

Dioecy in the Cerrado vegetation of Central Brazil

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Summary

Occurrence of dioecy in Cerrado, Neotropical savanna region in Central Brazil, is analyzed here. Frequency of dioecious species and their phenological and morphological characteristics were studied for a cerrado woody community near Brasilia, and a broader comparative survey was done using phytosociological data for different cerrado areas and vegetation physiognomies. Nine dioecious species were found in the studied community (15% of the species in the area), most with simple open flowers visited by small insects. Flowering phenology differed from species to species including long, sparse flowering and cornucopian strategies. Distance between flowering individuals varied from 13 to 70 m. Gender related differences in spatial distribution and in height or circumference were tested for three of the species and significant departure from random was found only for *Rapanea guianensis*. The regional survey showed frequencies of dioecy higher in denser woodlands and forest than in open cerrado areas. Most species presented small promiscuous flowers, probably associated to pollination by small insects, and fleshy fruits. Among the species occurring in the cerrado areas one could separate a group of dioecious shrubs and treelets really adapted to cerrado environment and another group of evergreen forest species which occur only in denser woodlands, the cerradão. Differences in the frequency of dioecy seems to be related to the occurrence of this latter group and the appearance of cerradão.

Key words: Pollination, breeding-system, savanna, plant-reproduction, dioecy

1. Introduction

Sexual dimorphism in plants, dioecy, is a relatively less common sexual system than hermaphroditism with a frequency among flowering plants worldwide estimated at 3–4% (YAMPOLSKY & YAMPOLSKY 1922 as cited by BAWA 1980a) and it has been considered a poorer alternative to cosexual system since unisexual individuals lose the possibility of fitness gain through the missing sexual function (LLOYD 1982). However, the singular characteristics of the dioecious mating system have motivated studies to understand the distribution patterns and possible factors affecting the occurrence of dioecy in different floras and habitats (BAWA 1980a). Geographical and altitudinal trends have been observed (BAKER 1955, CARLQUIST 1966, BAWA 1980a, SOBREVILLA & ARROYO 1982), links with specific pollination and dispersal mechanisms have been discussed (BAWA 1980a, 1980b, GIVINISH 1980, BEACH 1981, IBARRA-MANRIQUEZ & OYAMA 1992, RENNER & FEIL 1993, BAWA 1994), and possible ecological pressures selecting dioecious systems have been considered (JANZEN 1971,

LLOYD 1982). The incidence of dioecy has been shown to be high in some life forms, strata and formations of tropical vegetation, but studies carried out so far have been mostly for forest formations (BAWA 1974, RUIZ & ARROYO 1978, CROAT 1979, SOBREVILLA & ARROYO 1982, BAWA et al. 1985, BULLOCK 1985). Physiognomic differences between the two largest vegetation provinces in South America – lowland rain forest and neotropical savanna – pose an obvious question as to the relative frequency of dioecy in these formations which has not been successfully assessed as yet. In Central Brazil savannas, the cerrados, physiognomic gradients may lead from open cerrado areas to denser woodlands (Cerradão) and mesophyllous forest, associated or not with edaphic changes (GOODLAND 1971, GOODLAND & POLLARD 1973, FURLEY & RATTER 1988). A suggestion, specifically for some groups of Lauraceae, of possible trends relating dioecy with open vegetation has been put forward (KUBITZKI & KURZ 1984), but more detailed analysis are still lacking.

The aim here is to study the biology of dioecious woody species in cerrado both on a local community

base and also in regional terms. I compare the biology, population structure, and frequency of dioecious species in cerrado with contiguous gallery forest formations, and other plant communities in the neotropics.

2. Materials and methods

The study was based on a cerrado community data set (OLIVEIRA 1991) and in a Regional survey of the phytosociological information available for other cerrado areas in Brazil. A cerrado area in the Brasilia Botanic Garden was surveyed using the point centered quarter method (COTTAM & CURTIS 1956). The woody species included in the survey and another 10 species observed in the area were listed for the community. The floral biology of the dioecious species within this sample was studied. Phenology, flower longevity, main pollinators, and fruit-set by natural pollination were observed *in situ* (OLIVEIRA 1991). Fixed material in FAA was used for basic morphological analysis. Sex ratios, spatial distribution, and size relations were studied for three of the species, for which line transects were done in different areas during the flowering peak. Plant gender, stem circumference at 30 cm high, and height were noted for all the flowering individuals at sight range from the transect line. Differences in circumference and height between sexes were tested using t-tests. A run-test was used to check whether spatial sex distribution departed from random. Statistics were based on SOKAL & ROHLF (1981).

