ANALYSIS OF THE FLORISTIC COMPOSITION OF THE BRAZILIAN CERRADO VEGETATION II: COMPARISON OF THE WOODY VEGETATION OF 98 AREAS

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An analysis was made of the floristic composition of 98 areas of cerrado and Amazonian savanna, encompassing most of the area of such vegetation in Brazil. A total of 534 species of trees and large shrubs were recorded for these areas, of which 158 (30%) occurred at a single site only. Such unicates and taxa without determinations to specific level were excluded from the study since they provide no basis for comparison. The data were analysed by three techniques of multivariate analysis: (a) a divisive hierarchical classification by Two-way Indicator Species Analysis (TWINSPAN), (b) an agglomerative hierarchical classification by UPGMA (Unweighted Pair-Groups Method using Arithmetic Averages) using the Sørensen Coefficient of Community (CC) as a measure of similarity, and (c) an ordination by Detrended Correspondence Analysis (DCA). The results from all three methods showed great similarity, demonstrating a strong geographic pattern in the distribution of the flora of the cerrado biome and allowing the recognition of southern (São Paulo and S Minas Gerais), southeastern (largely Minas Gerais), central (Federal District, Goiás and parts of Minas Gerais), central-western (largely Mato Grosso, Goiás and Mato Grosso do Sul) and northern groups (principally Maranhão, Tocantins and Pará), as well as a disjunct group of Amazonian savannas. Soil type (mesotrophic or dystrophic) is an important factor in determining floristic composition. The study demonstrated that cerrado vegetation is extremely heterogeneous: none of the 534 species occurred at all sites and only 28 species were present at 50% or more.

Keywords. Amazonian savanna, cerrado, multivariate analysis, patterns of biodiversity.

Uma análise foi feita da composição florística de 98 áreas de cerrado e savana amazônica, englobando a maior parte da área desta vegetação no Brasil. Registrou-se um total de 534 espécies de árvores e arbustos grandes, com 158 espècies (30%) ocorrendo apenas em um local. Tais unicatas e taxa sem determinações até o nível de espécie foram eliminadas das análises por não oferecem uma base para comparação. Os dados foram analisados por três técnicas de análise multivariada: (a) uma classificação hierárquica divisiva por 'Two-Way Indicator Species Analysis' (TWINSPAN), (b) uma classificação hierárquica aglomerativa por UPGMA (Unweighted Pair-Groups Method using Arithmetic Averages) usando o Coeficiente de Comunidade de Sørensen como uma medida de semelhança, e (c) uma ordenação por

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Detrended Correspondence Analysis (DCA). Os resultados de todos os três métodos apresentaram grande semelhança, indicando um padrão geográfico bem forte na distribuição da flora do bioma Cerrado. Foi possível reconhecer grupos do sul (São Paulo e S Minas Gerais), sudeste (principalmente Minas Gerais), centro (Distrito Federal, Goiás e regiões de Minas Gerais), centro-oeste (na maioria Mato Grosso, Goiás e Mato Grosso do Sul) e norte (principalmente Maranhão, Tocantins e Pará), e ainda um grupo das savanas amazônicas separadas. O tipo de solo (distrófico ou mesotrófico) é um fator importante na composição florística. O estudo indicou mais uma vez que a vegetação do cerrado é extremamente heterogênea: nenhuma das 534 espécies ocorreu em todos os sítios e só 28 espécies ocorreram em 50% ou mais das áreas.

Palavras-chave. Análise multivariada, cerrado, padrões de biodiversidade, savana amazônica.

INTRODUCTION

In 1992 we reported a comparison of the woody species of 26 areas of cerrado, representing all the survey records available to us in 1986–87 (Ratter & Dargie, 1992). The present work is an extension of that study but is now able to compare 98 areas, demonstrating the great increase in interest and research in the cerrado biome during the last eight years.

