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A Hectare of Cerrado.
II. Flowering and Fruiting of Thick-Stemmed Woody Species

By

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With 7 Figures

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Summary

SILBERBAUER-GOTTSBERGER I. 2001. A hectare of cerrado. II. Flowering and fruiting of thick-stemmed woody species. – Phyton (Horn, Austria) 41 (1): 129–158, 7 figures. – English with German summary.

In a hectare of cerrado in the municipality of Botucatu, State of São Paulo, Brazil, individuals in flower and/or fruit were counted for 26 thick-stemmed woody species (stem-circumference of 10 cm or more at the height of 30 cm above ground) during 12 months, at intervals of 14 days, from April 1973 to March 1974. Although rainfall of the cerrado region is seasonal, the phenological events seem to be not well correlated with this seasonality, whether examined on the species level nor on the individual level. No doubt, the main flowering period was October and the first half of November, which is at the end of the dry season and the beginning of the rainy season, whereas during February, March, and April less flowering occurred. But across the year of the study, at least some individuals were on every census date in flower. The main fruiting period was during the rainy season, in the second half of December and first half of January. In total 53% of the individuals flowered, and of these, 72% produced ripe fruits. The majority of species have an annual flowering pattern. Duration of flowering, which was defined as the timespan between the flowering of the first individual of a species and the end of flowering of the last individual, was different for the species. Also the flower duration of the single individuals within one species was different. Extremely long-flowering seems to be characteristic of many thick-stemmed woody cerrado species. The long flower

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duration of a species may be achieved by long-flowering of the single individuals and also by low synchrony of flowering within the individuals of a species. Referring to the total of the species, duration of flowering of a species is not correlated with total number of its individuals, but the two species with the highest number of individuals also had the most of individuals with flowers and fruits. Within a species tall individuals flowered more frequently. The number of species and the number of individuals in flower (for each observation date) show also only moderate correlation. On a few observation dates the relationship was even reversed. During the dry season the few flowering species had the same number of individuals in flower as the many species at the beginning of the rainy season. Throughout the year, at all survey dates, one species dominated in terms of number of individuals flowering and the same was true for fruiting. In several species flowering stage and ripe fruiting stage overlapped, and the same was true for individual plants of *Styrax ferruginea*. The study also shows that phenological surveys of a complete census of a representative area give different insights into the phenological behavior of a community and its species than surveys based on selected individuals of selected species.

Zusammenfassung

SILBERBAUER-GOTTSBERGER I. 2001. Ein Hektar Cerrado. II. Blühen und Fruchten der dickstämmigen Holzarten. – Phyton (Horn, Austria) 41 (1): 129–158, 7 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Ein Jahr lang (vom April 1973 bis zum März 1974) wurden in einem Hektar Cerrado-Vegetation in der Nähe von Botucatu, im Staat von São Paulo, Brasilien, die Blüh- und Fruchtphänologie von 26 dickstämmigen Holzarten untersucht (Stammumfang ⩾ 10 cm, 30 cm oberhalb des Bodens). In 14-tägigen Abständen wurden alle Individuen gezählt, die Blüten, sowie unreife oder reife Früchte hatten. Obwohl sich in dem Gebiet des Cerrados eine wärmere Regen- mit einer kühleren Trockenzeit abwechselt, scheint die Phänologie der dickstämmigen Holzarten im Cerrado nicht streng mit diesen Jahreszeiten korreliert zu sein, weder wenn man die Arten, noch wenn man die Individuen berücksichtigt. Die Hauptblühzeit der Arten und Individuen war zwar gegen Ende der Trockenzeit oder zu Beginn der Regenzeit, im Oktober und der ersten Novemberhälfte, und im Februar, März und April blühten weniger Arten und Individuen, aber das ganze Jahr hindurch war an jedem der Aufnahmetage zumindestens einige Individuen in Blüte. Die Hauptfruchtzeit war die zweiten Hälfte Dezember und erste Hälfte Januar, das ist die Mitte der Regenzeit. Insgesamt blühten 53% der Individuen der 26 Arten und von diesen produzierten 72% reife Früchte. Die meisten Arten blühten einmal im Jahr. Die Blühdauer einer Art, die als Zeitraum zwischen dem Beginn des Blühens des ersten und Ende des Blühens des letzten Individuums definiert wurde, war für die einzelnen Arten sehr unterschiedlich. Unterschiedlich war auch die Dauer des Blühens der einzelnen Individuen der Arten. Extrem lange Blühzeiten scheinen für die dickstämmigen Holzarten des Cerrados charakteristisch zu sein. Die lange Blühdauer kommt sowohl durch ein stark asynchrones Hintereinanderblühen der Individuen zustande als auch durch ein langes Blühen einzelner Individuen. Wenn man alle Arten zusammen betrachtet, ist die Blühdauer einer Art zwar nicht mit der Gesamtzahl ihrer Individuen korreliert, aber die beiden individuenreichsten Arten blühten und fruchteten auch mit den meisten Individuen. Innerhalb einer Art blühten die hohen Individuen häufiger. Die Anzahl der Individuen in Blüte war nur schwach mit der Anzahl der Arten in Blüte korreliert. An einigen Aufnahmetagen war das Verhältnis sogar gegenläufig, nämlich in der Trockenzeit, in der wenige Arten mit fast ebenso vielen Individuen blühten, wie zahlreiche Arten zu Beginn der Regenzeit. An jedem Aufnahmetag während des Jahres dominierte eine der Arten das momentane Blüh- und Fruchtgeschehen. Diese Art hatte dann die grösste Anzahl an blühenden oder fruchtenden Individuen im Vergleich zu den anderen zu diesem Zeitpunkt blühenden oder fruchtenden Arten. Blühende Individuen und solche mit unreifen Fruchtstadien kamen bei vielen Arten nebeneinander vor und Blüten und unreife Früchte waren oft zusammen auf einem Individuum zu finden. Bei einigen Arten überlappten sich blühende Individuen mit solchen mit reifen Früchten und die Art, *Styrax ferruginea*, hatte sogar an einigen ihrer Individuen Blüten und reife Früchte gleichzeitig. Phänologische Studien, wie die vorliegende, bei denen die Gesamtindividuenzahl der Arten in einer repräsentativen Fläche berücksichtigt wurde, geben andere Ergebnisse in Bezug auf das Blüh- und Fruchtverhalten einer Vegetation und ihrer Arten als Untersuchungen an ausgewählten Individuen ausgewählter Arten.

Introduction

The cerrado, a species-rich xeromorphic, but not xerophytic, vegetation (EITEN 1972), adapted to periodic fires, originally covered about one fifth of Brazil, and has its core area on the Central Brazilian Plateau. The cerrado vegetation in all its physiognomic forms is a product of interaction of soils, climate, and topography (EITEN 1972, OLIVEIRA-FILHO & al. 1989). It is characterized by seasonal rainfall, with alternating wet and dry seasons and intermediate in amount between that of the formerly continuous humid Atlantic and Amazonian rainforests and that of the semi-arid caatinga of northeastern Brazil and the Chaco vegetation of Paraguay and Argentina. Cerrado vegetation occurs on infertile, water-permeable soils of any texture.

The first phenological data of Brazilian cerrado vegetation are from WARMING 1892, 1908, reporting flowering and fruiting time of species in respect to the seasons in the region of Lagoa Santa, State of Minas Gerais. Phenological observations, pollination and dispersal were compared for all angiosperm species of a cerrado in the Reserva Biológica de Mogi Guaçu, São Paulo State (MANTOVANI & MARTINS 1988). The phenology of trees of an Amazonian savanna (called cerrado) near Santarém in Pará State was studied at the individual level, but the results presented refer only to the number of species (MIRANDA 1995). One phenological study based on number of species and number of individuals for a Central Brazilian cerrado and gallery forest was done by GOUVEIA & FELFILI 1998 during one year.

Phenological data on cerrado plants are often presented in papers emphasizing dispersal or pollination. The fruiting time of all species of a hectare of cerrado are included in a study of seed dispersal (GOTTSBERGER &

SILBERBAUER-GOTTSBERGER 1983). A much larger number of studies treat the phenology of selected cerrado species (RIBEIRO & al. 1981), of a single species (BARRADAS 1972, BIANCO & PITELLI 1986, GRIBEL 1988, GRIBEL & HAY 1993, REZENDEL & al. 1990, FELFILI & al. 1999), or of a specific genus, tribe or family (ARISTA & al. 1997, BARBOSA 1983, BARROS & CALDAS 1980, CAMARGO & al. 1984, GOTTSBERGER & SILBERBAUER-GOTTSBERGER 1988a, 1988b, OLIVEIRA & al. 1991, 1992, OLIVEIRA & SILVA 1993, OLIVEIRA & GIBBS 1994, STEVENS 1994).