The Regional survey used phytosociological data from different physiognomies of cerrado in the Brasilia region (RIBEIRO et al. 1985, FELFILI & SILVA-Jr. 1992), from a floristic study lists also in Brasilia (RATTER 1985), and surveys available for other cerrado areas in Brazil (RATTER et al. 1973, OLIVEIRA-FILHO & MARTINS 1986, RATTER et al. 1988). Floristic lists for gallery forest sites in Brasilia were also analyzed for comparison (RATTER 1985 and FELFILI & SILVA-Jr. 1992 for

Agua Limpa Farm-FAL and PAULA et al. 1990 for the São Bartolomeu gallery forests). The sexual system was established for each taxon based on field observation, herbarium material and recent taxonomic revisions. Unidentified species were excluded from the final analysis.

3. Results

Dioecy has not been studied before for the cerrado flora and the results here depend to some extent on the field surveys and taxonomic accounts which were not specifically directed to this subject. Dioecy is often difficult to differentiate from partial dimorphism and gender polymorphism present in natural populations. Consequently, the data presented here have different degrees of precision which is probably highest for the local sexual system survey and lowest for the Regional survey since the latter was largely based on taxonomic information.

2.1. Local survey: The woody community study presented nine dioecious species (15% of the species in the area) of five different families ranging from small shrubs to relatively large trees of 10 m or more (Table 1). Except for *Neea theifera* OERST., which has a different flower structure, most of the plants have small, unspecialized flowers with easily available pollen and nectar in very small amounts. Sexual dimorphism was restricted to the flowers (Fig. 1) and vegetative features were similar, as far as it could be observed. Sex was maintained in consecutive reproductive seasons. Polygamous individuals were observed only in *Guapira graciliflora* (MART.) LUND. and intermediate floral morphs were present in *Ocotea spixiana* (NEES) MEZ and *Pouteria ramiflora* (MART.) RADLK.

Table 1. Flowering and reproductive parameters for the dioecious species included in the local community study. Estimates based on the phenological and phytosociological surveys of the area (OLIVEIRA 1991). Sex ratio (staminate-S/P-pistillate flowers) was obtained from a specific survey (see Fig. 2) and fruit set data is also from OLIVEIRA (1991).

Dioecious Species	Family	Growth form	Density Individuals/ha	Flowering Density	Average distance (m)	Sex ratio S/P	Fruit-set %
<i>Cybianthus detergens</i> MART.	Myrsinaceae	shrub	9*	9	69.47	*	–
<i>Guapira graciliflora</i> (MART.) LUND.	Nyctaginaceae	shrub	265	99	15.90	1.15	0.5
<i>Guapira noxia</i> (NETTO.) LUND.	Nyctaginaceae	shrub	119	63	22.72	0.57*	–
<i>Neea theifera</i> OERST.	Nyctaginaceae	shrub	18	3	70.54	*	8
<i>Ocotea spixiana</i> (NEES) MEZ.	Lauraceae	tree	27	5	51.37	4.5	1.6
<i>Phoebe erythropus</i> (NEES & MART.) MEZ.	Lauraceae	tree	9*	0	–	*	–
<i>Pouteria ramiflora</i> (MART.) RADLK.	Sapotaceae	tree	64	64	13.52	*	0.5
<i>Rapanea guianensis</i> AUBL.	Myrsinaceae	shrub	82	68	29.12	1.20	9
<i>Symplocos rhamnifolia</i> A.DC.	Symplocaceae	shrub	18	11	41.68	2.5*	4.6

* No direct data available. The smallest density obtained from the phytosociological survey was used.