The stimulus for more intensive research comes from the realization that the cerrado biome is a unique and extremely rich centre of biodiversity (estimated as having 160,000 species of plants, animals and fungi by Dias, 1992) and is highly endangered by agricultural development. As a result of this, many studies are being undertaken of which two interlinked initiatives should be mentioned, the 'Biogeography of the Cerrados' and the 'Biodiversity of the Cerrados' projects. The former is centred at the Forestry Department of the University of Brasília (UnB) and is led by Dr Jeanine Felfili, while the latter is a collaboration between UnB and the Brazilian government cerrado research station CPAC/EMBRAPA and is led by Dr J.F. Ribeiro. Much of the data compared in the present work comes from the surveys of these two projects and targets areas for which there was little or no previous information. Similar cerrado survey work is being carried out in the north-east of Brazil by Dr Alberto Jorge F. Castro of the Federal University of Piauí who is also working on general cerrado biogeography and has recently written a thesis on these subjects (Castro, 1994a, b). Readers are referred to Ratter & Dargie (1992) for a brief background to this study.

MATERIALS AND METHODS

Floristic and environmental data

Literature was searched for floristic lists which were added to those of the 26 areas analysed by Ratter & Dargie (1992). The majority came from works confined to cerrado vegetation, but some included other vegetation types (principally gallery forest) and the habitats of species were not always indicated. In such cases only species of known cerrado occurrence were selected. Many other records came from the 1993–94 fieldwork of the Biodiversity and Biogeography of the Cerrados projects in Maranhão, Tocantins, Pará, Goiás and Amapá. Unfortunately, as in our previous study (Ratter & Dargie, 1992), the sites compared vary greatly in size and sample methodology, but in the main floristic lists for very large areas were not included. The sites range in richness of woody species from those of the cerrado core area with more than 100 species (reaching 188 in the Chapada dos Guimarães) to Amazonian savannas with only seven species. In total, data were assembled from 98 sites, covering most of the cerrado domain and including some Amazonian cerrados. The localities are listed in Table 1 and shown on the map (Fig. 1).

Only species of tree or large shrub habit were entered in the comparisons. Small and slender shrubs with woody shoots of short duration produced from a long-lived rootstock (geoxyles or hemixyles), an important growth form in the cerrado, were

