REPRODUCTIVE PHENOLOGICAL PATTERNS OF CERRADO PLANT SPECIES AT THE PÉ-DE-GIGANTE RESERVE (SANTA RITA DO PASSA QUATRO, SP, BRAZIL): A COMPARISON BETWEEN THE HERBACEOUS AND WOODY FLORAS

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ABSTRACT

A natural vegetation area, with 1269 ha, composed mainly by cerrado, located at Santa Rita do Passa Quatro Municipality, São Paulo State, southeastern Brazil (21°36-39'S, 47°36-38'W), was studied. From September 1995 to February 1997, a floristic survey was carried out, when all vascular plant species at reproductive stage were collected. The flowering and fruiting patterns of the community were studied, comparing the herbaceous and the woody species. In the herbaceous component, 239 species were found and, in the woody one, 108 species. The woody species flowered mainly at the beginning of the rainy season, while the herbaceous ones produced flowers generally at the end of that season. The proportion of anemo and autochorous species was greater in the herbaceous component. The zoochorous ones, on the contrary, were more frequent in the woody component. At the dry season, when their dispersion is more efficient, the proportion of anemo and autochorous species producing fruits was higher. During the rainy season, when their fruits become attractive for longer time, the zoochorous species fruited more intensely.

Key words: cerrado, savanna, phenology, Pé-de-Gigante, São Paulo, Brazil.

RESUMO

Padrões fenológicos reprodutivos das espécies de um cerrado disjunto: comparação entre as floras herbáceo-subarbustiva e arbustivo-arbórea

Foi estudada uma área de vegetação natural, de 1269 ha, composta principalmente por cerrado, situada no munícipio de Santa Rita do Passa Quatro, estado de São Paulo (21°36-39'S, 47°36-38'W). Entre setembro de 1995 e fevereiro de 1997, realizou-se um levantamento florístico, em que foram amostradas as espécies vasculares de plantas em fase fértil. A partir dos dados desse levantamento, estudaram-se os padrões de floração e frutificação da comunidade, comparando as espécies herbáceo-subarbustivas com as arbustivo-arbóreas. No componente herbáceo-subarbustivo, foram encontradas 239 espécies e, no componente arbustivo-arbóreo, 108 espécies. As espécies arbustivo-arbóreas floresceram principalmente no início da estação chuvosa, enquanto as herbáceo-subarbustivas produziram flores, de modo geral, apenas no final da estação úmida. A proporção de espécies anemo e autocóricas foi maior no componente herbáceo-subarbustivo, ao contrário das zoocóricas, mais freqüentes no componente arbustivo-arbóreo. Na estação seca, quando sua dispersão é mais eficiente, a proporção de espécies anemo e autocóricas em frutificação foi maior. Já durante a estação chuvosa, as espécies zoocóricas frutificaram com maior intensidade, uma vez que seus frutos carnosos podem se manter atraentes por mais tempo.

Palavras-chave: cerrado, savana, fenologia, Pé-de-Gigante, São Paulo, Brasil.

INTRODUCTION

Savannas are tropical and subtropical formations where the grass layer is continuous, interrupted by shrubs and trees in varying proportions, and where the main growth patterns are closely associated with alternating wet and dry seasons (Bourlière & Hadley, 1983). In tropical savannas, the temporal patterns in growth and reproduction are linked to the climatic seasonality (Williams *et al*., 1997).

The so-called "cerrado" occupies approximately 2 millions km^2 of the Brazilian territory (Ratter *et al*., 1992). It refers to several structural types, from grasslands to tall woodlands, most of which fit the definition of tropical savannas (Sarmiento, 1983).

Coutinho (1978), in his "woodland-ecotone-grassland" concept of cerrado, stated that there are in this vegetation type two floras, the herbaceous and the woody ones, which are perfectly distinct and antagonic.

The cerrado species, like those of other savannas, present periodic variations concerning flower and fruit production that may represent adaptations to biotic and abiotic factors (Schaik *et al*., 1993), determined by intrinsic genetic characters (Salisbury & Ross, 1992).

The relation between the phenological patterns of the cerrado plant species and seasonality has already been discussed by Warming (1892). Since this pioneer study, several papers discuss some aspects of the cerrado species phenology (Barradas, 1972; Coutinho, 1977, 1982; Aoki & Santos, 1980; Barros & Caldas, 1980; Ribeiro *et al*., 1982; Gottsberger & Silberbauer-Gottsberger, 1983; Oliveira & Sazima, 1990; Oliveira & Moreira, 1992; Miranda, 1995), but few of them do it at the community level (Mantovani & Martins, 1988; Batalha *et al*., 1997).

Scholes & Archer (1997) hypothesized that the climate seasonal pattern of tropical savannas, with alternating warm dry seasons with hot wet seasons, provides a potential axis of niche separation by phenology for the herbaceous and the woody components.

The aim of this study was to observe the reproductive phenological patterns of the plant species in a disjunct cerrado area at the community level, comparing the herbaceous and the woody floras.

MATERIAL AND METHODS

This study was carried out at the Pé-de-Gigante Reserve, at Santa Rita do Passa Quatro Municipality, São Paulo State, between 21°36-39'S and 47°36-38'W, under Köppen's Cwag' climate, at 660 to 730 m high, on Red-Yellow Latosol (Pivello *et al*., 1998). Its name ("Pé-de-Gigante" or "Giant's foot") was given after a foot-shaped geomorphological formation decurrent in the Paulicéia Stream drainage. The study area has 1,269 ha, 1,060 of which constitute the Reserve. According to Brazilian legislation, it's classified as an ARIE ("Área de Relevante Interesse Ecológico" or "Area of Relevant Ecological Interest"). The main vegetation type in the Reserve is the cerrado, covering 98% of the total area. A more detailed characterization of the study area can be found in Pivello *et al*. (1998).

The flowering and fruiting patterns of the cerrado species were analysed from data obtained in the floristic survey carried out from September 1995 to February 1997 (Batalha & Mantovani, submitted). The botanical material at reproductive stage was collected with the walking-and-gathering method. The collected exsicata were deposited at São Paulo State Botanical Institute herbarium (SP), with doubles at São Paulo State Forestry Institute (SPSF) and Biosciences Institute of São Paulo University (SPF) herbaria.

The species at reproductive stage were observed whether they were flowering or fruiting. The observations were simply qualitative: for example, on a certain month, if at least one individual of a determined species was found producing flowers, the species was considered to be in its flowering period.

These informations were compared with climatic data collected from 1986 to 1995, at the Santa Rita do Passa Quatro meteorological station (21°43'09''S and 47°28'22''W), from which a climatic diagram following Walter (1986) was constructed.