The idea to do a survey of individuals in flower and fruit of certain species within a hectare during one year, was given by the late Prof. A. B. JOLY, University of São Paulo.

Site and Vegetation Characteristics

The study was carried out in the municipality of Botucatu, State of São Paulo, Brazil, in a hectare of cerrado vegetation at the Fazenda Treze de Maio (22°45' S, 48°25' W), 18 km north of Botucatu and 14 km east of São Manuel, at an altitude of 550 m. The hectare was in the middle of an area of about 700 hectares of cerrado which were left of a larger disjunct cerrado area typical for the southern edge of the cerrado province. Unfortunately we are forced to communicate the total destruction of the natural vegetation in this area for *sugar cane plantation*.

The soil is of the most common type for cerrado, very deep, a red latosol, sandy, without stones, and somewhat clayey. Its pH 4.4 to 4.9 is a common range of values for cerrado. The soil is poor in exchangable ions and organic matter, and contains an appreciable amount of available aluminum (SILBERBAUER-GOTTSBERGER & EITEN 1987).

The physiognomy of the hectare was a "low tree and scrub woodland" with 3–8 m tall trees that formed a slightly uneven open canopy layer which admitted abundant light to treelets, shrubs, and groundlayer. For details of quantitative data on species composition, species importance, patterns of distribution within the hectare, and vegetation profiles, see SILBERBAUER-GOTTSBERGER & EITEN 1978, 1983, 1987.

Climate

The nearest weather station is at Fazenda Edgardia, 8 km south of the hectare at almost 700 m altitude. Weather data are shown for 1971–1974 (Fig. 1). The daily means of temperature through the year ranged from 16.5 °C to 26.3 °C, the lowest in July and the highest in February. The annual average is 19.8 °C. Precipitation is about 1200 mm per year, but up to 40% departures from this long term average may occur in either direction in a particular year (Fig. 1). At Edgardia, precipitation was 963 mm in 1971, but 1648 mm in 1972. The driest months were July or August with minimum monthly 0.0 mm in July 1974 and 8.4 mm in August 1971. There

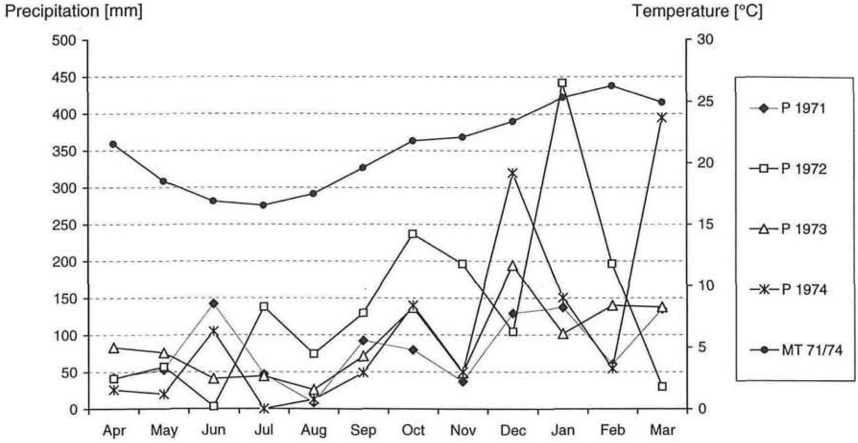

Fig.1. Monthly precipitation and mean temperature for the years 1971–1974, Fazenda Edgardia, Botucatu, SP. – P = precipitation, MT = mean temperature

is a single wet season; the rainiest months are December to January with maximum monthly 320 mm in December 1974 and 441 mm in January 1972. Air humidity varies from 57–75% in the dry season to 82–88% in the wet season. Full sunlight varies from 101 to 287 hours per month.

Methods

Phenological data were recorded from the first half of April 1973 to the last half of March 1974. Individuals of woody species were considered which had a stem-circumference of 10 cm and more, at a height of 30 cm above the ground (SILBERBAUER-GOTTSBERGER & EITEN 1983). Of the 54 species, which occurred in this growth form, 26 were chosen for the phenological observations. Considering the importance index of the species published in the cited paper, we chose the first 12 species (index<12>4), leaving out *Stryphnodendron barbatimam*, as it has been cut for tannery, in 1972, and *Sclerolobium aureum*, a species which was flowering there only with few tall trees. The next 8 species with an importance value of<4 but>1.1 were also choosen, and furthermore 6 species of the category with importance values<1>0.2. In intervals of more or less fourteen days, for the chosen species, all individuals in flower or in fruit were counted. Three reproductive stages were recorded: F, with flowers, when the first and the last flower were open; U, with unripe fruits, when the first fruit-swelling could be distinguished and when the last flower was in this stage. R, with ripe fruits, when the first and last ripe fruit was noticed. Often individual plants had both flowers and unripe fruits, or unripe fruits and ripe fruits together, or rarely, they presented all three stages at once. Such individuals were counted in each of the reproductive stages. The actual number of individuals in flower and ripe fruits also were counted for each of the 26 species. Duration of flowering or fruiting was determined as the time from the first individual which entered the phenophase till the last individual which left it. The number of species in flower is different from the number in fruit, because for six of the flowering species fruiting was not observed at the sample days.

Table 1. Flowering and fruiting of selected thick-stemmed woody species in a hectare of cerrado, Botucatu, SP (1973/74)

NI = number of individuals in the hectare
NF = number of individuals with flowers during the year
NR = number of individuals with ripe fruits during the year
SF (surveyed-flowering) = number of individuals with flowers, sum of the 24 survey dates
SF% = percentage of surveyed-flowering of each species of the total of all species
SU (surveyed-unripe-fruiting) = number of individuals with unripe fruits, sum of the 24 observation dates
SU% = percentage of surveyed-unripe-fruiting of each species of the total of all species
SR (surveyed-ripe-fruiting) = number of individuals with ripe fruits, sum of the 24 observation dates
SR% = percentage of surveyed-ripe-fruiting of each species of the total of all species
ASF = average SF (SF divided by 24)

SPECIES	NI	NF	NF/NI%	NR	NR/NI%	NR/NF%	SF	SF%	SU	SU%	SR	SR%	ASF
Erythroxylum suberosum	860	600	70	500	58	83	1052	23.9	1004	26.1	493	34.1	43.8
Styrax ferruginea	250	213	85	164	77	77	946	21.5	1206	31.3	233	16.1	39.4
Ouratea spectabilis	242	82	34	74	31	90	407	9.2	224	5.8	91	6.3	17.0
Myrcia lasiantha	187	170	91	160	86	94	314	7.1	139	3.6	232	16.1	13.1
Byrsonima coccolobifolia	221	125	57	78	35	62	285	6.5	174	4.5	23	1.6	11.9
Eugenia aurata	183	90	49	55	30	61	274	6.2	193	5	34	2.4	11.4
Qualea grandiflora	183	70	38	20	11	29	185	4.2	337	8.8	47	3.3	7.7
Eriotheca gracilipes	39	30	77	14	36	47	161	3.7	48	1.3	8	0.6	6.7
Piptocarpha rotundifolia	80	59	74	49	61	83	147	3.3	63	1.6	72	5.0	6.1
Roupala montana	75	71	95	30	40	42	126	2.9	111	3	26	1.8	5.3
Erythroxylum tortuosum	134	85	64	81	60	95	112	2.5	81	2.1	93	6.4	4.7
Caryocar brasiliense	48	47	98	45	94	96	88	2.0	88	2.3	29	2.0	3.7
Diospyros hispida	81	54	76	11	14	20	74	2.0	18	0.5	6	0.4	3.1
Byrsonima verbascifolia	37	24	57	nc	–	–	41	0.9	58	1.5	10	0.7	1.7
Licania humilis	44	17	39	11	25	65	37	0.8	20	0.5	16	1.1	1.5
Qualea multiflor	12	9	75	nc	–	–	25	0.6	nc	–	nc	–	1.0
Annona crassiflora	103	18	18	nc	–	–	23	0.5	18	0.5	nc	–	1.0
Bowdichia virgiliodes	26	8	8	8	31	100	19	0.4	12	0.3	6	0.4	0.8
Tabebuia caraiba	15	11	73	nc	–	–	15	0.3	nc	–	nc	–	0.6
Aspidosperma tomentosum	164	6	4	nc	–	–	14	0.3	nc	–	nc	–	0.6
Annona coriacea	22	5	23	nc	–	–	13	0.3	nc	–	nc	–	0.5
Couepia grandiflora	122	14	12	9	7	64	11	0.2	14	0.4	3	0.2	0.5
Machaerium acutifolium	29	14	48	10	34	71	11	0.2	15	0.4	10	0.7	0.5
Dimorphandra mollis	54	9	17	7	13	78	9	0.2	15	0.4	10	0.7	0.4
Xylopia aromatica	7	7	100	7	100	100	7	0.2	10	0.3	2	0.1	0.3
Tabebuia ochracea	255	3	1	nc			6	0.14	nc		nc		0.3
Total	3473	1841	53	1333	38	72	4402	100.0	3848	100.2	1444	100.0	