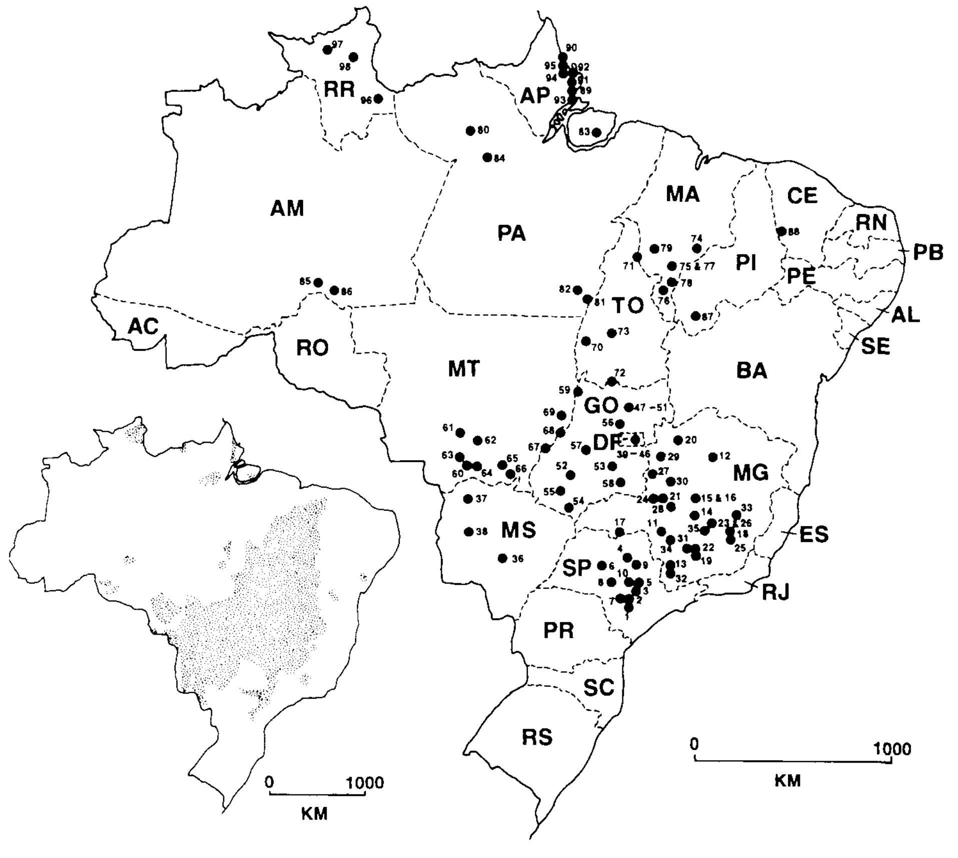

FIG. 1. Map showing sites compared in the study. See Table 1 for reference to the numbers. The inset map shows the approximate distribution of cerrado and Amazonian savanna in Brazil.

TABLE 1. Areas of cerrado (and Amazonian savanna) compared in the study. Figures in parentheses are the numbers of species recorded at only a single site; Meso. spp. = no. of indicator species of mesotrophic soils; Meso. index = no. of mesotrophic indicator species/total no. of species. Biodiv. = Biodiversity of the Cerrados project; Biogeog. = Biogeography of the Cerrados project. Asterisks indicate sites not entered in the ordination (DCA) analysis.

No.	Code	Locality	Co-ord.	No. of spp.	Meso. spp.	Meso. index	Ref.
1	SPA	Angatuba, SP	23°28'S 48°28'W	70 (5)	1	0.01	Ratter et al. (1988a)
2	SPB	Botucatu, SP	22°45'S 48°25'W	53 (2)	1	0.02	Silberbauer-Gottsberger & Eiten (1983)
3	SPC	Faz. Campininha, SP	22°15'S 47°10'W	103 (3)	3	0.03	Gibbs et al. (1983), Eiten (1963)
4	SPD	Itirapina, SP	22°08'S 47°47'W	42	0	0	Durigan et al. (1994)
5	SPE	Emas, SP	22°02'S 47°30'W	33	0	0	Ferri & Coutinho (1958)
6	SPF	Corumbataí, SP	22°15'S 47°00'W	92 (12)	3	0.03	Cesar et al. (1988)
7	SPI	Brotas-Itirapina, SP	22°15'S 47°49'W	38	0	0	Souza (1977)
8	SPL	Luis Antonio Expt. Stn, SP	21°40'S 47°49'W	62	1	0.02	Toledo-Filho (1984)
9	SPM	Mojí-Mirim, SP	22°26'S 46°57'W	90 (12)	3	0.03	Toledo-Filho et al. (1989)
10	SPV	Vaçununga, SP	21°41'S 47°37'W	70	0	0	Castro (1987)
11	MGA	Araxá, MG	19°46'S 46°55'W	39	0	0	Brandão & Gavilanes (1992)
12	MGB	Montes Claros, MG	16°45'S 43°52'W	76	9	0.12	Brandão & Gavilanes (1992)
13	MGC	Lagoa Santa, MG	19°39'S 43°44'W	110 (7)	9	0.08	Warming (1892), Brandão & Gavilanes (1992)
14	MGD	Curvelo, MG	18°45'S 44°27'W	59	6	0.1	Brandão & Gavilanes (1992), Rizzini (1975)
15	MGE	Corinto, MG	18°22'S 44°27'W	54	5	0.09	Brandão & Gavilanes (1992)
16	MGF	Felixlândia, MG	18°45'S 44°52'W	55	5	0.09	Brandão & Gavilanes (1992)
17	MGG	Triângulo Mineiro, MG	19°29'S 48°50'W	116 (13)	9	0.03	Goodland (1970)
18	MGH	Prudente de Morais, MG	19°36'S 44°04'W	58	4	0.07	Brandão & Gavilanes (1992)
19	MGI	Itumirim, MG	21°18'S 44°48'W	47	2	0.04	Brandão & Gavilanes (1992)
20	MGJ	Januária, MG	15°20'S 44°23'W	38 (1)	8	0.21	Ratter et al. (1977)
21	MGK	Patos de Minas, MG	18°34'S 46°31'W	33	1	0.03	Brandão & Gavilanes (1992)