* Data not available or based on small samples

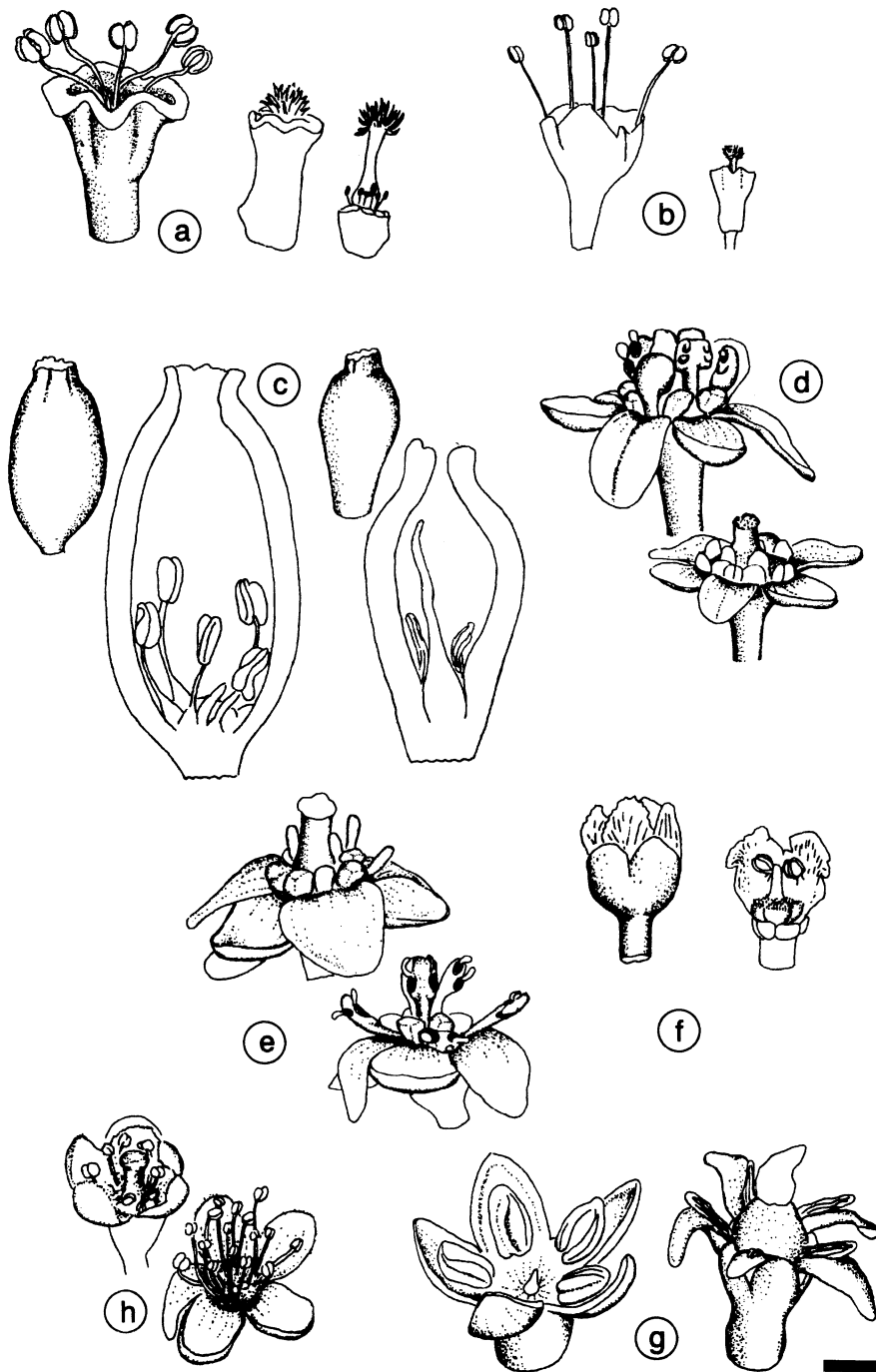


Figure 1. Floral morphology of the dioecious species in the BBG study area (except *Cybianthus detergens*). (a) *Guapira noxia*, staminate, pistillate flowers and internal detail of the pistil and reduced stamens. (b) *Guapira graciliflora*, staminate and pistillate flowers. (c) *Nea theifera*, staminate, pistillate flowers and details of their internal chamber. Note details are enlarged 2x. (d) *Ocotea spixiana*, staminate and pistillate flowers. (e) *Phoebe erythropus*, pistillate and staminate flower. (f) *Pouteria ramiflora*, flowers observed in the area did not present marked dimorphism and fruit-bearing individuals had flowers with normal stamens. (g) *Rapanea guianensis*, staminate and pistillate flowers. (h) *Symplocos rhamnifolia*, pistillate with less stamens and staminate flowers with pistil absent. Scale bar = 2 mm or 1 mm in the case of (d), (g) and details in (c).