Results

1) Flowering

1a) Main flowering period, number of species and individuals

During the single year of observation, for the 26 species surveyed, 4402 individuals with flowers were registered (Tab. 1). This number is the sum over the year of the flowering individuals at each of the 24 survey dates ("survey-flowering" = SF). The survey-flowering for one species is also given in Table 1. This SF number evidently is not the actual number of individuals of a species in flower during the year, as in the SF one individual was counted repeatedly, if its flowering extended over various survey dates. For the actual number of individuals in flower (NF) of one species see also Table 1. Of the 3473 individuals (NI) by which the 26 spp. were represented in the hectare, 1841 individuals (53%) were in flower during the year (Tab. 1). The SF of each species, divided by the number of observation dates (24), gives a kind of "average of survey-flowering" (ASF; Table 1).

The main flowering period was October and the first half of November, which is at the end of the dry season and the beginning of the rainy season, whereas during February, March, and April less flowering occurred (Tab. 2, Fig. 2). But across the year of the study, at least some individuals were in flower on every census date. The minimum was 8

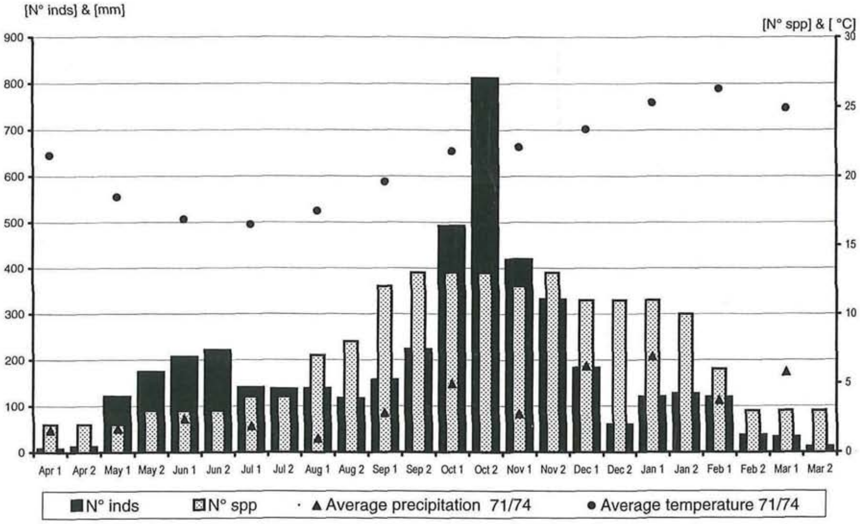

Fig. 2. Flowering of thick-stemmed woody species in a hectare of cerrado, Botucatu, SP (1973/74; 26 spp.). Flowering data are in intervals of 14 days. 1 = first survey date of that month and 2 = second survey date. In this graph the monthly values of precipitation and temperature are averages from the years 1971–1974 (for the separate monthly values of the 4 years see Fig. 1 also).

individuals (2 spp.) in the first half of April and the maximum was 812 individuals (13 spp.) in the second half of October. The number of species and the number of individuals in flower (for each observation date) show only moderate correlation [Spearman rank correlation R = 0.65 ($p<0.000$), n = 24]. The highest number of species in flower (13 spp.) coincided with the highest numbers of individuals in flower (492 in the first half of October, and 812 in the second half of October), as did the lowest number of species in February, March, and April (3 spp., 3 spp., 3 spp. 2 spp., 2 spp., 37 individuals, 33 individuals, 12 individuals, 8 individuals, and 13 individuals) But on few observation days the relationship was reversed. For instance, in the second half of June, which is in the first third of the dry season, 3 spp. flowered with nearly the same number of individuals (221 individuals) as 13 species in the second half of September (223 individuals), which is the beginning of the rainy season.

Table 2. Number of individuals in flower (SF) on each of the 24 observation days in a hectare of cerrado, Botucatu, SP (1973/74)

	Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec		Jan		Feb		Mar	
	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Styrax ferruginea	3	10	109	154	181	191	101	41	20	12	11	24	27	19	18	16	8	1						
Eriotheca gracilipes			12	19	24	26	26	23	15	12	4													
Ouratea spectabilis				1	2	4	6	17	36	43	59	73	68	64	25	9								
Roupala montana							7	56	63															
Bowdichia virgilioides									2	3	3	8	1	2										
Tabebuia caraiba									1	3	8	3												
Licania humilis									1	8	11	10	2	3	1	1								
Erythroxylum suberosum	5	3								32	43	60	315	477	103								5	9
Erythroxylum tortuosum										4	6	8	17	56	21									
Byrsonima coccolobifolia											4	17	28	30	37	44	74	15	9	6	6	5	8	2
Eugenia aurata											3	7	19	55	81	62	47							
Tabebuia ochracea											3	3												
Aspidosperma tomentosum											2	7	3	2										
Byrsonima verbascifolia												2	2	3	14	11	3	2	2	2				
Couepia grandiflora												1	1	2	3	4								
Myrcia lasiantha													6	51	91	158	8							
Diospyros hispida													3	48	21	2								
Caryocar brasiliensis															4	12	27	22	19	3	1			
Annona crassiflora																9	8	4	1	1				
Annona coriacea																3	5	2	2	1				
Machaerium acutifolium																1	1	7	2					
Dimorphandra mollis																	1	1	4	3				
Xylopia aromatica																	1	1	1	1	1	2		
Qualea grandiflora																		3	59	66	57			
Qualea multiflora																		2	8	8	7			
Piptocarpha rotundifolia																			13	36	47	30	20	1
Sum individuals in flower	8	13	121	174	207	221	140	137	138	117	157	223	492	812	419	332	183	60	120	127	119	37	33	12
Sum species in flower	2	2	2	3	3	3	4	4	7	8	12	13	13	13	12	13	11	11	11	10	6	3	3	3

1b) "Importance" of a species during flowering

The relationship between the species was calculated by the number of survey-flowering (SF) of a species to the total of the SFs of all species (SF%; Tab. 1). The percentages show that *Erythroxylum suberosum* and *Styrax ferruginea,* which were by far the most numerous in the hectare, also dominated flowering, with about 24% and 22% respectively. The following species were *Ouratea spectabilis* and *Myrcia lasiantha*, with 9% and 7% of the total SF, respectively. Five species accounted for 6.5% to 3.3% of the flowering individuals, four had less than 3% but more than 1%, and 13 species had 1% to 0.1%. The sequence of the species remains the same if the percentage of the actual number of individuals in flower versus the total of the actual number of individuals in flower (NF/Total NF) is calculated. *Erythroxylum suberosum* is the most important species with 32.6%, followed by *Styrax ferruginea* (11.6%), *Myrcia lasiantha* (9.2%), and *Byrsonima coccolobifolia* (6.8%). Evidently the survey-flowering numbers (SF) and the real numbers of flowering individuals (NF) are correlated (Spearmans rank R = 0.924; $p<0.000$). The actual number of indivduals in flower (NF) and the number of individuals by which a species was represented in the hectare (NI) are only weakly correlated (Spearmans rank R = 0.604; $p<0.001$]. Although the species with the highest number of flowering individuals were also those with the most individuals (NF/NI 85% and 70%), some species with many individuals had relatively few of them in flower (e.g., *Annona crassiflora, Dimorphandra mollis*, *Tabebuia ochracea*). On the other hand, the species with 100% of its individuals in flower, *Xylopia aromatica*, was represented by only 7 individuals, which flowered synchronously. Among the other species which had 98% of its individuals flowering (e.g., *Caryocar brasiliense)*, or 95% (*Roupala montana)*, 91% *(Myrcia lasiantha*), 70% (*Qualea grandiflora*), 73% (*Tabebuia caraiba*) are species with a high, medium or even low number of individuals (Tab. 1).