Pteridophytes were classified following Tryon & Tryon (1982), while angiosperms were included in families according to Cronquist (1988). The species were classified in life forms in accordance with Raunkiaer's system adapted by Mueller-Dombois & Ellenberg (1974). The dispersion syndromes were classified according to Pijl (1972).

The chamaephytes, epiphytes, geophytes, hemicryptophytes, lianas, vascular parasites, vascular hemi-parasites and therophytes species were considered as belonging to the herbaceous component, while the phanerophytes species as belonging to the woody one.

The flowering and fruiting periods were related to climatic variations and diaspore dispersion syndrome, comparing the herbaceous and the woody floras.

RESULTS

The climatic diagram (Fig. 1) shows that the dry period of the year lies between June and August, and the wet one between September and May. Mean annual rainfall and mean monthly temperature are, respectively, 1499 mm and 21.5°C.

During the floristic survey, 239 herbaceous species (Table 1), belonging to 57 families, and 108 woody species (Table 2), representing 44 families, were found at reproductive stage.

The proportion of flowering herbaceous species was lower on August, increased till February, and decreased till August (Fig. 2). The proportion of flowering woody species peaked on September, and remained high until December. The lowest proportions of flowering species in this component were found from March to August. In the herbaceous component, the flower production was more intense at the end of the rainy season, while in the woody component it was concentrated at the beginning of this season.

The fruit production presented a similar pattern than the flower production, but slightly delayed (Fig. 3). The proportion of fruiting herbaceous species was lower on August, when it started to rise, reaching its peak on April, and then falling till August again. In the woody component, the lowest proportion of fruiting species was found also on August, when it quickly increased, peaking on November. From December to February, the proportions remained high, when it decreased quickly till August.

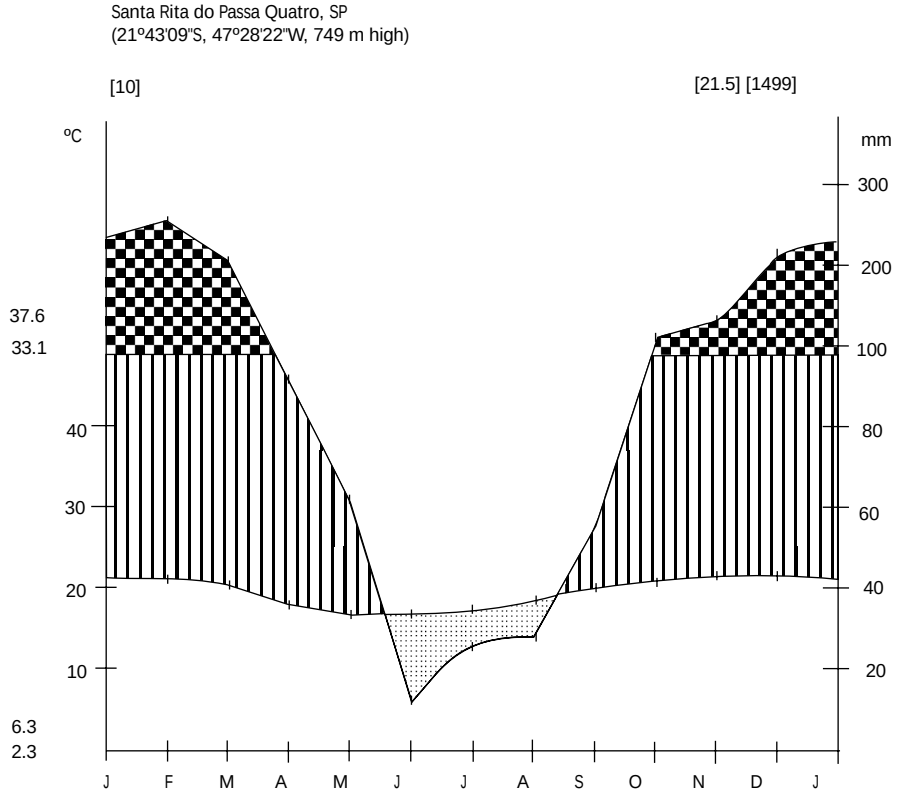

Fig. 1 — Climatic diagram following Walter (1986), constructed from data obtained at DAEE C4-107 meteorological station, located at Santa Rita do Passa Quatro (21°43'09''S, 47°28'22''W, 749 m high), from 1986 to 1995.

TABLE 1

List of collected herbaceous species at the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, SP (21°36-39'S, 47°36-38'W). Disp. = dispersal syndrome, ANE = anemochorous, AUT = autochorous, ZOO = zoochorous; fl. per. = spores production or flowering period, 1 = january, 2 = february, ..., 11 = november and 12 = december; fruiting per. = fr. period, 1 = january, 2 = february, ..., 11 = november and 12 = december. The hyphen (–) represents continuity between months while the comma (,) means interruption.

Family	Species	disp.	fl. per.	fr. per.
Acanthaceae	*Hygrophila brasiliensis* (Spr.) Lindau	AUT	3	6
	Ruellia geminiflora H.B.K.	AUT	—	4
Amaranthaceae	*Alternanthera brasiliana* (L.) Kuntze	AUT	12-4	2-5
	Froelichia lanata (H.B.K.) Moq.	AUT	11-4	12-6
	Gomphrena virgata Mart.	AUT	10-5	3-11
	Pfaffia jubata Mart.	AUT	10	10
Anacardiaceae	*Anacardium humile* A. St-Hil.	ZOO	9	9-10
Annonaceae	*Annona coriacea* Mart.	ZOO	9-12	9-12
	A. dioica A. St-Hil.	ZOO	11-12	1
Apiaceae	*Eryngium junceum* Cham. & Schltdl.	AUT	12-1	4
Apocynaceae	*Forsteronia glabrescen* Müll. Arg.	ANE	10-3	12-9
	Mandevilla vellutina (Mart.) Woods.	ANE	12-1	1
	Odontadenia lutea (Vell.) Markgr.	ANE	1-9	5-10
	Rhodocalyx rotundifolius Müll. Arg.	ANE	12	—
	Temnadenia violacea (Vell.) Miers	ANE	10-4	10-5
Arecaceae	*Attalea geraensis* Barb. Rodr.	ZOO	4, 10-11	—
	Syagru flexuosa (Mart.) Becc.	ZOO	9	9-11
	S. petraea (Mart.) Becc.	ZOO	3-7	12
Aristolochiaceae	*Aristolochia giberti* Hook.	ANE	2	—
Asclepiadaceae	*Astephanus carassensi* Malme	ANE	4-5	—
	Blepharodon nitidum (Vell.) J. Macbr.	ANE	10-2	—
	Ditassa acerosa Mart.	ANE	3-6	—
	D. nitida Fourn.	ANE	4-6	8
	Oxypetalum appendiculatum Mart. & Zucc.	ANE	—	9
Asteraceae	*Acanthospermum australe* (Loefl.) Kuntze	ZOO	—	12
	Achyrocline satureoides (Lam.) A. DC.	AUT	3-6	4-10
	Aspilia reflexa Baker	AUT	11-1	11-1
	Baccharis dracunculifolia A. DC.	ANE	12-4	1-7
	B. humilis Sch. Bip.	ANE	11-4	11-6
	B. rufescens Spreng.	ANE	—	9
	Bidens gardneri Baker	ZOO	12-7	12-8
	Chaptalia integerrima (Vell.) Burk	ANE	3-4	3-4
	Conyza canadensis (L.) Cronquist	ANE	12-3	12-3
	Dasyphyllum sprengelianu (Gardner) Cabrera	ANE	6-11	6-11
	Elephantopus biflora Less.	ANE	2-5	5-6
	E. mollis L.	ANE	2-3	6-9
	Emilia coccinea (Simns) Sweet	ANE	11-3	11-3
	Eremanthus sphaerocephalu Baker	ANE	7	7-10