Actually, *P. ramiflora* is a puzzling species since PENNINGTON (1990) described it as dioecious but no clear dimorphism was observed between flowers in the study area. Flowers from fruit producing trees each bore a pistil and anthers with pollen which contrasted with the description of clear sexual dimorphism in the taxonomic revision. Other individuals, however, flowered massively but did not produce fruits though possibly functional flowers were present. Since it was not possible to assess the problem specifically during the field work, the species is treated as dioecious throughout the present study.

Dioecious species were visited by small insects (bees, flies and wasps) and very small insects (thrips and other insects smaller than 5 mm) in the case of *Pouteria ramiflora* and *Neea theifera*. This latter species presents a rather different flower structure with a gamosepalous calix forming a chamber open only by a narrow pore. Thrips (Thysanoptera) were the only common visitors directly observed in these flowers (and also in *Pouteria ramiflora*) and could be involved in the pollination of these plants.

The small shrubs and treelets had an extended flowering period but were poorly visited during the study, while the trees *O. spixiana* and *P. erythropus* flowered in a cornucopian fashion (sensu GENTRY 1974) for one or more weeks and received more visitors. This was particularly the case with some male individuals of the fly-pollinated *Phoebe erythropus* (NEES, MART. & SIX) MEZ which showed a continuous noise of visitor's movement similar to that observed in bee pollinated cornucopian flowers.

Phytosociological parameters of the nine dioecious species are present in the Table 1. Flowering density was estimated from the phenological observations in the study area during their peak flowering. Average distance between flowering individuals was calculated from the flowering density estimates and varied from 13 to 70 metres. Actual mate distance is possibly greater than these values suggest since sex ratios were often biased.

Possible gender related spatial distributions in three species were tested and spatial distribution did not depart significantly from random in the community area (Fig. 2). No difference in size (height and circumference) was found between flowering, possibly adult, pistillate and staminate plants for the three species at the population level (Fig. 2). Another population of *Rapanea guianensis* AUBL. in another area inside the Brasilia Botanic Garden showed, however, a different spatial distribution. This species was represented in this second area only by pistillate (female) individuals where it was overwhelmingly dominant, indeed, almost the sole woody species in an open cerrado area. The population flowered uniformly in 1989, and all individuals sampled were pistillate. Extended searches did not locate any

staminate individual (male) in the area. Nevertheless, these plants presented fruits later on in the reproductive season (presence and viability of the seeds were not verified). *Rapanea guianensis* in the community study area also seemed to present a clustered gender distribution and statistics were a borderline case (significantly different from random at 6%). Thus, it seems that although distributions in the study area did not depart from random, some differences in sex ratio and distribution may occur between populations of the studied dioecious species. Furthermore, the kind of sex distribution in *Rapanea guianensis*, suggests that some sort of agamospermy or vegetative propagation may be present.

Ocotea spixiana is a less common tree and the sample obtained was much smaller. The sex ratio was male biased but no significantly grouped distributions could

Guapira gracilliflora

Population 1 (N=56)

±P S P P S P S P S S S P P S P S P S S S S S S P S S S P P S S P P S P P P P S S S S
S S P P S P S P S S S S P S S

Runs=30, t=0.6468 (NS) Sex ratio = 1.55

Height P → 229cm. (± 13.0) t = 0.784 (NS)

S → 215cm. (± 11.7)

Circumf. P → 10.6cm. (± 0.58) t = 1.079 (NS)

S → 9.73cm. (± 0.52)

Population 2

P P P S S P S P P S S ± S P P P S S P S P S S ± S S P P P P S P P P S P P P
P P P P P S S P P P S S P S P S P S S S S S P P P P S P S S P S P S S S S P P P S
S S P S S S P P P S S P P S P S P S P S P P P S P S

Runs=53, t=1.2973 (NS) Sex ratio = 0.95

Height P → 192cm (± 7.7) t = 0.77 (NS)

S → 183cm (± 8.2)

Circumf. P → 7.6cm (± 0.36) t = 0.37 (NS)

S → 7.8cm (± 0.34)

Rapanea guianensis

Population 1 (N=44)

P P P P P P P P S S S P P S P P S S S P P S S S S S S S S S S S P P P S S S P S S
S S S S S S S P P P P P P S P S P P S S P P S