To show the relationship between the species in flower on a particular observation date, the percentage of their number of flowering individuals to the total number of individuals in flower on that day was calculated (Fig. 3). About half the year, from January to the first half of July flowering in the hectare was "dominated" by one species (defined as having more than 50% from the total number of individuals on each sample date). *Styrax ferruginea* dominated flowering with 77% of the total flowering individuals in the second half of April, and with around 90% until the first half of July. *Erythroxylum suberosum* accounted for more than 50% of all flowering individuals in October and also during its second flowering period in March and April. This second episode of flowering involved only 3–5 individuals but occurred during a period of sparse flowering together with *Styrax ferruginea*. *Piptocarpha rotundifolia* dominated with 86% the

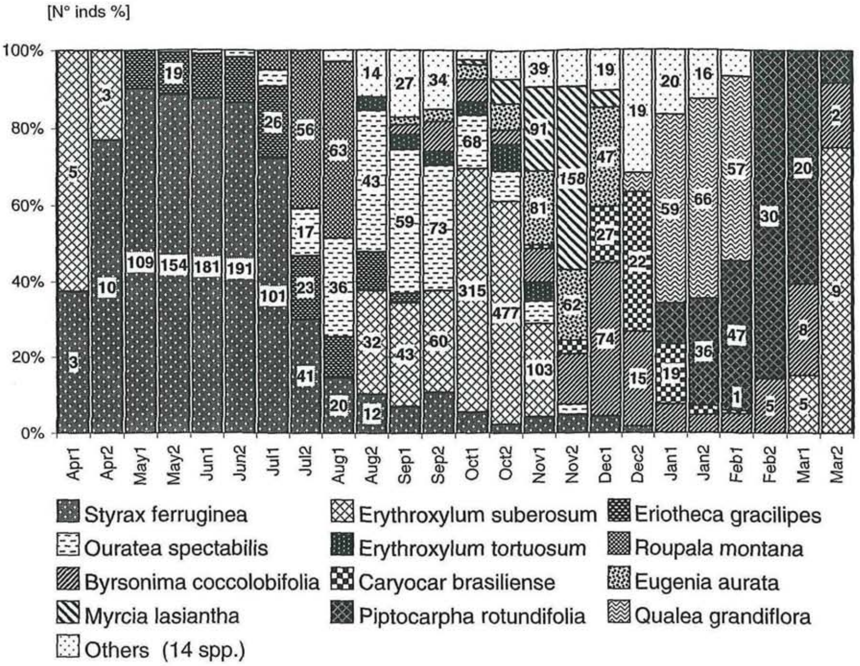

Fig. 3. Monthly distribution of individuals in flower (% for one observation date) in a hectare of cerrado, Botucatu, SP (1973/74). The numbers in the columns are numbers of respective individuals.

second half of February, and with 60% in the first half of March. *Qualea grandiflora* and *Myrcia lasiantha,* dominated during three months and one month, respectively. The group "other species" composed of the other 14 species, which flowered with only few individuals, had as the highest only once 31%, which was in the second half of December.

1c) Duration of flowering of species and individuals

Of 250 individuals of *Styrax ferruginea* 213 flowered during the year. The survey-flowering (sum of the number of flowering individuals on each survey date) of this species is 946 (SF Tab. 1), which is 4.4 times its actual number of individuals in flower (NF; Tab.1). This relation is relatively high, compared to the other species, first because the single individuals of *Styrax* flowered longer than those of other species, and second, flowering of *Styrax* was very asynchronous. At least one individual was in flower on 18 observation dates spanning 9 months (Tab. 2). The single individual flowered between 4 to 5 months, unripe fruits were visible almost two months after the initiation of flowering. The last 2-month-flowering coincided with the unripe fruit stage. After flowering had ceased, the unripe fruit stage was present another 1 to 2 months; the ripe fruits were present for one month only. In comparison, the SF of *Erythroxylum suberosum* is 1052, which is about 1.6 times the NF (Tab. 1). This species flowered during 10 observation dates (5 months). Mean duration of flowering per individual was 2.5 months. Although *Machaerium acutifolium* flowered for 2.5 months (SF = 11, NI is 14), some of its individuals flowered for less than half a month (i.e., were observed in flower on only one observation day). The species with identical SF and NF values, were those where each individual flowered during the whole flowering period of the species, e. g. in *Dimorphandra mollis*, two months, or in *Xylopia aromatica*, three months.

The minimum flowering time of a species was one month (*Tabebuia ochracea*), and the maximum was 9 months (*Styrax ferruginea*). Most species flowered during 2 to 4 months (Tab. 3). The minimum flowering time of one individual was fourteen days or less (*Machaerium acutifolium, Tabebuia ochracea*) and the maximum was 5 months (*Styrax ferruginea*).

Table 3. Duration (numbers of survey dates) of reproductive stages of thick-stemmed woody species in a hectare of cerrado, Botucatu, SP (1973/74); n.c. = not counted

	Flowers	Unripe fruits	Ripe fruits
Styrax ferruginea	18	12	8
Byrsonima coccolobifolia	14	11	4
Ouratea spectabilis	13	7	2
Erythroxylum suberosum	10	9	6
Byrsonima verbascifolia	9	7	8
Eriotheca gracilipes	9	7	2
Licania humilis	8	7	7
Eugenia aurata	7	10	10
Caryocar brasiliense	7	6	5
Erythroxylum tortuosum	6	8	6
Piptocarpha rotundifolia	6	3	3
Xylopia aromatica	6	3	2
Bowdichia virgilioides	6	4	2
Annona coriacea	5	n.c.	n.c.
Annona crassiflora	5	4	n.c.
Myrcia lasiantha	5	3	3
Couepia grandiflora	5	4	2
Qualea multiflora	4	n.c.	n.c.
Tabebuia caraiba	4	n.c.	n.c.
Aspidosperma tomentosum	4	n.c.	n.c.
Diospyros hispida	4	6	3
Dimorphandra mollis	4	7	5
Machaerium acutifolium	4	7	5
Qualea grandiflora	4	8	8
Roupala montana	3	6	4
Tabebuia ochracea	2	n.c.	n.c.

Although the duration of flowering of a species varied among individuals, there was one flowering period per year for each species, except *Erythroxylum suberosum* which had a second flowering involving a few individuals. These individuals flowered a second time and started 4 months after the main flower period of the species and finished 4 months before they started to flower once more. The flowering of *Styrax ferruginea* had two peaks. The main peak with most of individuals in flower was in June, and a second one, with much less individuals in October (Tab. 2).

1e) Flowering Patterns (Fig. 4a, b)

Flowering pattern of a species depends on flowering time of each of its individuals as well as on the fact how synchronous is the flowering of the individuals. The following patterns were observed:

Pattern 1 – "Symmetrical": Flowering curves of these species have more or less the same inclination (the same number of observation days) in the increasing phase as in the decreasing phase. Species and the number of individuals with such a pattern are the following (the numbers are the number of survey dates the species were in flower; species marked with a star (*) are shown in Fig. 4a and 4b): *Byrsonima coccolobifolia* 14*, *Byrsonima verbascifolia* 9, *Eriotheca gracilipes* 9*, *Eugenia aurata* 7, *Caryocar brasiliense* 7, *Bowdichia virgilioides* 6, *Piptocarpha rotundifolia* 6*, *Aspidosperma tomentosum* 4*, *Machaerium acutifolium* 4*, *Tabebuia caraiba* 4*, *Roupala montana* 3*.

Pattern 2 – "Asymmetrical": Steep increase to the maximum and a more flat decreasing curve. Species: *Styrax ferruginea* 18*, *Licania humilis* 8, *Annona coriacea* 5, *Annona crassiflora* 4, *Diospyros hispida* 4, *Dimorphandra mollis* 4*.

Pattern 3 – "Asymmetrical": Flat rise to maximum and steeper fall. Species: *Ouratea spectabilis* 13*, *Erythroxylum tortuosum* 6, *Erythroxylum suberosum* 6 (if only the main flowering period of this species is considered; both on Fig. 5), Myrcia *lasiantha* 5.

Pattern 4 – Rise to maximum and then stop. (Includes cases of last survey day having a very slight reduction from the maximum on the previous observation day). Species: *Couepia grandiflora* 5, *Qualea multiflora* 4, *Qualea grandiflora* 4*.

