fairly even over the year with higher correlation between the fruiting phases and rainfall. Besides rainfall, fire also stimulated reproductive events.

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