TABLE 1 (*Continued*)

Family	Species	disp.	fl. per.	fr. per.
Asteraceae	*Eupatorium chlorolepsis* Baker	ANE	4	—
	E. maximiliani Schrad.	ANE	4-7	1-12
	E. squalidum A. DC.	ANE	3-6	4-10
	Gochnatia barrosii Cabrera	ANE	8-10	9-10
	G. pulchra Cabrera	ANE	2-8	6-11
	Kanimia oblongifolia Baker	ANE	9-2	9-2
	Mikania cordifolia (L.) Willd.	ANE	12-6	2-10
	Orthopappus angustifolius (Sw.) Gleason	ANE	12-3	2-11
	Porophyllum angustissimum Gardner	ANE	4-6	6-9
	P. ruderale (Jacq.) Cass.	ANE	3	3
	Pterocaulon rugosum (Vahl) Malme	ANE	3-4	3-4
	Trichogonia salviifolia Gardner	ANE	12-8	12-8
	Vernonia apiculata Mart.	ANE	2-4	4-10
	V. bardanoides Less.	ANE	2-6	2-10
	V. cephalotes A. DC.	ANE	8	—
	V. ferruginea Less.	ANE	7	—
	V. herbacea (Vell.) Rusby	ANE	1-3	2-4
	V. holosericea Mart.	ANE	6-9	9
	V. lappoides Baker	ANE	3-4	3-4
	V. obtusata Less.	ANE	6	6-7
	V. onopordioides Baker	ANE	3-5	3-6
	V. polyanthes (Spr.) Less.	ANE	10-11	10-7
	V. rubriramea Mart.	ANE	1-6	6-10
	V. scabra Pers.	ANE	9	7-9
	Viguiera discolo Baker	AUT	1-5	2-5
	Wulffia stenoglossa A. DC.	AUT	1-5	2-5
Bignoniaceae	*Anemopaegma arvense* (Vell.) Stellfeld	ANE	—	10
	A. chamberlaynii (Simns) Bur. & K. Schum.	ANE	—	8
	Arrabidaea brachypoda (A. DC.) Bur.	ANE	10-4	4
	A. craterophora (A. DC.) Bur.	ANE	1-5	4-11
	A. florida A. DC.	ANE	12-3	7-9
	Cremastus pulcher (Cham.) Bur.	ANE	5-6	—
	Distictella mansoana (A. DC.) Urban	ANE	11-4	1-12
	Jacaranda caroba (Vell.) A. DC.	ANE	3-10	7-1
	J. decurrens Cham.	ANE	10-11	—
	J. rufa Silva Manso	ANE	12	—
	Memora peregrina (Miers.) Sandwith	ANE	9-3	9-3
	Pyrostegia venusta (Ker) Bur.	ANE	5-11	7-12
Bixaceae	*Cochlospermum regium* (Mart.) Pilg.	ANE	9	9-11
Boraginaceae	*Cordia corymbosa* (L.) G. Don.	ANE	4	—
Bromeliaceae	*Aechmea bromeliifolia* (Rudge) Baker	ANE	10	11
	Ananas ananassoides (Baker) L.B. Sm.	ZOO	9-12	9-5

TABLE 1 (*Continued*)

Family	Species	disp.	fl. per.	fr. per.
Bromeliaceae	*Bromelia balansae* Mez	ZOO	9-12	9-7
	Dickia tuberosa (Vell.) Beer	ANE	10	11
	Tillandsia geminiflora Brogn.	ANE	11	4-5, 9
Cactaceae	*Epyphyllum phyllanthus* (L.) Haw.	ZOO	—	11
Caesalpiniaceae	*Chamaecrista campestris* Irwin & Barneby	AUT	1-4	1-4
	C. cathartica (Mart.) Irwin & Barneby	AUT	12-6	6
	C. debilis (Vogel) Irwin & Barneby	AUT	11-7	1-12
	C. desvauxii (Collad.) Killip	AUT	1-7	2-7
	C. flexuosa (L.) Greene	AUT	9-4	2-9
	C. rotundifolia (Pers.) Greene	AUT	5	5-6
Caryophyllaceae	*Polycarpaea corymbosa* (L.) Lam.	AUT	12-4	3-6
Chrysobalanaceae	*Parinari excelsa* Sabine	ZOO	9-12	9-12
Commelinaceae	*Commelina erect* L.	AUT	9-6	9-6
Convolvulaceae	*Ipomoea procurrens* C.F.W. Meissn.	AUT	2-6	—
	Jacquemontia tamnifolia (L.) Griseb.	AUT	8-3	8-3
Cucurbitaceae	*Cayaponia espelina* (Cogn.) Silva Manso	ZOO	11	12-2
Cyperaceae	*Bulbostylis hirtella* (Schrad.) Urban	AUT	9-5	2-7
	B. sphaerocephala (Boeck.) C.B. Clarke	AUT	12-2	2-6
	Cyperus cayennensis (Lam.) Britton	AUT	11-4	1-5
	C. diffusus Vahl	AUT	11-5	3-10
	Rhynchospora exaltata Kunth	AUT	5-1	10-7
	Scleria comosa (Nees) Steud.	AUT	11-7	12-8
Dilleniaceae	*Davilla rugosa* A. St-Hil.	AUT	4	4, 11
Euphorbiaceae	*Croton eriocladus* Müll. Arg.	AUT	12-5	12-7
	C. pohlianus Müll. Arg.	AUT	11	4
	C. sclerocalyx Müll. Arg.	AUT	12-2	1-6
	Manihot caerulescens Pohl	AUT	11	12-4
	M. tripartita Müll. Arg.	AUT	2	11
	Phyllanthus orbiculatus Müll. Arg.	AUT	11-6	11-6
	Sapium glandulatum (Vell.) Pax	ZOO	—	1-2
	Sebastiania serrulata Müll. Arg.	AUT	10-3	1-5
Fabaceae	*Aeschynomene marginata* Benth.	ANE	10-6	1-12
	Andira laurifolia Benth.	ZOO	9-10	12
	Centrosema venosum Mart.	AUT	3	—
	Clitoria falcata Lam.	AUT	2-3	2-4
	C. laurifolia Poir.	AUT	11	12-3
	Crotalaria vitellina Ker Gawl.	AUT	1-3	2-4
	Deguelia nitidul (Benth.) Az.-Tozzi	AUT	5-7	6-8
	Galactia decumbens (Benth.) Hassl.	AUT	11	—
	G. grewiifolia (Benth.) Taub.	AUT	10-4	10-4
	Indigofera suffruticosa Mill.	AUT	—	5-7
	Macroptilium gracile (Benth.) Urban	AUT	3-6	6