Runs=26, t=1.9334 (0.05 < p < 0.06) Sex ratio = 1.2

Height: P → 226cm (± 13) t = -0.674 (NS)

S → 238cm (± 14)

Circumf. P → 11.6cm (± 1.05) t = 0.818 (NS)

S → 12.7cm (± 0.95)

Population 2

83 pistillate individuals sampled

Ocotea spixiana (N=33)

S S S S S S S P S S S S S P S S S S S S S S P P P S S S S P S S

Runs=9, t=1.1054 (NS) Sex ratio = 4.5

Height: P → 667cm (± 84.3) t = 0 (NS)

S → 667cm (± 28.7)

Figure 2. Sampling sequence in populations of three dioecious woody cerrado species. P = pistillate individual, S = staminate individual and ± = monoecious individuals. Underlining shows the sequences of individuals of the same sex (runs). Monoecious (±) individuals were excluded from the statistical analysis. Significant departure from random distributions was tested at 5%. Average height and circumference is present for pistillate and staminate plants. Size differences between gender were tested using t-test at 5% of significance. NS = not significant.

Table 2. Percentage of occurrence of some reproductive features in different physiognomies of cerrado in Brasília (Oliveira 1991). Based on the phytosociological data from RIBEIRO et al. 1985 in the Centro de Pesquisas Agropecuárias de Cerrado (CPAC) cerrado areas, FELFILI & SILVA-Jr. 1992 in the Fazenda Água Limpa (FAL) cerrado areas and OLIVEIRA (1991) in the Brasília Botanic Garden (BBG) study area. Numbers in parentheses correspond to species showing the feature and the total of species observed in the area. Tree density and coverage increases from the Campo Cerrado area (C. Cerrado) to the Cerradão woodland.

	C. CERRADO CPAC	CERRADO CPAC	CERRADO FAL	CERRADO BBG	CERRADÃO FAL	CERRADÃO CPAC
Dioecy	11 (3/26)	6 (4/64)	8 (5/61)	15 (9/59)	15 (9/60)	26 (19/74)
Pollination						
Small insects	35 (9/26)	38 (22/58)	38 (23/61)	44 (26/59)	45 (27/60)	40 (25/63)
Large bees	35 (9/26)	33 (19/58)	39 (24/61)	32 (19/59)	37 (22/60)	36 (23/63)
Bats	8 (2/26)	5 (3/58)	5 (3/61)	3 (2/59)	3 (2/60)	5 (3/63)
Dispersal						
Anemochory	54 (14/26)	45 (29/64)	41 (25/61)	34 (20/59)	38 (23/60)	34 (26/76)
Others	46 (12/26)	55 (35/64)	59 (36/61)	66 (39/59)	62 (37/60)	66 (50/76)

be identified. A male biased sex ratio was also observed for *Cybianthus detergens* MART. and for the few flowering individuals of *Phoebe erythropus* observed out of the study area. Only three pistillate trees of *P. erythropus* could be found in the Botanic Garden area after a fairly intensive search during the flowering period of 1989.

All nine species produce fleshy fruits most of which are characteristically bird dispersed and all of them are zoochorous. Except for *Ocotea spixiana*, where an individual with a massive number of fruits was observed with a relatively high degree of synchrony in fruit maturation, most plants produced relatively small fruit-set which matured slowly. *Rapanea guianensis*, particularly, had fruits at different stages of development which matured at different periods of the year. Average fruit-set of six of these dioecious species (the other species either presented no pistillate individual in the area or, in the case of *Guapira noxia* (NETTO) LUND., had very weak flowering) was small (4%) when compared with a sample of zoochorous hermaphrodite species in the area (17%, n = 22).

2.2. Regional survey: The occurrence of dioecy varied along the cerrado physiognomic gradients (Table 2) but cannot be related directly to the changes in woody biomass or coverage since some dioecious species were present even in open cerrado. Higher frequencies of dioecy were found, however, in dystrophic cerradão

Table 3. Frequency of dioecy in different areas of cerrado and Gallery forest in Central Brazil.