22	MGL	Lavras, MG	21°14′S 44°59′W	69 (1)	5	0.07	Brandão & Gavilanes (1992)
23	MGM	Paraopeba, MG	19°20′S 44°20′W	60 (1)	7	0.11	Silva Junior (1984)
24	MGN	Coromandel, MG	18°20′S 47°12′W	43	1	0.02	Brandão & Gavilanes (1992)
25	MGO	Sete Lagoas, MG	19°32′S 44°06′W	69	4	0.06	Brandão & Gavilanes (1992)
26	MGP	Paraopeba, MG	19°18′S 44°25′W	60	5	0.08	Brandão & Gavilanes (1992)
27	MGQ	Paracatú, MG	17°00′S 46°45′W	53	1	0.02	Felfili & Silva Junior (1993)
28	MGR	Patrocínio, MG	18°47′S 46°25′W	57	1	0.02	Felfili & Silva Junior (1993)
29	MGS	Sagarana, MG	16°00′S 47°00′W	48	14	0.27	Ratter et al. (unpubl.)
30	MGT	Trés Marias, MG	18°12′S 45°10′W	55	6	0.11	Brandão & Gavilanes (1992)
31	MGU	Uberaba, MG	19°47′S 47°57′W	35	0	0	Brandão & Gavilanes (1992)
32	MGV	Campo do Meio, MG	21°06′S 45°50′W	56	1	0.02	Carvalho (1987)
33	MGW	Alpinópolis, MG	20°55′S 46°15′W	46	0	0	Carvalho (1987)
34	MGX	Pimenta, MG	20°30′S 45°50′W	73	4	0.05	Carvalho (1987)
35	MGY	Pedro Leopoldo, MG	19°39′S 44°03′W	28	2	0.07	Rizzini (1975)
36	MSF	Campo Grande, MS	20°24′S 54°35′W	25	2	0.08	Ferri & Coutinho (1958)
37	MSP	Fazenda Acurizal, MS	17°45′S 57°37′W	57 (11)	18	0.3	Prance & Schaller (1982)
38	MSR	Fazenda Nhumirim, MS	18°59′S 56°39′W	88 (2)	17	0.19	Pott et al. (1986)
39	DFB	São Bartolomeu, DF	15°50′S 47°30′W	137	6	0.04	Pereira et al. (1985)
40	DFE	E. E. das Aguas Emendadas, DF	15°31′S 47°32′W	65	1	0.01	Felfili & Silva Junior (1993)
41	DFF	Fazenda Agua Limpa, DF	15°45′S 47°57′W	130	4	0.03	Ratter (1986)
42	DFG	APA Gama. da Cab. Vead., DF	15°52′S 47°50′W	59	1	0.02	Felfili & Silva Junior (1993)
43	DFI	Res. Ecol. do IBGE, DF	15°55′S 47°53′W	114 (1)	6	0.05	Pereira et al. (1993)
44	DFJ	Jardim Botânico, Brasília, DF	15°48′S 47°50′W	79	5	0.06	Fundação Zoobotânica (1990)
45	DFN	Brasília National Park, DF	15°37′S 47°54′W	52	0	0	Felfili & Silva Junior (1993)
46	DFP	Planaltina, DF	15°39′S 47°38′W	111 (1)	1	0.01	Ribeiro et al. (1985)
47	GOA	Chapada dos Veadeiros, GO	14°07′S 47°31′W	54	1	0.02	Biodiv. & Biogeog. (unpubl.)
48	GON	Chapada dos Veadeiros, GO	14°07′S 47°13′W	59	15	0.25	Biodiv. & Biogeog. (unpubl.)