TABLE 1 (*Continued*)

Family	Species	disp.	fl. per.	fr. per.
Fabaceae	*Periandra mediterrane* (Vell.) Taub.	AUT	3-6	5-6
	Rhynchosia melanocarpa Grear	ZOO	1-3	1-3
	Stylosanthes gracili H.B.K.	AUT	10-7	11-8
	S. guianensis Sw.	AUT	5	5
	Zornia latifolia Sm.	AUT	11-4	11-4
Iridaceae	*Trimezia juncifolia* (Kl.) Kunth	AUT	2-4, 10	—
Lamiaceae	*Hyptis brevipes* Poit.	AUT	—	5
	H. cana Pohl ex Benth.	AUT	9	9
	H. eriophylla Pohl	AUT	5-8	6-9
	H. mutabili (A. Rich.) Briq.	AUT	—	5
	H. reticulata Mart.	AUT	1-12	1-12
	H. rugosa Benth.	AUT	2-9	3-10
	Peltodon tomentosus Pohl	AUT	12-6	2-9
Lauraceae	*Cassytha americana* Nees	ZOO	—	8
Liliaceae	*Alstroemeria pulchella* L. f.	AUT	1-4	3-4
Loganiaceae	*Strychnos bicolor* Progel	ZOO	11-2	11-5
Loranthaceae	*Psittacanthus robustus* Mart.	ZOO	12-2	10
Lythraceae	*Cuphea carthaginensi* (Jacq.) Macbr.	AUT	11-3	1-3
Malpighiaceae	*Banisteriopsis argyrophylla* (A. Juss.) B. Gates	ANE	4-5	—
	B. campestris (A. Juss.) Little	ANE	1-6	2-10
	B. laevifolia (A. Juss.) B. Gates	ANE	12-5	5-9
	B. pubipetala (A. Juss.) Cuatrec.	ANE	7-1	9-1
	B. stellaris (Griseb.) B. Gates	ANE	12-7	2-7
	B. variabili B. Gates	ANE	9	9-11
	Heteropteris umbellat A. Juss.	ANE	10-2	11-2
	Mascagnia cordifolia (A. Juss.) Griseb.	ANE	—	10-11
	Peixotoa tomentosa A. Juss.	ANE	2-7	7
Malvaceae	*Pavonia communis* A. St-Hil.	AUT	2	2
	P. hexaphylla (S. Moore) Krapov.	AUT	1-5	2-5
	Peltaea edouardii (Hochr.) Krapov. & Cristóbal	AUT	1-3	3
	Sida glaziovii K. Schum.	AUT	9	9-10
	S. linifolia A. Juss.	AUT	2-5	3-5
	S. rhombifolia L.	AUT	1-3	3
	S. urens L.	AUT	3	3
Melastomataceae	*Miconia fallax* DC.	ZOO	2-10	9-2
Menispermaceae	*Cissampelos ovalifolia* Ruiz & Pav.	ZOO	10-2	2
Mimosaceae	*Mimosa debilis* Humb. & Bonpl.	ZOO	1-3	2-5
	M. gracili Benth.	AUT	1-2	—
	M. pigra L.	ZOO	12	—
	M. xanthocentra Mart.	AUT	9-2	1-7
Myrtaceae	*Psidium australe* Cambess.	ZOO	9-10	11-1
	P. cinereum Mart.	ZOO	10-11	10-4

TABLE 1 (*Continued*)

Family	Species	disp.	fl. per.	fr. per.
Orchidaceae	*Galeandra montana* Barb. Rodr.	ANE	11-4	4
	Ionopsis paniculata Lindl.	ANE	8	—
Oxalidaceae	*Oxalis physocallyx* Zucc.	AUT	11-5	12-5
Poaceae	*Andropogon leucostachy* H.B.K.	AUT	11	12-7
	Aristida jubata (Arechav.) Herter	ANE	3-5	5-9
	Axonopus barbigerus (Kunth) Hitchc.	ZOO	2	4-5, 9-10
	A. marginatus (Trin.) Chase	ZOO	2-3	4-5
	Brachiaria decumbens Stapf	ZOO	12-2	1-8
	Chloris barbata (L.) Sw.	ZOO	1-2	5
	Digitaria insularis (L.) Fedde	ANE	12-2	—
	Echinolaena inflexa (Poir.) Chase	ZOO	12-4	4-11
	Eragrostis airoide Ness	ZOO	12-2	2-4
	E. articulata (Schrank) Nees	ZOO	1-4	4
	E. maypurensis (H.B.K.) Steud.	ZOO	4	4
	Gymnopogon foliosus (Willd.) Nees	ANE	4-6	5-9
	Ichnanthus sericeus Hack.	ZOO	9-5	1-12
	Loudetiopsis chrysothrix (Nees) Conert	ZOO	2-3	4-11
	Melinis minutiflora P. Beauv.	ANE	6-7	6-11
	Panicum cayennensis Lam.	ZOO	—	3-6
	P. maximum Jacq.	ZOO	4-5	5-7
	P. olyroides H.B.K.	ZOO	11-3	3-11
	P. parvifolium Lam.	ZOO	12-3	3-10
	P. procurrens Nees	ZOO	3	—
	P. repens L.	ZOO	12-1	6
	Rhynchelitrum repens (Nees) C.E. Hubb.	ANE	5-2	5-2
	Schyzachirium condensatum (Kunth) Nees	ANE	3	3-10
	Setaria geniculata (L.) P. Beauv.	ZOO	—	5
	Sporolobus indicus (L.) R. Br.	ZOO	12-5	5
	Tristachya leiostachya Nees	ZOO	2-3	5-7
Polypodiaceae	*Polypodium latipe* Langsd. & Fisch.	ANE	1-12	—
Polygalaceae	*Securidaca tomentosa* A. St-Hil.	ANE	9-12	10-12
Portulacaceae	*Portulaca hirsutissima* Cambess.	AUT	11-2	12-2
	P. mucronata Link	AUT	11-12	—
	Tallinum paniculatu (Jacq.) Gaertn.	AUT	11-2	11-4
Pteridaceae	*Adiantum fructuosum* Spreng.	ANE	9-3	—
Rhamnaceae	*Crumenaria polygaloides* Reissek	ANE	—	9
Rubiaceae	*Alibertia sessili* (Vell.) K. Schum.	ZOO	6-9	10-12
	Borreria verticilata (L.) Mey.	AUT	1-4	2-4
	B. warmingii K. Schum.	AUT	12-1	1-2
	Coccocypselum lanceolatum (Ruiz & Pav.) Pers.	ZOO	1-2	3-4