Pattern 5 – "Steady" (more or less the same number of species in flower each observation day). Species: *Xylopia aromatica* 6, *Tabebuia ochracea* 2.

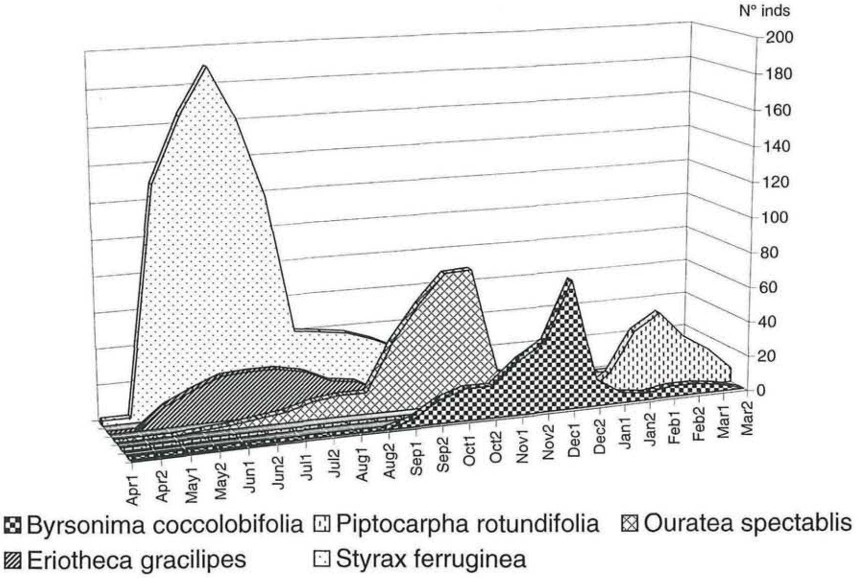

Fig.4a. Flowering of long-flowering species in a hectare of cerrado, Botucatu, SP (1973/74)

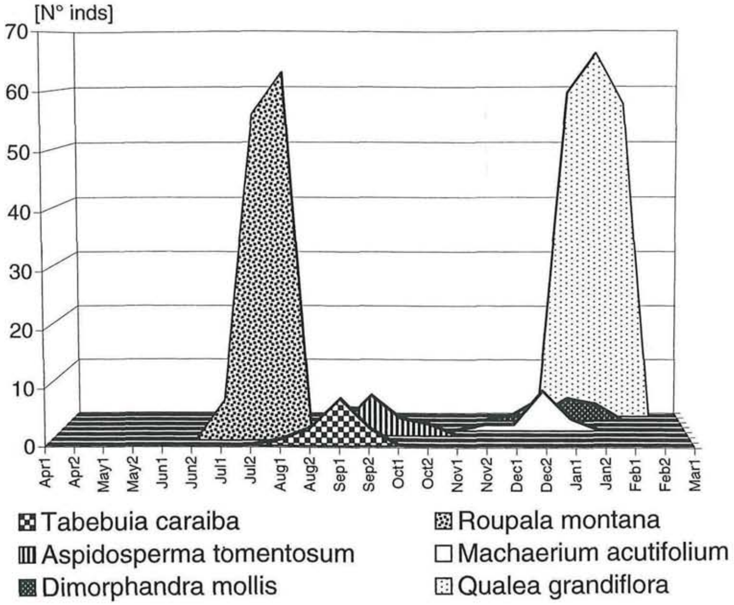

Fig.4b. Flowering of short-flowering species, in a hectare of cerrado, Botucatu, SP (1973/74)

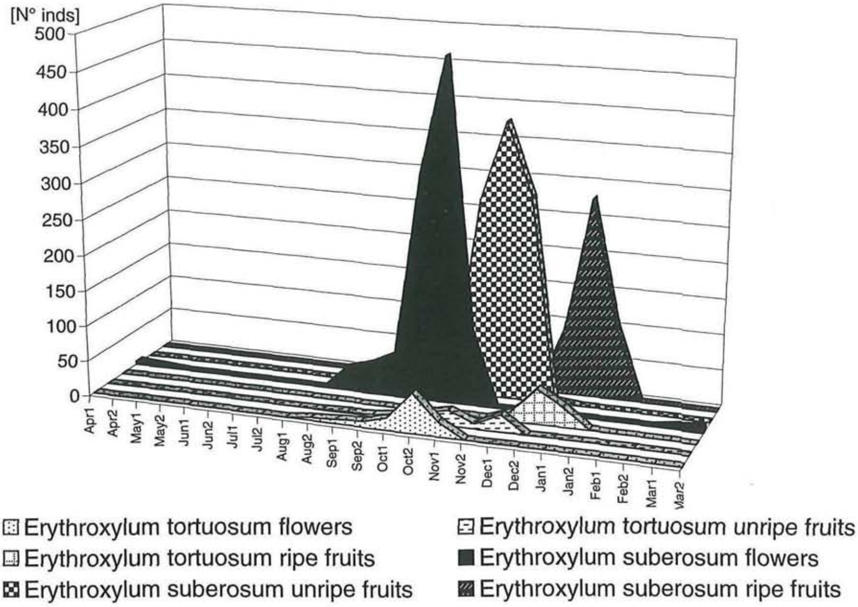

Fig. 5. Flowering and fruiting of the two *Erythroxylum* species in a hectare of cerrado, Botucatu, SP (1973/74)

Most of the species flowered following the "symmetrical" pattern 1. The patterns seem to be more or less independent of the length of the flowering period of a species and are shown independently by "long-flowering" species and by "short-flowering" species (Fig. 4a, 4b).

1f) Height of species when in flower ("Reproductive height")

The species were represented in the hectare by taller (⩾3 m) and smaller individuals (<3 m), which had all a stem-circumference of ⩾10 cm, 30 cm above ground. In general more of the taller individuals flowered. In *Qualea multiflora, Annona crassiflora, Aspidosperma tomentosum, Bowdichia virgilioides, Dimorphandra mollis, Machaerium acutifolium*, and *Qualea grandiflora* all the individuals that flowered were taller than 3 m. Only one individual of *Annona crassiflora* and *Couepia grandiflora*, which flowered, was shorter than 3 m. In *Caryocar brasiliense, Roupala montana, Styrax ferruginea, Xylopia aromatica* besides all the individuals taller than 3 m were flowering, also individuals of lower height flowered. In those species with few tall individuals, as *Byrsonima verbascifolia, Diospyros hispida, Erythroxylum suberosum, E. tortuosum*, and *Myrcia lasiantha*, all tall ones flowered and also many of those individuals shorter than 3 m.

2) Unripe fruit stage

During the 24 survey days 3848 individuals of 21 species were registered having unripe fruits (SU; Tab. 1). As in the countings of flowering also, the survey number of unripe fruits is the sum of all individuals counted on each survey date. Thus individuals which had unripe fruits for a longer time, were counted repeatedly. Five of of the 26 flowering species were not observed in the unripe fruit stage. *Tabebuia ochracea* did not set fruits, and to see fruits in the other species, the observation period was too short.

The main period of incipient fruiting was November and first half of December, with about 400 to 530 individuals and 13 to 14 species bearing unripe fruits. In the second half of June, only *Eriotheca gracilipes* and *Styrax ferruginea* had unripe fruits (5 and 191 individuals, respectively). Individuals with unripe fruits often had flowers also. The correlation between individuals and species with unripe fruits is only moderate (Spearmans rank $R = 0.54$ $p < 0.006$, $n = 24$). In August 3 spp. had even more individuals with unripe fruits (199 individuals) than 8 spp. in January (126 individuals).

The unripe fruit stage within a species lasted 1.5 months (3 spp.), 2–3 months (6 spp.), 3.5 months (6 spp.), and 4–4.5 months (3 spp; Tab. 3). *Eugenia aurata* had 5 months unripe fruits, *Byrsonima coccolobifolia* was 5.5 months in the unripe fruit stage and the longest was *Styrax ferruginea* with 6 months.

3) Ripe fruit stage

3a) Main ripe fruiting period, number of individuals and species

Individuals of 20 species with ripe fruits were surveyed 1444 times. This number is the sum of the survey number of individuals in ripe fruit over all survey dates (SR; Tab. 1), in which "longer"-fruiting individuals entered in the countings repeatedly. The period of production of ripe fruits overlapped that of unripe fruits. Most individuals of the 20 species had ripe fruits from the second half of December, through January, with 209, 451, and 244 individuals, and 10, 10, and 7 species respectively on the 3 survey days of this period (Tab. 4, Fig. 6). The correlation between number of species and amount of individuals in ripe fruit (SF) is strong (Spearmans rank $R = 0.8$; $p < 0.000$; $n = 20$).