TABLE 1. *(cont.)*

No.	Code	Locality	Co-ord.	No. of spp.	Meso. spp.	Meso. index	Ref.
49	GOR	Chapada dos Veadeiros, GO	14°07'S 47°16'W	89	27	0.3	Biodiv. & Biogeog. (unpubl.)
50	GOT	Chapada dos Veadeiros, GO	13°55'S 47°23'W	62 (18)	0	0	Biodiv. & Biogeog. (unpubl.)
51	GOV	Chapada dos Veadeiros, GO	14°02'S 47°26'W	51	0	0	Biodiv. & Biogeog. (unpubl.)
52	GOC	Caiapônia, GO	16°57'S 51°49'W	125 (2)	22	0.17	Biodiv. & Biogeog. (unpubl.)
53	GOG	Goiânia, GO	16°43'S 49°18'W	29	0	0	Ferri & Coutinho (1958), Rizzo et al. (1972)
54	GOJ	Jataí, GO	17°58'S 51°45'W	61	6	0.1	Biodiv. (unpubl.)
55	GOM	Caiapônia & Mineiros, GO	17°22'S 52°10'W	58	15	0.26	Biodiv. (unpubl.)
56	GOP	Padre Bernardo, GO	15°15'S 48°30'W	83 (2)	15	0.18	Ratter et al. (1977)
57	GOS	Serra Dourada, GO	16°22'S 50°20'W	40	0	0	Rizzo (1970)
58	GOW	Silvânia, GO	16°30'S 48°30'W	64	2	0.03	Felfili & Silva Junior (1993)
59	MTB	Base Camp, MT	12°49'S 51°46'W	129 (12)	19	0.14	Ratter et al. (1973)
60	MTC	Chapada das Guimarães, MT	15°21'S 55°49'W	188 (12)	19	0.1	Oliveira-Filho (1984)
61	MTG	Mun. de Cuiabá, MT	15°32'S 56°05'W	23	4	0.17	Guarim Neto et al. (1994)
62	MTN	Cuiabá, MT	15°36'S 56°06'W	37	3	0.08	Nascimento & Saddi (1992)
63	MTO	Baixada Cuiabana, MT	15°30'S 56°02'W	111	21	0.18	Oliveira-Filho & Martins (1991)
64	MTP	Poconé, MT	16°16'S 56°37'W	34 (1)	18	0.51	Ratter et al. (1988b)
65	MTR	Rondonôpolis, MT	16°29'S 54°37'W	94	15	0.16	Biodiv. (unpubl.)
66	MTS	Serra da Petrovina, MT	16°47'S 54°06'W	94	20	0.21	Biodiv. (unpubl.)
67	MTT	Torixoreu,MT	15°53'S 52°23'W	53 (1)	18	0.33	Furley et al. (1988)
68	MTV	Vale de Sonhos, MT	15°00'S 52°13'W	72	12	0.16	Ratter et al. (1977)
69	MTX	Nova Xavantina, MT	14°45'S 52°20'W	121 (1)	14	0.11	Ratter et al. (1973)
70	TOA	Ilha do Bananal, TO	10°26'S 50°25'W	106 (7)	13	0.12	Ratter (1987)
71	TOB	Fazenda Bragança, TO	06°53'S 47°48'W	34	2	0.06	Biodiv. (unpubl.)