TABLE 1 (*Continued*)

Family	Species	disp.	fl. per.	fr. per.
Rubiaceae	*Declieuxia fruticosa* (Willd.) Kuntze	ZOO	12-5	12-7
	Diodia schumanii Standl.	AUT	11-1	2-5
	D. teres Walt.	AUT	6	6-7
	Palicourea coriacea (Cham.) K. Schum.	ZOO	9-2	11-4
	Psychotria barbiflora A. DC.	ZOO	—	4-6, 12
	P. capitata Ruiz & Pav.	ZOO	9-11	9-5
	P. deflexa A. DC.	ZOO	12	—
	P. tricholoba Müll. Arg.	ZOO	11-12	4-5
	Sabicea brasiliensis Wernham	ZOO	6	6, 11
Sapindaceae	*Paullinia elegans* Cambess	ANE	7-10	—
	Serjania erecta Radlk.	ANE	11-2	11-2
	S. lethalis A. St-Hil.	ANE	9	9-10
	S. reticulata Cambess	ANE	2-9	5-10
	Talisia angustifolia Raddi	ZOO	9-11	1
	Toulicia tomentosa Radlk.	ANE	4-6	5-10
Sapotaceae	*Pouteria subcaerulea* Pierre ex Dubard	ZOO	9-1	12-2
	Pradosia brevipes (Pierre) Penn.	ZOO	10	—
Schizaeaceae	*Anemia ferruginea* H.B.K.	ANE	2-4	—
Scrophulariaceae	*Buchnera lavandulacea* Cham. & Schltdl.	ANE	4	4
Smilacaceae	*Smilax cissoides* Mart. ex Griseb	ZOO	9-12	11-2
Solanaceae	*Solanum lycocarpu* A. St-Hil.	ZOO	9-2	1-2
	S. palinacanthu Dunal	ZOO	8-1	8-3
Sterculiaceae	*Byttneria sagittifolia* A. St-Hil.	AUT	11-2	2-5
	Helicteres sacarolha A. St-Hil.	AUT	3	—
	Waltheria americana L.	AUT	1-10	1-10
	W. communis L.	AUT	12-4	2-4
Turneraceae	*Piriqueta rosea* (Cambess.) Urban	AUT	12-1	12-1
Verbenaceae	*Lantana camara* L.	ZOO	12-3	12-3
	L. fucata Lindl.	ZOO	11	11
	Lippia lasiocalycina Cham.	AUT	10-3	11-3
	L. lupulina Cham.	AUT	9-11	9-11
	L. salviifolia Cham.	AUT	1-4	5-9
	Stachytarpheta maximilliani Schauer	AUT	12-3	2-3
Vitaceae	*Cissus erosa* Rich.	ZOO	12-4	2-4, 9
	C. inundata (Baker) Planch.	ZOO	11-12	11-12

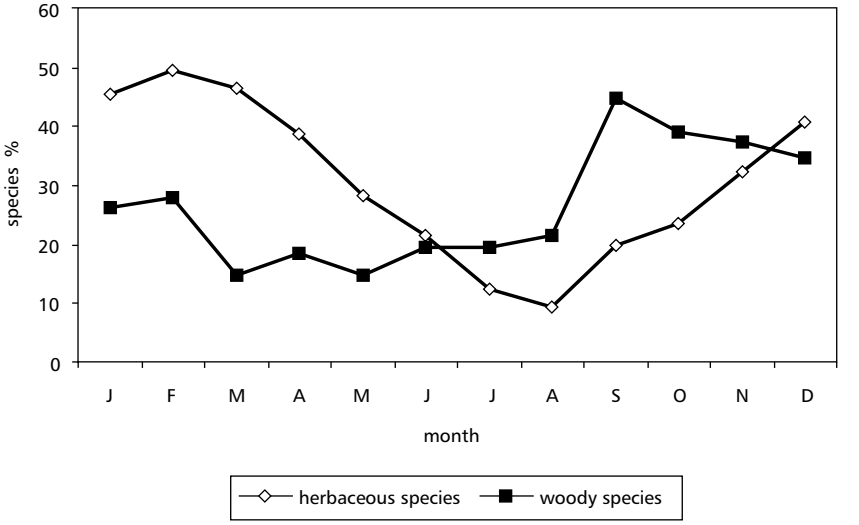

Fig. 2 — Percentage of cerrado species flowering through the year at the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, São Paulo (21°36-39'S, 47°36-38'W).

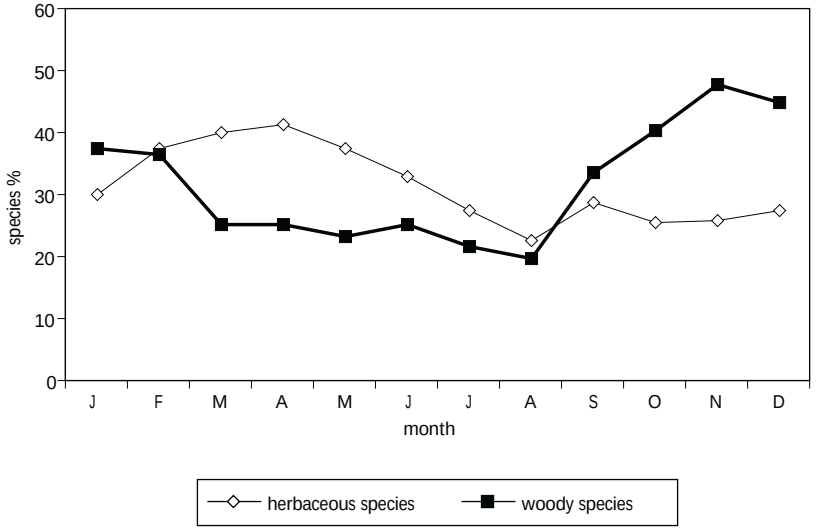

Fig. 3 — Percentage of cerrado species fruiting through the year at the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, São Paulo (21°36-39'S, 47°36-38'W).