The actual total number of individuals with ripe-fruits was 1341, which means that nearly 73% of the flowering individuals ripened at least some fruits. The percent of flowering individuals which set ripe fruits for most species was also high (Tab. 1; NR/NI%), exceptions were *Diospyros hispida* (20%) and *Qualea grandiflora* (29%).

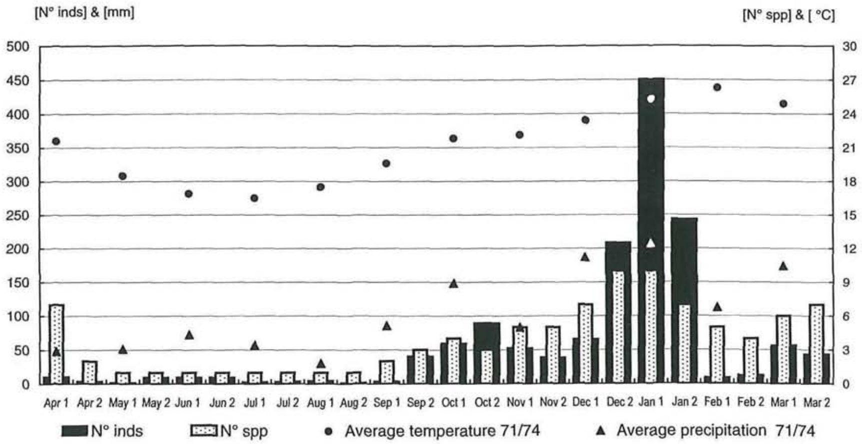

Fig. 6. Ripe-fruiting of thick-stemmed woody species in a hectare of cerrado, Botucatu, SP (1973/74; 20 spp.). In this graph the monthly values of precipitation and temperature are averages from the years 1971–1974 (for the separate monthly values of the 4 years see Fig. 1 also).

Table 4. Number of individuals with ripe fruits (SR) on each of the 24 observation days in a hectare of cerrado, Botucatu, SP (1973/74)

	Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec		Jan		Feb		Mar	
	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Dimorphandra mollis	2	2	2																				2	2
Diospyros hispida	2	2																						2
Styrax ferruginea	1										2	33	51	69	46	30	1							
Eugenia aurata	2														1	1	1	1	1	3	4	6	10	4
Machaerium acutifolium	2																				1	2	1	4
Xylopia aromatica	1																							1
Piptocarpha rotundifolia	1																						41	30
Erythroxylum suberosum															2	4	6	92	279	110				
Qualea grandiflora			3	10	10	10	3	4	5	2														
Eriotheca gracilipes												4	4											
Ouratea spectabilis																	42	49						
Roupala montana											2	4	3	17										
Bowdichia virgilioides																		3	3					
Erythroxylum tortuosum															1	1	13	49	28	1				
Licania humilis													2	4	3	3	2	1	1					
Caryocar brasiliense																			11	12	1	4	1	
Couepia grandiflora																		2	1					
Byrsonima verbascifolia																	1	1	1	1	2	1	2	1
Myrcia lasiantha																		8	114	110				
Byrsonima coccolobifolia																		3	12	7	1			
Sum individuals in ripe fruit	11	4	5	10	10	10	3	4	5	2	4	41	60	90	53	39	66	209	451	244	9	13	57	44
Sum species in ripe fruit	7	2	2	1	1	1	1	1	1	1	2	3	4	3	5	5	7	10	10	7	5	4	6	7

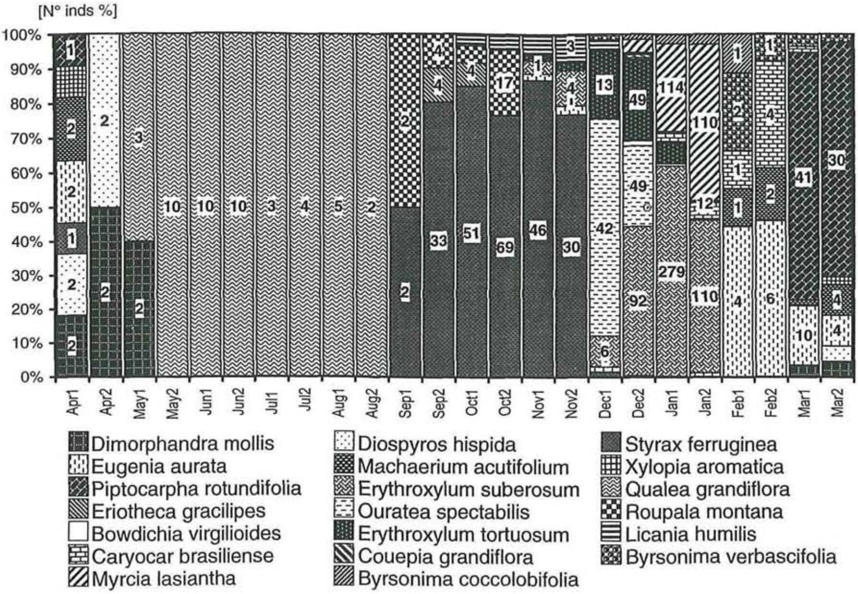

Fig. 7. Monthly distribution of individuals with ripe fruits (% for one observation date) in a hectare of cerrado, Botucatu, SP (1973/74). The numbers in the columns are the numbers of fruiting individuals.

3b) "Importance" of a species in the fruiting event

As in flowering, the percentages of number of individuals in ripe fruit (SR) to the total show that *Erythroxylum suberosum* and *Styrax ferruginea* dominated ripe fruiting too, with about 34% and 16% respectively (SR/Total SF; Tab. 1). *Myrcia lasiantha* had also 16%, and the following species were, *Erythroxylum tortuosum* (6.4%), *Ouratea spectabilis* (6.3%), *Piptocarpha rotundifolia* (5%), *Qualea grandiflora* (3.3%), *Eugenia aurata* (2.5%), *Roupala montana*, and *Caryocar brasiliense* (approx. 2% each). The remaining species participated in the fruiting event with ⩽1% of fruiting individuals.

The importance of a fruiting species on a particular survey day was calculated as the percent of the number of its individuals in fruit on that day in relation to the total number of individuals in fruit on this respective date (Fig. 7). Species dominance during fruit production on one survey date was still more marked than for flowering. *Qualea grandiflora* was the only species with ripe fruits during the second half of May till the second half of August. *Styrax ferruginea* dominated September, October and November with 80%, 85%, and 77% of all individuals with ripe fruits in these months; during the second half of February and all of March *Pitocarpha rotundifolia* was the dominant species with about 70%.

3c) Duration of production of ripe fruits (Tab. 3)

The longest period when a species had ripe fruits were 5 months. This was the case in *Eugenia aurata*. Single individuals had a much shorter ripe fruit stage than the species. More than half the species flowered for a much longer time than they had ripe fruits. Exceptions were *Eugenia aurata, Qualea grandiflora, Dimorphandra mollis,* and *Machaerium acutifolium*, which had a longer ripe fruit stage than the flowering stage. In six species the unripe-fruit stage was longer than flowering and ripe fruiting (Tab. 3).

4) Delimitation and overlap of flowering and fruiting by species and by individuals

There was no sharp delimitation of flowering and fruiting periods among species. In 19 species individuals with flowers and others with unripe fruits co-occurred for a long time. In most of these flowers and unripe fruits were also present on the same individual (e.g., *Styrax ferruginea*, *Erythroxylum* and *Byrsonima* spp., *Dimorphandra mollis, Bowdichia virgilioides, Caryocar brasiliense,* and *Licania humilis*). In contrast, *Qualea grandiflora, Diospyros hispida, Roupala montana,* and the *Myrtaceae* species never had flowers and unripe fruits together on one individual. Nearly all species had individuals with ripe fruits and with unripe fruits at the same time. In some species flowering individuals overlapped for a short time with individuals with ripe fruits (e.g., *Styrax ferruginea, Licania humilis, Byrsonima coccolobifolia, B. verbascifolia, Piptocarpha rotundifolia)*. In *Styrax ferruginea* this situation lasted for 3 months; some individuals started to flower at the end of the main flower period, when the majority of its individuals had ripe fruits. *Styrax* even had a few cases of flowers and ripe fruits together on the same individual for a short time. The individuals of most other species ripened their fruits only after flowering on that individual had totally ceased. There was almost no (only in 1 ind.) overlap between flowering- and ripe-fruit periods in individuals of *Bowdichia virgilioides, Ouratea spectabilis, Erythroxylum suberosum, E. tortuosum*, *Caryocar brasiliensis, Eugenia aurata, Myrcia lasiantha, Qualea grandiflora*, and *Dimorphandra mollis*.