72	TOF	10km S of Figueirópolis, TO	12°04′S 49°10′W	76 (1)	13	0.17	Biodiv. (unpubl.)
73	TOH	Fazenda Belo Horizonte, TO	10°05′S 48°55′W	60	9	0.15	Biodiv. (unpubl.)
74	MAB	Rio Balsinha, MA	07°30′S 46°05′W	43	1	0.02	Biodiv. (unpubl.)
75	MAC	Carolina, MA	07°07′S 47°25′W	63	2	0.03	Biodiv. (unpubl.)
76	MAF	Fazenda Parnaiba, MA	07°30′S 46°05′W	60	11	0.18	Biodiv. (unpubl.)
77	MAM	Carolina, MA	07°07′S 47°25′W	21	9	0.41	Biodiv. (unpubl.)
78	MAP	Pé de Galinha, MA	07°45′S 45°50′W	62	10	0.16	Biodiv. (unpubl.)
79	MAQ	Pedra Caída, MA	06°57′S 47°28′W	62 (1)	1	0.02	Biodiv. (unpubl.)
80	PAA*	Ariramba, PA	01°10′S 55°35′W	24	0	0	Egler (1960)
81	PAC	Fazenda Chocolate, PA	08°21′S 50°00′W	64 (1)	9	0.14	Biodiv. (unpubl.)
82	PAG	Fazenda de Prof. Getulinho, PA	08°21′S 50°06′W	66	8	0.12	Biodiv. (unpubl.)
83	PAM*	Marajó, PA	00°45′S 48°30′W	20	1	0.05	Bastos (1984)
84	PAS	Alter do Chão, PA	02°36′S 54°56′W	49 (1)	2	0.04	Sanaiotti (1991), Branch & Silva (1983), Miranda (1993)
85	AMG*	Humaitá, AM	07°31′S 63°00′W	17	0	0	Gottsberger & Morawetz (1986)
86	AMH	Humaitá, AM	07°40′S 63°00′W	46 (9)	1	0.02	Janssen (1980)
87	PIC	Uruçuí-Una, PI	08°50′S 44°10′W	37 (1)	2	0.05	Castro (1986)
88	CES*	Sertão de Salgado, CE	06°38′S 39°30′W	20	2	0.1	Figueiredo (1987)
89	APA*	APA de Curiaú, AP	00°20′N 51°03′W	17	0	0	Sanaiotti et al. (1996)
90	APC*	5km S of Calçoene, AP	02°27′N 50°33′W	6 (1)	0	0	Sanaiotti et al. (1996)
91	APE*	EMBRAPA Stn., AP	00°37′N 51°05′W	19	1	0.05	Sanaiotti et al. (1996)
92	APG*	Gleba de Pedreira, AP	00°40′N 51°45′W	19 (1)	0	0	Sanaiotti et al. (1996)
93	APM*	36km N of Macapá, AP	00°20′N 51°05′W	15	0	0	Sanaiotti et al. (1996)
94	APN*	114km N of Macapá, AP	00°46′N 51°18′W	11	0	0	Sanaiotti et al. (1996)
95	APT*	Tartarugalzinho, AP	01°40′N 50°50′W	7	0	0	Sanaiotti et al. (1996)
96	RRD*	Roraima, RR	03°48′N 59°46′W	6 (1)	0	0	Dantas & Rodrigues (1982)
97	RRM*	Ilha da Maracá, RR	03°22′N 61°26′W	8 (3)	0	0	Milliken & Ratter (1989)
98	RRT*	Boa Vista, RR	03°20′N 61°26′W	11	1	0.09	Takeuchi (1960)

excluded. In some cases it is difficult to decide whether a species should qualify for inclusion or not and readers may disagree with some of the choices. As yet, data are insufficient to allow extensive phytogeographic comparisons including species of the 'ground layer' ('vegetação rasteira'). In the rare instances where detailed floristic lists including the ground layer are available (e.g. Ratter, 1986; Pereira et al., 1993), they record four to six times the number for small species as for trees, and thus collection of data is a much greater task. A list of the taxa used in the analyses is given in Appendix 1; all are identified to species level since taxa with less complete determinations (vernacular name, etc.) do not provide a reliable basis for comparison.