TABLE 2

List of collected woody species at the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, SP (21°36-39'S, 47°36-38'W). Disp. = dispersal syndrome, ANE = anemochorous, AUT = autochorous, ZOO = zoochorous; fl. per. = spores production or flowering period, 1 = january, 2 = february, ..., 11 = november and 12 = december; fr. per. = fruiting period, 1 = january, 2 = february, ..., 11 = november and 12 = december. The hyphen (–) represents continuity between months while the comma (,) means interruption.

Family	Species	disp.	fl. per.	fr. per.
Anacardiaceae	*Tapirira guianensis* Aubl.	ZOO	9-10	—
Annonaceae	*Annona crassiflora* Mart.	ZOO	11-12	11-12
	Duguetia furfuracea (A. St-Hil.) Benth. & Hook.	ZOO	11-7	1-12
	Xylopia aromatica A. St-Hil.	ZOO	1-12	1-12
Apocynaceae	*Hancornia speciosa* Gomez	ZOO	9-11	9-11
	Himatanthus obovatus (Müll. Arg.) Woods.	ANE	12-6	—
Araliaceae	*Didymopanax vinosum* (Cham. & Schltdl.) Seem	ZOO	2-11	2-11
Arecaceae	*Butia paraguayensis* (Barb. Rodr.) Bailey	ZOO	4, 10-12	—
	Syagrus romanzoffiana (Cham.) Glass.	ZOO	9-2	2-11
Asteraceae	*Eremanthus erythropappa* Sch. Bip.	ANE	5-7	7-9
	Piptocarpha rotundifolia (Less.) Baker	ANE	12-4	1-12
Bignoniaceae	*Tabebuia aurea* (Silva Manso) S. Moore.	ANE	9-10	—
	T. ochracea (Cham.) Standl.	ANE	9	—
	Zeyhera montana Mart.	ANE	4	—
Bombacaceae	*Eriotheca gracilipes* (K. Schum.) A. Robyns	ANE	7-8	9-12
Burseraceae	*Protium heptaphyllum* (Aubl.) March	ZOO	6-8	8-2
Caesalpiniaceae	*Bauhinia rufa* Steud.	AUT	12-3	1-12
	Copaifera langsdorffii Desf.	ZOO	—	9-6
	Dyptichandra aurantiaca Tul.	ANE	11-12	1-11
	Hymenaea stigonocarpa Mart.	ZOO	1	7-10
	Senna rugosa (G. Don.) Irwin & Barneby	AUT	2-6	4-11
	S. sylvestris (Vell.) Irwin & Barneb	AUT	2-3	9
Caryocaraceae	*Caryocar brasiliense* Cambess.	ZOO	9-11	11-2
Celastraceae	*Plenckia populnea* Reissek	ANE	12	—
Chrysobalanaceae	*Couepia grandiflora* (Mart. & Zucc.) Benth.	ZOO	8-11	10-2
	Licania humilis Cham. & Schltdl.	ZOO	6-10	10-12
Clusiaceae	*Kielmeyera rubriflora* Cambess.	ANE	4-6	—
	K. variabilis Mart.	ANE	12-2	5-11
Connaraceae	*Rourea induta* Planch.	ZOO	8-12	11-4
Dilleniaceae	*Davilla elliptica* A. St-Hil.	AUT	4-6	6-1
Ebenaceae	*Diospyros hispida* A. DC.	ZOO	—	11-2
Erythroxylaceae	*Erythroxylum campestre* A. St-Hil.	ZOO	10	10-2
	E. cuneifolium (Mart.) O.E. Schulz	ZOO	—	10-11
	E. suberosum A. St-Hil.	ZOO	9-11	10-2
	E. tortuosum Mart.	ZOO	11	—
Fabaceae	*Acosmium subelegans* (Mohl) Yakovlev	ANE	11	—
	Andira anthelmia (Vell.) J. Macbr.	ZOO	9	2

TABLE 2 (*Continued*)

Family	Species	disp.	fl. per.	fr. per.
Fabaceae	*Bowdichia virgilioides* H.B.K.	ANE	8-10	—
	Dalbergia miscolobium Benth.	ANE	9-2	5-10
	Machaerium acutifolium Vogel	ANE	9-10	9-6
	Platypodium elegans Vogel	ANE	12	—
	Pterodon pubescens Benth.	ANE	9-10	1-12
Flacourtiaceae	*Casearia grandiflora* Cambess.	ZOO	6-2	9-2
	C. sylvestris Sw.	ZOO	7-10	9-10
Hippocrateaceae	*Peritassa campestris* (Cambess.) A.C. Sm.	ZOO	7-9	11
	Tontelea micrantha (Mart.) A.C. Sm.	ZOO	9-12	—
Lauraceae	*Ocotea corymbosa* (Meiss.) Mez	ZOO	11-12	3-4
	O. pulchella Mart.	ZOO	1-4	2-7
Loganiaceae	*Strychnos pseudoquina* A. St-Hil.	ZOO	10	—
Lythraceae	*Lafoensia pacari* A. St-Hil.	AUT	4	—
Malpighiaceae	*Byrsonima coccolobifolia* A. Juss.	ZOO	11-2	12-2
	B. crassa Nied.	ZOO	—	2
Malpighiaceae	*B. intermedia* A. Juss.	ZOO	9-5	10-6
	B. verbascifolia (L.) Rich ex A. Juss.	ZOO	6-10	11
	Heteropteris byrsonimifolia A. Juss.	ANE	7-2	9-4
Melastomataceae	*Leandra lacunosa* Cogn.	ANE	9-11	11-7
	Miconia albicans Triana	ZOO	4-11	6-1
	M. ligustroides Naudin	ZOO	11-6	1-7
	M. rubiginosa (Bonpl.) A. DC.	ZOO	7-2	9-6
	M. stenostachya A. DC.	ZOO	9-10	11
	Tibouchina stenocarpa (A. DC.) Cogn.	ANE	2-9	5-10
Mimosaceae	*Anadenanthera falcata* (Benth.) Speg.	AUT	9-1	1-12
	A. peregrina (L.) Speg.	AUT	2, 9	4, 12
	Dimorphandra mollis Benth.	AUT	12-1	1—9
	Enterolobium gummiferum (Mart.) Macbr.	AUT	10	—
	Plathymenia reticulata Benth.	ANE	—	12
	Stryphnodendron polyphyllum Benth.	AUT	12-1	6-12
Monimiaceae	*Siparuna guianensis* Aubl.	ZOO	7-11	—
Moraceae	*Brosimum gaudichaudii* Trècul	ZOO	9-10	9-11
	Ficus citrifolia Mill.	ZOO	12	12
Myristicaceae	*Virola sebifera* Aubl.	ZOO	1-4	5-11
Myrtaceae	*Campomanesia pubescens* (A. DC.) O. Berg	ZOO	9-11	10-2
	Eugenia aurata O. Berg	ZOO	11	3
	E. bimarginata A. DC.	ZOO	5-7	9-12
	E. hiemalis Cambess.	ZOO	5	—
	E. langsdorfii O. Berg	ZOO	11	11
	E. livida O. Berg	ZOO	8	12
	E. punicifolia (Kunth) A. DC.	ZOO	1	2-4