Discussion

Community Level and General Considerations

In the hectare of cerrado, flowering occurred throughout the year, but it peaked at the end of the dry season and early in the rainy season. Such a pattern is consistent with other cerrados (Miranda 1995, Mantovani & Martins 1988, Gouveia & Felfili 1998), as well as with other vegetation types in the tropics with a more or less seasonal climate (Frankie & al. 1974, Opler & al. 1976, Hilty 1980, Mori & al. 1982, Lieberman 1982, MORELLATO & al. 1989, 1990, BULLOCK & SOLIS-MAGALLANES 1990, HEIDEMAN 1989, LAMPE & al. 1992, MACHADO & al. 1997). It has been shown in many studies that there are multiple factors influencing flowering (RATHCKE & LACEY 1985). For instance, rainfall and increase of temperature (e.g. OPLER & al. 1976, BULLOCK & SOLIS-MAGALLANES 1990), soil moisture and water availability (FRIEDEL & al. 1993), or seasonal variation in tree-water status (REICH & BORCHERT 1984, BORCHERT 1994a, 1994 b). Tree-water status may be important for flowering of thick-stemmed woody species in the cerrado (BARROS & CALDAS 1980). Most of the thick-stemmed woody cerrado species do not suffer strong water stress, because they reach soil water with their deep tap roots (RAWITSCHER 1942, RAWITSCHER & al. 1943, FERRI 1944, 1961, 1963). These species could theoretically flower in the dry season. Some species in the hectare started to flower with a few individuals before its peak of flowering ("pre-flowering"); these individuals perhaps were better adapted to conditions at this special timespan (e.g. *Styrax, Eriotheca, Roupala).* Other species continuated to set flower after their peak was over already long ago (e.g, *Licania humilis*). Some species even initiated their flowering with a few individuals in the dry season, but had their flowering peak in the rainy season, e.g. *Ouratea spectabilis*, *Erythroxylum suberosum*. They started to flower in May, June and July, months that have a very low precipitation or no precipitation in some years. These months also have very low temperatures in many years. These species therefore could not be stimulated by the increase of rainfall and temperature, but, perhaps contrarily, by their diminuation (FRANKIE & al. 1974, ASHTON & al. 1988), or by dry soil conditions (KINNAIRD 1992).

The two most numerous species in the hectare occupy climatically different niches in respect to flowering. *Styrax ferruginea* is a "dry-season-flowering" species and *Erythroxylum suberosum* a "wet-season-flowering" one, although a few individuals of *Erythroxylum* started to flower towards the end of the dry season. Surprisingly, *E. suberosum* had a second flowering at the beginning of the dry season (March). This was of shorter duration than its main flowering period, and involved only five individuals or 0.6% of the total number of individuals of that species. Thus at least some individuals of *E. suberosum* flowered during 5 months of this year.

Other factors may also be involved in the timing of flowering, including increasing daylength (MORI & al. 1982), or insolation (WRIGHT & SCHAIK 1994). STEEGE & PERSAUD 1991 found in a Guyana forest that flowering seems to be correlated with the peak of insolation, while fruiting is related to maximum rainfall. Timing of flowering and fruiting may also be controlled by internal factors rather than by environmental changes (BORCHERT 1983), and competition may also play a role (PRIMACK 1980). Separation in flowering time of different species may also lead increased fitness for individual species involved (ÅGREN & FAGERSTRÖM 1980). These factors are difficult to test and were beyond the scope of the present study.

It is necessary to distinguish, in regard to time of flowering of a species, between the weather of the year during which observations were made (perhaps including the few years previous) and long-time climatic averages over the last few tens of thousand of years. Populations may have evolved to fit the long-term average for the beginning of the rainy season so that a species may begin to flower before the first rain of a particular season, if the first rain is later than the long-time average. The date of first flowering caused by this internal clock may be modified by the present year's weather.

Seasonality, periodicity, and patterns of flowering and fruiting have been shown to be related to pollinators or seed dispersers activity periods in cerrados (MANTOVANI & MARTINS 1988), and other vegetations (e.g., BAWA 1983, BULLOCK & SOLIS-MAGALLANES 1990, JANZEN 1967, WHEELWRIGHT 1985, WILLIAMS-LINERA 1997, WRIGHT & CALDERON 1995). However, whether availability of pollinators is a cause or an effect of flowering is uncertain (RATHCKE & LACEY 1985). Plant species may even gain advantage in pollination by mimicry of their flowers with flowers of co-flowering species, by which more pollinators may be attracted (FEINSINGER 1987, OLLERTON & LACK 1992). Among the thick-stemmed woody species of the cerrado hectare there was no convincing correspondence of flowering season and pollination at the general level of pollination modes. Most thick-stemmed woody plants are pollinated by insects, and only very few by hummingbirds and/or bats; there were no anemophilous species (SILBERBAUER-GOTTSBERGER & GOTTSBERGER 1988). Most of the cerrado species may be pollinated by animals of different groups (families or orders). Such "joint pollination" for instance, by bees and hummingbirds, or even these plus flies, sphingids, moths, and bats is not infrequent. As there are plants in flower during the entire year, pollinators would have a continuous supply of flowers, although the resource is reduced in quantity during the dry season where fewer individuals and species flower (MACHADO & al. 1997). Moreover, most of the pollinators are not dependent exclusively on cerrado plants because they can find their food supply in plants of gallery forests, semideciduous forests, or marshes, which often occur intermixed with cerrados.

Still some plant-pollination links with flower time can be noted (SILBERBAUER-GOTTSBERGER & GOTTSBERGER 1988). Certain species with a nocturnal anthesis and specialized pollinators such as sphingids or moths (*Couepia grandiflora, Diospyros hispida, Qualea grandiflora*) and beetles (*Annona* spp.) flowered only during the warm rainy period. On the other hand, species with poricidal anthers pollinated by buzzing bees flowered only in or at the end of the dry period (*Ouratea spectabilis*). Interdependence of species' phenophases with pollinators and dispersers may appear when pollination studies do not consider animal orders as taxonomic level, but genera or species (FEINSINGER 1987, GENTRY 1974).

Seasonality of flowering probably is related to life forms rather than to competition for pollinators (KOCHMER & HANDEL 1986). LIEBERMAN 1982 and MONASTERIO & SARMIENTO 1976 showed that flowering and fruiting patterns are related to habitat, growth- and life forms. Many shrubs, vines, and especially the groundlayer plants have a completely different flowering rhythm, having the peaks often even opposite to that of thick-stemmed woody species (AKPO 1997, MANTOVANI & MARTINS 1988). As these other growth forms make-up about 80% of cerrado species, it is necessary in phenological studies to include them, to get an actual picture.

Fruiting of the studied woody species is somewhat more synchronous than flowering (see also GUITIAN & GUITIAN 1990, HILTY 1980). Most species and individuals had their fruiting peaks during the rainy season, and only a few in the dry season. The two most important species in the hectare fruited during the rainy season. The phenomenon that only a single species fruited in July and August was certainly due to the fact that fruiting of all species was not captured due to the sampling interval and of the observation period being only one year. A special situation of this particular year was, that the two species, *Machaerium acutifolium* and *Dimorphandra mollis* set fruits in April and May respectively, and not in June and July as they did in other years.