Detailed soil data are available for some studies but there is no information for many sites. However, presence of mesotrophic soils in areas where no soil analyses are available is inferred by the occurrence of indicator species of richer soils (see Ratter et al., 1977, 1978), marked in bold in Appendix 1. A 'Mesotrophic Index' consisting of the no. of mesotrophic soil indicator species/total no. of species was calculated for all sites as a basis for comparison. Such an index is of some use, but a 'Mesotrophic Importance Index' based on Importance Value Index, Cover Value Index or basal area would be much better, since in many mesotrophic communities the indicator species have high values for these parameters, while many other species are present but relatively unimportant as constituents of the total vegetation. Unfortunately, however, data are not available to calculate a mesotrophic importance index for most of the sites considered.

Data analysis

The general approach used is the same as in Oliveira-Filho & Ratter (1995), which is essentially similar to that of Ratter & Dargie (1992) but with the addition of the agglomerative hierarchical classification based on the Sørensen Coefficient of Community.

Three techniques of multivariate analysis, corresponding to different methodological approaches, were used. The purpose was to seek patterns that could be accentuated in common by different analytical procedures. The techniques were: (a) a divisive hierarchical classification by Two-way Indicator Species Analysis (TWINSPAN) (Hill, 1979), (b) an agglomerative hierarchical classification by UPGMA (Unweighted Pair-Groups Method using Arithmetic Averages) using the Sørensen Coefficient of Community (CC) as a measure of similarity (Kent & Coker, 1992), and (c) an ordination by Detrended Correspondence Analysis (DCA) (Hill & Gauch, 1980).

For DCA and TWINSPAN, we used the versions contained in the package VESPAN 11 (Malloch, 1988). The floristic matrix analysed by both methods had 376 species and 98 areas as a result of the elimination of 158 species occurring in only one area, following the procedures described in Ratter & Dargie (1992). However, we carried out UPGMA analyses using both the floristic matrix with elimination of unicates, as used for DCA and TWINSPAN, and the full matrix with 534 species. The CCs were calculated with a program written in FORTRAN and processed by the package NTSYS (Rohlf, 1992) in order to produce the clustering dendrogram.

RESULTS AND DISCUSSION

A total of 534 species were recorded in the 98 areas, of which 158 (30%) are unicates occurring only at a single locality. Appendix 1 gives a list of species occurring at more than one site and the number of sites at which they occurred, while Appendix 2 lists the unicates. Space does not allow the table of species occurrence at all sites to be reproduced here but copies are available from the authors. As in our previous study (Ratter & Dargie, 1992), none of the species occurs at all sites, but the most widespread species is again *Qualea grandiflora* which has 80 occurrences (=81.6%). Only the 28 species listed in Table 2 were recorded at 49 (50%) or more of the sites.

It is interesting that Ratter & Dargie (1992) recorded 485 species from only 26 areas and of these 230 were unicates. Thus, despite a near quadrupling of the number of sample sites, species recorded have only increased by 10% while, as expected, the number of unicates has fallen quite steeply: clearly the species/site curve is flattening off. However, the number of species occurring at a high percentage of sites has actually declined with the increase of the comparison from 26 to 98 areas. Ratter & Dargie (1992) recorded 27 species occurring in 15 or more sites (=58% of the 26 sites sampled); however, it is more logical to use the figure for 50% (13 sites) and this increases the number of species in common to 41. Thus, in these terms, we see an increase in heterogeneity, since 41 species were common to 50% of the sites in

TABLE 2. Species occurring at 49 (50%) or more sites. The figures indicate the percentage of sites where the species occurs, with equivalent values from Ratter & Dargie (1992) in parentheses.