	Total	Dioecious	% Dioecy
Species	418	77	18
Gallery forest S. Bart. ¹	79	17	22
Gallery forest FAL ²	130	30	23
Cerrado-MT ³	96	7	7
Cerradão-MT ³	103	11	11
Cerrado-Angatuba ⁴	63	7	11
Cerradão-Angatuba ⁴	70	12	17
Cerrado-FAL ⁵	89	10	11
Cerradão-FAL ⁵	99	16	16
Brasília Botanic Garden JBB	121	20	17
Cerrado-Ch. dos Guimarães ⁶	129	13	10
Cerradão-Ch. dos Guimarães ⁶	155	32	21
Cerrado Species	327	54	17
Strictly cerrado species	251	30	12
Strictly forest species	167	47	28

1 – PAULA et al. 1990, 2 – RATTER 1985 and FELFILI & SILVA-Jr. 1992, 3 – RATTER et al. 1973, 4 – RATTER et al. 1988, 5 – RATTER 1985, 6 – OLIVEIRA-FILHO & MARTINS 1986.

areas (*sensu* FURLEY & RATTER 1988). The studied plot presented an intermediate result.

Regionally (Table 3), cerradão woodland areas showed a percentage of dioecy which was consistently higher than those of their sympatric cerrado areas, but frequencies varied from site to site. The list of species

Table 4. List of the dioecious species observed in the Regional survey for the cerrados of Brazil.

ANACARDIACEAE	MYRSINACEAE
<i>Astronium fraxinifolium</i> SCHOTT	<i>Rapanea guianensis</i> AUBL.
<i>Tapirira guianensis</i> AUBL.	<i>Rapanea lancifolia</i> MEZ.
<i>Tapirira marchandii</i> ENGL.	<i>Rapanea umbellata</i> MEZ.
AQUIFOLIACEAE	<i>Weigeltia densiflora</i> MEZ. (= <i>Cybianthus detergens</i> MART.)
<i>Ilex affinis</i> GARDN.	NYCTAGINACEAE
<i>Ilex asperula</i> MART.	<i>Guapira noxia</i> (NETTO) LUND.
<i>Ilex conocarpa</i> REISS.	(= <i>Pisonia noxia</i> NETTO)
<i>Ilex cerasifolia</i> REISS.	<i>Guapira graciliflora</i> (MART.) LUND. (= <i>Pisonia</i> <i>graciliflora</i> MART.)
BURSERACEAE	<i>Neea theifera</i> OERST.
<i>Protium almecega</i> MARCH.	OPILIACEAE
<i>Protium elegans</i> ENGL.	<i>Agonandra brasiliense</i> MIERS.
<i>Protium heptaphyllum</i> (AUBL.) MARCH.	POLYGONACEAE
<i>Protium pilosissimum</i> ENGL.	<i>Coccoloba mollis</i> CASAR
EBENACEAE	RUBIACEAE
<i>Diospyros burchellii</i> HIERN	<i>Alibertia concolor</i> (CHAM.) K. SCH.
<i>Diospyros coccolobifolia</i> MART.	<i>Alibertia edulis</i> (L. RICH.) A. RICH.
<i>Diospyros hispida</i> A. DC.	<i>Alibertia</i> cf. <i>sessilis</i> (CHAM.) K. SCHUM.
<i>Diospyros sericea</i> DC.	<i>Alibertia verrucosa</i> MOORE
EUPHORBIACEAE	<i>Amaioua guianensis</i> AUBL.
<i>Alchornia triplinervia</i> MÜLL.-ARG.	RUTACEAE
<i>Jatropha vitifolia</i> MILL.	<i>Fagara rhoifolia</i> (LAM.) ENGL.
<i>Pera glabrata</i> (SCHOTT) BAILL.	<i>Fagara ridelianum</i> ENGL.
GUTTIFERAE	SAPINDACEAE
<i>Clusia sellowii</i> SCHLECHT.	<i>Dilodendron bipinnatum</i> RADLK.
LAURACEAE	SAPOTACEAE
<i>Ocotea spixiana</i> (NEES) MEZ	<i>Pouteria ramiflora</i> (MART.) RADLK.
<i>Ocotea pulchella</i> MART.	MONIMBIACEAE
<i>Phoebe erythropus</i> (NEES & MART.) MEZ	<i>Siparuna guianensis</i> AUBL.
MENISPERMACEAE	MORACEAE
<i>Abuta selloana</i> EICHL.	<i>Cecropia</i> cf. <i>cinerea</i> MIQ.
MONIMBIACEAE	<i>Cecropia pachystachya</i> TRÉC.
<i>Siparuna guianensis</i> AUBL.	<i>Ficus gardnerianum</i> (MIQ.) MIQ.
MORACEAE	<i>Ficus guianensis</i> AUBL.
<i>Cecropia</i> cf. <i>cinerea</i> MIQ.	<i>Pseudolmedia laevigata</i> TRÉC.
<i>Cecropia pachystachya</i> TRÉC.	MYRISTICACEAE
<i>Ficus gardnerianum</i> (MIQ.) MIQ.	<i>Virola malmei</i> A. C. SMITH
<i>Ficus guianensis</i> AUBL.	<i>Virola sebifera</i> AUBL.
<i>Pseudolmedia laevigata</i> TRÉC.	
MYRISTICACEAE	
<i>Virola malmei</i> A. C. SMITH	
<i>Virola sebifera</i> AUBL.	