Rhythm of fruiting and seed dispersal in the cerrado was more strongly linked to the seasonal climate than was flowering and pollination. Of the five anemochorous species, three (*Machaerium acutifolium*, *Piptocarpha rotundifolia*, *Qualea grandiflora*) fruited at the beginning of the dry season and in the dry season, and all of the zoochorous species in the rainy season. This was also observed for cerrado and other vegetations forms in Brazil by MORELLATO & al. 1989, 1990, MORELLATO & LEITÃO FILHO 1996, and in other countries and vegetation types by FRANKIE & al.1974. To fully characterize seasonality of dispersal events in the cerrado, especially in its more open forms (campo cerrado), it will be necessary to include not only the thick-stemmed woody species, but also plants of other life- and growth forms. If all angiosperm species of the hectare are considered, it is seen, that most of the anemochorous species fruited during the dry months from April to June, and only a few anemochorous species fruited in the rainy season. Some epichorous, autochorous, and endo- and synzoochorous species have their ripe fruits during the dry season, but most endo- and synzoochorously-dispersed species fruit in the warm wet season. A comparison of dispersal modes of cerrado and cerradão showed that differences in fruit dispersal are directly correlated with growth forms, which, in turn, are related to the vegetation structure (GOTTSBERGER & SILBERBAUER-

GOTTSBERGER 1983, SILBERBAUER-GOTTSBERGER & GOTTSBERGER 1988). Time of fruit maturation certainly is not only related to dispersal mechanisms but also to seed dormancy and physiology of germination and establishment (KINNAIRD 1992).

Species Level

For vegetation that is more or less in a climax situation, one could hypothesize that species with the largest population sizes might also be the "best" when considering reproduction. This was more or less the case in the studied hectare, but there were also some species with a relatively high number of individuals, in which only a few individuals flowered (e.g., *Tabebuia ochracea*). Flowering in this species always occurs within 3 to 4 weeks. Species with many individuals may have few flowering individuals if only a few individuals of the appropriate stage (e.g., age, height) were present (e.g. *Qualea grandiflora, Byrsonima coccolobifolia*). On the other hand, most of the thick-stemmed woody species in the cerrado also flowered at low height, some even when they were only half a meter tall. But in species with both tall and short individuals, more of the taller individuals flowered.

Duration of flowering of a species was determined as the interval between the initiation of the first individual and the termination of the last individual to flower (MACHADO & al 1997). Many of the thick-stemmed woody species had medium-long to very long flowering periods, a phenomenon which is not common in other seasonal vegetations, and may be characteristic of cerrado. In a deciduous forest in Mexico, for instance, among trees, duration of flowering of one month was the most common (BULLOCK & SOLIS-MAGALLANES 1990). The duration of flowering of a species expresses more or less the degree of synchronization among their individuals (RATHCKE & LACEY 1985), expresses also duration for individuals, and the time of overlapping of flowering with individuals with unripe and ripe fruits. In species that flowered for less than 2.5 months (35%), individuals flowered more synchronously than did those of longer-flowering species (23%). But species with a long-flowering phase (42%) had different levels of synchrony of their individuals. For instance, the flowering of the longest-flowering species *Styrax ferruginea* (9 months) was not well synchronized, but rather staggered among individuals. Flowering of single individuals lasted up to 5 months. During the long flowering period, single individuals started to flower while others had already faded; and some started to flower even when others already had ripe fruits. During most of the time, individuals had both flowers and unripe fruits, or, in some cases also even ripe fruits at the same time. In contrast, the flowering phase of the medium-long flowering species (5.5 months) *Erythroxylum suberosum,* started with few individuals, reached its peak relatively quickly and ended flowering rather abruptly. There was nearly no overlap between the flowering and ripe-fruit period in this species, and flowers and ripe fruits were never seen together on one individual. Synchronization in flowering was also marked in short-flowering species. All short-flowering species had one prominent flowering peak and did not show "pre"- or "post-flowering", as many of the long-flowering species did. In some species the same individuals flowered over the whole flowering period.

There was a slight tendency for species that flowered in the dry season to have a longer duration of flowering than those that flowered in the rainy season. This was also found by MORELLATO & al. 1989 for a Brazilian tall mesophyllous semideciduous forest. This is certainly not the case in *Bignoniaceae* species with short-flowering periods, during the dry season (see also GENTRY 1974).

Duration of flowering in the area is not correlated with density of species. Among the three most numerous species were a long-, a medium-long and a short-flowering species.

During the year, participation of species in flowering and fruiting of the hectare differed. It is true that the two most numerous species were also the most important both in flowering and fruiting. However, among the longer-flowering species there were those that dominated flowering during nearly all the months they flowered, others dominated only in a few months, and a third group never dominated. On the other hand, there were also short-flowering species that dominated overall flowering in the hectare during more than half of their flowering time. In most months a single species dominated flowering with about 50% or more of all flowering individuals in that month (of the 26 spp.) (Fig. 4).

Although flowering time of species and individuals varied, there was one continuous flowering period per year for all species, with one exception. *Erythroxylum suberosum* had a second separate flowering period involving a few individuals. Therefore, all species observed, except *E. suberosum*, may be classified as "annual" flowering (NEWSTROM & al. 1994). There may, however, be other patterns that could not be detected because the observation time of one year was too short. Such flowering patterns may occur on the species level and perhaps even individual level, because individuals of one species may behave differently in different years. Only studies over many years would reveal such patterns. The results of the many-year project in Costa Rica show very impressively how complicated the flowering patterns in tropical habitats may be (NEWSTROM & al. 1994).

In our hectare, 72% of flowering individuals of the 26 species studied had ripe fruits on at least one census date. The presentation period of ripe fruits in the species was on average much shorter than the flowering period, although the "longest flowering" species was also the "longest fruiting" one. More short-fruiting species than long-fruiting species ripened their fruits in the dry season.

The relation between flowering and fruiting time is also species dependent but is linked to the duration of the two phenophases. Among those species that presented a longer flowering period, flowering and fruiting occurred in parallel.

The monthly dominance of a species in the fruiting event was still more striking than in flowering. In most months a single species dominated fruiting, and contained 70% to 90% of all individuals fruiting that month.

Methodology

Phenological studies in both tropical and temperate regions are often based on counting phenological events of species, or of selected individuals of the most common species. For Brazilian vegetation such phenological studies by demarcation of tree individuals, but evaluated only on species level, were done among others by MORI & al. 1982 for a wet forest in southern Bahia, MORELLATO & al. 1989, 1990 for a montane and a submontane forest in the Serra de Japi, Jundiaí, São Paulo State, and by MORELLATO & LEITÃO FILHO 1996 for climbers in a forest in São Paulo State.

Results based on studies at the individual level (ARROYO 1990, BULLOCK & SOLIS-MAGALLANES 1990, MACHADO & al. 1997), as also the present study, showed that the correlation between phenophases of number of species and number of individuals especially for the flowering phase is weak. A redundant example in the hectare is, that during the months of May and June (Fig. 2) the number of individuals of all 26 woody-layer species that were in flower, was greater than in December and January, yet the first period had only 3–4 species in flower, whereas the second period had 6 to 13. This lack of correspondence between different seasons was to some extent due to the high absolute number of flowering or fruiting individuals of only 2 or 3 species. This phenomenon was also related by HEIDEMANN 1989, MACHADO & al. 1997 for the vegetation they studied. This weak correlation of flowering of species and individuals can be expected for all cerrados, cerradões, and even dry forests, as in all the areas studied by RIZZINI 1975, GIBBS & al. 1983, RIBEIRO & al. 1985, OLIVEIRA-FILHO & MARTINS 1986, 1991, CESAR & al. 1988, RATTER 1987, RATTER & al. 1988, FURLEY & al. 1988, PAGANO & al. 1989a, 1989b, ENCINAS & RIBEIRO MONTE 1989, FELFILI & SILVA JR. 1993, GUARIM NETO & al. 1994, one to four species were dominant in respect to number of individuals. It is very probable that these species with a high density also reproduce with numerous individuals.

Therefore, to understand the phenological patterns in a vegetation, especially in the context of pollination and seed dispersal, studies of selected species or individuals must be extended to a complete phytosociological survey of a representative area. Still more promising is to extend the observations to more details, such as number of flowers and fruits (ARROYO M.T.K. & al. 1982, ARROYO, J. 1990, GUITIAN & GUITIAN 1990, KRATOCHWIL 1983, ROTENBERRY 1990, STRUCK 1994, SUN & al. 1996), and their size, as well as the quality and quantity of rewards. These kinds of studies are necessary because the majority of these variables are not correlated (HEIDEMANN 1989, PRIMACK 1980). It was also even shown for the rainforest that the number of species in flower or fruit were no good indicators for number of individuals (HILTY 1980, HEIDEMANN 1989). This is contrary to SUN & al. 1996, and van SCHAIK & al. 1993, who showed for a tropical montane forest in Rwanda: "that phenology patterns expressed as the number of species, number of individuals or some ad hoc indices are highly correlated". It may be that correlations of flowering and fruiting times considering number of species, individuals, and even flowers may be stronger for an aseasonal vegetation than for a seasonal one.

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