TABLE 2 (*Continued*)

Family	Species	disp.	fl. per.	fr. per.
Myrtaceae	*Myrcia bella* Cambess.	ZOO	9-12	9-2
	M. lasiantha A. DC.	ZOO	9-11	9-6
	M. lingua O. Berg	ZOO	9-12	12-4
	M. tomentosa (Aubl.) A. DC.	ZOO	9-11	11-12
	M. uberavensis O. Berg	ZOO	7-12	10-1
Nyctaginaceae	*Guapira noxia* (Netto) Lund	ZOO	10	10-11
	Neea theifera Oerst.	ZOO	—	11-1
Ochnaceae	*Ouratea castaneaefoli* (A. DC.) Engl.	ZOO	9	—
	O. spectabilis (Mart.) Engl.	ZOO	6-10	10-1
Polygalaceae	*Bredemeyera floribunda* Willd.	AUT	1-6	5-10
Proteaceae	*Roupala montana* Aubl.	AUT	9	—
Rosaceae	*Prunus sellowii* Sm.	ZOO	12	—
Rubiaceae	*Alibertia macrophylla* K. Schum.	ZOO	9	11-12
	Amaioua guianensis Aubl.	ZOO	—	2-5
	Palicourea rigida H.B.K.	ZOO	11-2	1-6
	Rudgea viburnoides (Cham.) Benth.	ZOO	—	6
	Tocoyena formosa (Cham. & Schltdl.) K. Schum.	ZOO	11-2	2-7
Sapindaceae	*Magonia pubescens* A. St-Hil.	ANE	—	1-3
Sapotaceae	*Pouteria ramiflora* (Mart.) Radlk.	ZOO	6-9	12-2
	P. torta (Mart.) Radlk.	ZOO	6-9	9-3
Solanaceae	*Solanum erianthum* D. Don	ZOO	10-6	12
Styracaceae	*Styrax ferrugineus* Nees & Mart.	ZOO	2-9	7-9
Tiliaceae	*Luehea divaricata* Mart.	AUT	9-10	11-12
Verbenaceae	*Aegiphila lhotzkiana* Cham.	ZOO	11-12	—
Vochysiaceae	*Qualea dichotoma* Warm.	ANE	—	10
	Q. grandiflora Mart.	ANE	9-2	5-12
	Q. multiflora Mart.	ANE	12-2	—
	Q. parviflora Mart.	ANE	11-2	9-4
	Vochysia cinamomme Pohl	ANE	2-4	2-12
	V. tucanorum Mart.	ANE	12-2	4

Of the total herbaceous species, 38.07% are anemochorous, 36.98% are autochorous and 25.95% are zoochorous (Fig. 4). In the woody component, 25.92% of the species are anemochorous, 12.04%, autochorous and the majority, 62.04%, are zoochorous. Of the total anemochorous species, 76.47% belong to the first component, as well as 86.87% of the autochorous species. On the other side, the zoochorous species were distributed more evenly among the components, with 48.06% of them in the herbaceous component and 51.94% in the woody one. In the herbaceous component, the anemochorous species fruited specially from June to October, the autochorous ones from February to June, and the zoochorous ones from November to May (Fig. 5). In the woody component, the anemochorous species fruited mainly from September to November, the autochorous ones from June to September, and the zoochorous ones from October to February (Fig. 6).

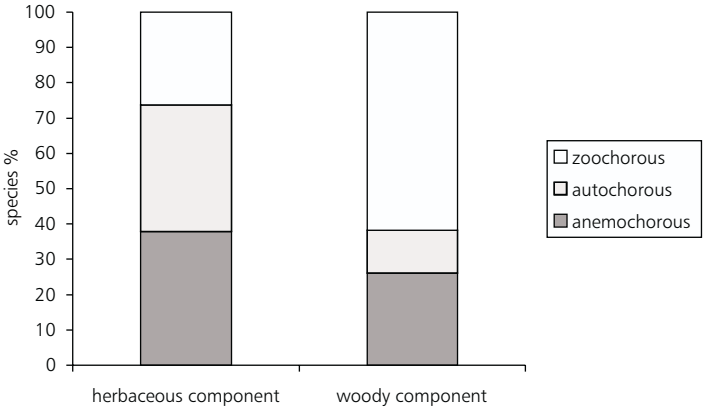

Fig. 4 — Percentual distribution of dispersion syndrome in the herbaceous and woody component of the cerrado species at the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, São Paulo (21°36-39'S, 47°36-38'W).

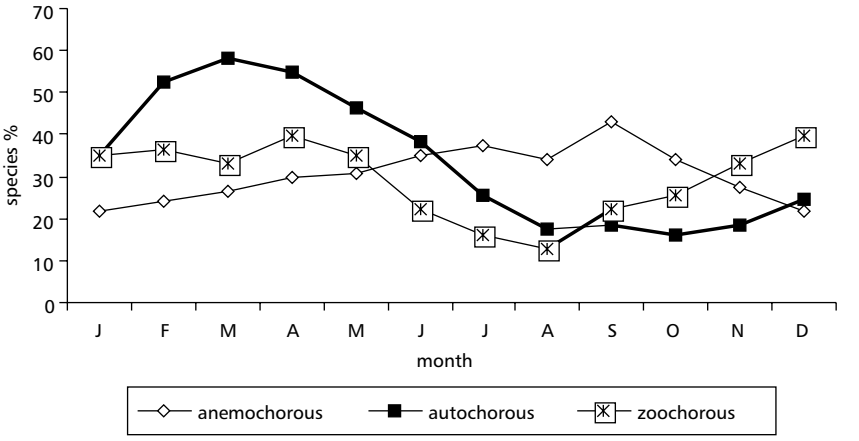

Fig. 5 — Percentual distribution of fruiting herbaceous species through the year at the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, São Paulo (21°36-39'S, 47°36-38'W), according to their dispersion syndrome.