occurring in the Brasilia Botanic Garden included both cerrado and cerrado woody flora and showed a frequency of dioecy higher than the one obtained for the community area only. Data from gallery forest areas around Brasilia showed a higher occurrence of dioecy than the cerrado and cerrado areas in the region. The frequency of dioecy for exclusive cerrado species was lower than for the complete group of species occurring in cerrado. The gallery forest flora showed the highest percentage of dioecy. Dioecious groups in the cerrado flora included the ones present in the community study area and others which were not observed locally. *Alibertia* and *Amaioua* (Rubiaceae), for example, are important moth pollinated understorey trees in mesophilous forest and also occur in different cerrado areas. Predominantly dioecious forest groups such as Burseraceae (*Protium* spp.), Monimiaceae (*Siparuna* spp.), Moraceae (*Cecropia* spp.), and Myristicaceae (*Virola* spp.) were also important groups in the cerrado. A list of all dioecious species in the regional survey is presented in the Table 4.

The pollination systems of the dioecious species (inferred from size of the flowers and from pollination observations for some taxa) are mostly related to small insects, and flowers are usually also small, though the blooming display can be impressive in some species such as *Simarouba versicolor* ST. HIL. and *Fagara rhoifolia* (LAM.) ENGL. For most of the taxa reported here, information on floral biology and pollination is still lacking. Dispersal is mainly zoochorous. The only potentially wind dispersed dioecious species, as far as was possible to assess, is *Astronium fraxinifolium* SCHOTT. Small fleshy fruits suggest that bird dispersal is important but large, probably mammal-dispersed fruits, are also frequent (e.g. *Diospyros* spp.).

3. Discussion

3.1. Local trends: The result presented here show some interesting trends which in one way or another are similar to data from other tropical communities. Male biased sex ratios, pollination by small unspecialized insects and dispersal by animals are common features of tropical dioecious woody plants (BAWA 1980a, IBARRA-MANRÍQUEZ & OYAMA 1992, but see RENNER & FEIL 1993). The species observed in the cerrado area also shared some of these features. Small unspecialized flowers visited and probably pollinated by small unspecific insects were present in most species. Only *Neea theifera* presented a rather different flower structure which may be functionally similar to that of the dioecious *Diospyros* spp. (Ebenaceae). These species are probably visited and pollinated either by very small insects, small enough to penetrate the narrow pore

which gives access to the interior of the flower, or by small Lepidoptera (as suggested by SILBERBAUER-GOTTSBERGER & GOTTSBERGER 1988). Thrips may be a pollinator of this species and also of *Pouteria ramiflora*. These insects, however, are generalist flower dwellers and are present in many different flowers of diverse pollination system. Thrip pollination activity has been recognized and studied in other tropical habitats (APPANAH 1990) but their importance in neotropical pollination is still unknown. In this study, I did not test the species for wind pollination and BULLOCK (1994) has showed that some dioecious species with unspecific pollination system may be actually wind pollinated in Central America forests. He even cited species of *Guapira* as wind pollinated, and this suggests that some of the species studied here may be facultatively wind pollinated.

All species are zoochorous but present relatively small fruit set and scattered fruit maturation. This seems to reinforce the idea that high fruit-set in order to attract dispersers is not a well defined feature of dioecious species (HERRERA 1982, LLOYD 1982).

In the studied cerrado community, the dioecious species presented male biased population but no defined spatial gender distribution pattern. Gender grouping observed in *Rapanea guianensis* is probably the result of vegetative reproduction, but was not common among the studied species. Reproductive density results in inter plant distances (13 to 70 m) smaller than the distances of 40 to 100 metres obtained for rain forest Myristicaceae in Central Amazonas (ACKERLY et al. 1990), but always larger than those cited for deciduous forest trees in Costa Rica which were under 10 metres (BAWA & OPLER 1977). Smaller distances in the latter study are probably the result of a less species rich community in Costa Rica and may turn wind pollination of dioecious species, as suggested by BULLOCK (1994), more plausible in those forests.

3.2. General trends: Dioecy has been seen as a sexual system which is characteristic of later stages of succession and primary forest. Contrastingly, it has also been related to colonizing species which invade habitats where specialized pollinators are absent such as islands or tropical high altitude areas (BAWA 1980a, LLOYD 1982, BAWA 1990). Dioecy would be the easiest way for these supposedly self-compatible invaders to increase outcrossing and genetic variability (BAWA 1980a and discussion in RENNERT & FEIL 1993 and BAWA 1994). This idea was used to suggest that dioecy would be established from dichogamous systems during the invasion of semi-open vegetation and disturbed habits by *Ocotea* and *Nectandra* species and would, consequently, be more common in these habitats (KUBITZKI & KURZ 1984). ROHER (1986) observed, however, that

dioecy in *Ocotea* was more clearly related with primary forest than with open formations.

Dioecy in the analyzed cerrado areas seems to be correlated with dense woodlands (cerradão) and gallery forests rather than with open cerrado physiognomies. These differences, however, may be simply a consequence of other reproductive characteristics associated with dioecy. Since animal dispersal seems to be less important in open cerrado than in dense woodlands and forests (GOTTSBERGER & SILBERBAUER-GOTTSBERGER 1983, OLIVEIRA & MOREIRA 1992) and dioecy is closely associated with zoochory, its frequency may be simply linked to this general pattern. Advantages of wind dispersed plants to colonize widely the cerrado areas, seasonal climate which affects animal activity, and patchy distribution of trees which reduce efficiency of animal dispersers may contribute to this general distribution of dispersal strategies (GOTTSBERGER & SILBERBAUER-GOTTSBERGER 1983, OLIVEIRA & MOREIRA 1992).

One could imagine that patchiness of floral resources, together with fire disturbance and environmental constraints in the cerrado vegetation (FURLEY & RATTER 1988), may affect the less mobile fauna which pollinates dioecious inconspicuous flowers and make pollination service unpredictable. However, these vectors also pollinate other hermaphrodite species (SILBERBAUER-GOTTSBERGER & GOTTSBERGER 1988, OLIVEIRA 1991) and are too widespread to be a specific limiting factor for the distribution of dioecious taxa. Furthermore, wind pollination, which may be an alternative for some dioecious species, would be favored in cerrado open physiognomies.

In the cerrados of Brasilia and perhaps within the cerrado region as a whole two different groups of dioecious species can be delimited. First, the treelets and shrubs of Ebenaceae (*Diospyros*), Nyctaginaceae (*Neea* and *Guapira*), Myrsinaceae (*Cybianthus* and *Rapanea*), Sapotaceae (*Pouteria*) and Symplocaceae (*Symplocos*) which are widespread in open cerrado areas. They are brevidiciduous plants (except *Rapanea guianensis* and *Pouteria*) which present irregular, inconspicuous flowering and fruit-set. Locally biased sex ratio as observed for Myrsinaceae may be common among these plants and perhaps related with vegetative regeneration. These plants will respond for the 12% of dioecious species among exclusively cerrado species.

A second group is formed by the Lauraceae (*Ocotea* and *Phoebe*), Myristicaceae (*Virola*), Rubiaceae (*Alibertia* and *Amaioua*), Simaroubaceae (*Simarouba*), Monimiaceae (*Siparuna*) which are usually forest trees occurring in gallery forests and dense woodlands (locally "cerradão") areas but also as isolated trees in cerrado. Their phenological behaviour, and also the available information on germination and establishment (A. MO-

REIRA, pers. com.) are similar to those of *Emmotum nitens* (BENTH.) MIERS., whose evergreen dense canopy and drought sensitive seedlings (MOREIRA 1987) differ from successfully adapted cerrado plants. These plants are only marginal components of open cerrado and are more closely related with the physiognomic changes towards dystrophic cerradão (FURLEY & RATTER 1988). The frequency of dioecy is thus related, in Central Brazil cerrado region, with the occurrence of such species and with dense woodlands and forest environments.

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