During the dry season, in both components, the proportions of fruiting anemo and autochorous species were higher than those of zoochorous species.

DISCUSSION

The flowering and fruiting patterns of the herbaceous species, late in the rainy season, are found in other tropical savannas too (Sarmiento & Monasterio, 1983).

Tenório (1969) observed that the vegetative development of grasses allows carbohydrates accumulation that will be used in flowering and fruiting.

The carbohydrates accumulation of herbaceous species before flowering was also observed by Figueiredo & Dietrich (1981). Sarmiento & Monasterio (1983) hypothesized that this strategy would guarantee the reproduction in the safest period in respect of water availability: during the period of water shortage, the aerial biomass rapidly decays, and then as the rainy season progresses they gradually develop their shoots and reproductive structures, to reach the maximum growth rates during the reproductive phenophases that occur in the period with higher water availability.

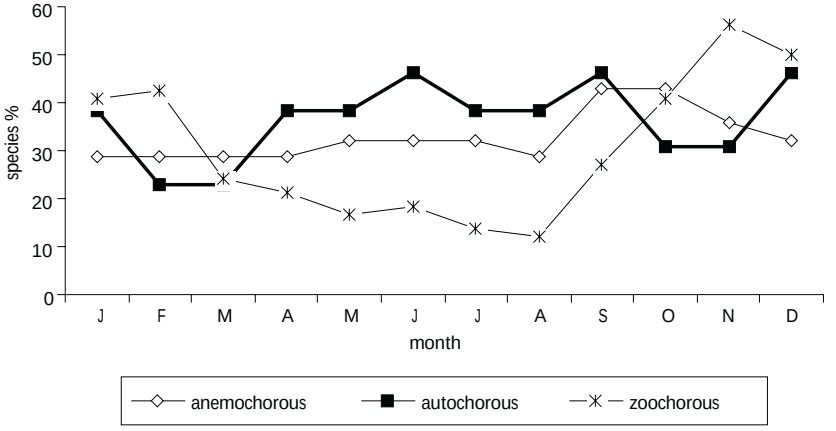

Fig. 6 — Percentual distribution of fruiting woody species through the year at the Pé-de-Gigante Reserve, Santa Rita do Passa Quatro, São Paulo (21°36-39'S, 47°36-38'W), according to their dispersion syndrome.

This strategy shows the importance of vegetative reproduction in mantaining the space occupied by the individual, since the underground storage reserves are utilized in flushing (Figueiredo & Dietrich, 1981; Sarmiento & Monasterio, 1983; Mantovani & Martins, 1988).

The reproductive pattern found in the herbaceous species were quite different of those observed in the woody ones. The flowering period of the woody species was concentrated at the beginning of the rainy season. These results are in agreement with Mantovani & Martins (1988) and Batalha *et al*. (1997). At lower latitudes, however, a distinct pattern was found: at Federal District (Aoki & Santos, 1980) and at Pará State (Miranda, 1995), most species flower at the dry period of the year, what could be explained by the lower variations in temperature and day length through the year at these regions. Sarmiento & Monasterio (1983) suggested that if trees and shrubs, through development of deep root systems, have water access during the whole year, what was observed by Rawitscher (1942) and Ferri (1944), there would be an advantage in reproducing during the period of water shortage, and leaving to the rainy season the function of storing reserves to support the dry season's activities. In accordance with Janzen (1980), the pollinating insects activity would be favoured at this time of the year, due to the lack of heavy rains that would damage the flowers and to the leaf fall that would make the flowers more visible.

Although several phenological patterns can be outlined within each component (Sarmiento & Monasterio, 1983), a major distinction between them seems to exist. Scholes & Archer (1997) stated that the coexistence of herbaceous and woody species in the savannas is a result of the interaction of several stresses and disturbances, acting differentially on each component and patchily in time and space. According to these authors, niches of herbaceous and woody species differ in both rooting depth and phenology, but there is more opportunity for phenological separation.

The diaspore syndrome proportions found at Santa Rita do Passa Quatro were close to those obtained by Batalha *et al*. (1997) at Pirassununga. Mantovani & Martins (1988) found at Moji Guaçu a higher proportion of autochorous species and a lower one of zoochorous species. These authors, however, considered many grass species, here treated as zoochorous, autochorous. Gottsberger & Silberbauer-Gottsberger (1983) found also a higher proportion of anemo and autochorous species in the herbaceous component and of zoochorous species in the woody one.

During the driest months, in both components, the proportion of fruiting anemochorous and autochorous species was higher than those of zoochorous ones, what was also found by Gottsberger & Silberbauer-Gottsberger (1983), Mantovani & Martins (1988), Miranda (1995) and Batalha *et al*. (1997). The anemochorous and autochorous fruits are generally dry and therefore

their pericarp dehydrate in the drought, releasing the seeds. Augspurger & Franson (1987) observed that, at seasonal climate areas, the anemochorous diaspore dispersion is more efficient at the dry season. The leaf fall observed mainly in the anemochorous species facilitates the diaspore dispersion as well (Matthes *et al*., 1988).

It could be noted for the zoochorous species that they fruited principally during the wettest and hottest period of the year, when their fleshy fruits can be kept attractive for a long time, showing the same pattern observed by Gottsberger & Silberbauer-Gottsberger (1983), Mantovani & Martins (1988), Miranda (1995) and Batalha *et al*. (1997).

Previous works with the woody component in other seasonal vegetation types (Frankie *et al*., 1974; Morellato *et al*., 1989) showed similar patterns, that is, flowering after first rainfalls, fructification of anemo and autochorous species at the dry season, and fructification of zoochorous species dispersed along the whole rainy season. Frankie *et al*. (1974), however, found more species flowering at the dry season than at the rainy one, as in other cerrado areas located at lower latitudes (Aoki & Santos, 1980; Miranda, 1995).

CONCLUSIONS

The results found at the Pé-de-Gigante Reserve show the distinct flowering and fruiting patterns of the herbaceous and woody species. The herbaceous species flowered mainly at the end of the rainy season, while the woody ones at the beginning of this season. The proportion of anemo and autochorous species was higher in the herbaceous component, but the zoochorous species were more frequent in the woody component. During the dry season, the proportion of anemo and autochorous species producing fruits were higher, since their dispersion is facilitated at this time of the year. During the wet season, on the other hand, the zoochorous fruited more intensely, since their fruits can be kept attractive for a longer time.

These results, however, are only qualitative and therefore cannot provide secure answers to the questions raised. To accept or reject the hypothesis of niche separation by phenology for the herbaceous and the woody components, quantitative and experimental work is needed. Anyway, the results here presented can be taken as guidelines for some phenological patterns of the cerrado plant species, principally at the community level, where few works have been carried out.

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