Acosmium dasycarpum	60% (53%)	*Hymenaea stigonocarpa*	66% (58%)
Annona crassiflora	52% (42%)	*Kielmeyera coriacea*	65% (58%)
Astronium fraxinifolium	52% (54%)	*Lafoensia pacari*	62% (58%)
Bowdichia virgilioides	76% (73%)	*Machaerium acutifolium*	55% (58%)
Brosimum gaudichaudii	53% (50%)	*Pouteria ramiflora*	51% (58%)
Byrsonima coccolobifolia	71% (77%)	*Qualea grandiflora*	82% (88%)
B. verbascifolia	55% (61%)	*Q. multiflora*	54% (61%)
Caryocar brasiliense	66% (69%)	*Q. parviflora*	60% (69%)
Connarus suberosus	60% (69%)	*Roupala montana*	62% (50%)
Copaifera langsdorfii	51% (50%)	*Salvertia convallariodora*	53% (54%)
Curatella americana	71% (77%)	*Tabebuia aurea*	56% (69%)
Dimorphandra mollis	65% (65%)	*T. ochracea*	57% (35%)
Erythroxylum suberosum	54% (65%)	*Tocoyena formosa*	58% (73%)
Hancornia speciosa	51% (42%)	*Xylopia aromatica*	57% (58%)
			Total: 28 species

Ratter & Dargie (1992) but only 28 species in the present more extensive study. Percentage occurrences for these 28 species in both studies are given in Table 2; in the main they show a high degree of correspondence.

Seventeen species recorded with an occurrence of 50% or more in Ratter & Dargie (1992) are not in the present top 28 (Table 2). These are, with percentage occurrences in this study followed by those in Ratter & Dargie (1992) in parentheses: *Annona coriacea* 42% (50%), *Aspidosperma tomentosum* 42% (65%), *Casearia sylvestris** 48% (65%), *Cochlospermum regium** 20% (50%), *Davilla elliptica** 40% (61%), *Eriotheca gracilipes* 32% (50%), *Erythroxylum tortuosum** 37% (58%), *Magonia pubescens* 38% (61%), *Plathymenia reticulata* 47% (58%), *Sclerolobium aureum* 40% (54%), *Strychnos pseudoquina* 40% (50%), *Stryphnodendron adstringens* 44% (54%), *Terminalia argentea* 38% (58%), *Vatairea macrocarpa* 41% (54%), and *Vernonia ferruginea** 21% (54%). Of these, the species marked with an asterisk are usually small and have probably been excluded from many surveys because they failed to reach qualifying size.

The species list (Appendix 1) can be used to give an idea of the most abundant and widespread cerrado tree species; for instance, the 98 species with 20 or more occurrences could be taken as a reasonable working list of the commonest tree species of the cerrado. It is interesting that some of these widely dispersed species seem in our experience to be always of sparse occurrence, e.g. *Cybistax antisyphilitica* and, to a lesser extent, *Agonandra brasiliensis*.

Multivariate analyses

The multivariate analyses of the floristic data show a great deal of coincidence in the patterns arising from the three techniques used. All demonstrate a similar geographic pattern in the groupings obtained. A detailed description and discussion of the results are given below.

1. Divisive hierarchical classification (TWINSPAN) site hierarchy

The site hierarchy produces 12 groups after four levels of division (Fig. 2). A fifth level of division gives 19 groups but, in the main, those produced by only four divisions are more meaningful and for this reason are the groups we discuss below. Details of the divisions and the indicator species on which they are partly based are too lengthy to reproduce here but are available from the authors. The groupings produced by the analysis are mapped in Fig. 3.

Interpretation of grouping. The main features of groups and group sets are as follows:

Group 1: This group comprises three diverse localities in São Paulo, Mato Grosso do Sul and Goiás, all recorded in the pioneer study of Ferri & Coutinho (1958), together with one from Humaitá, Amazonas (86 AMH). The species totals of the first three localities are low (33, 24 and 29 respectively) and they are the only sites

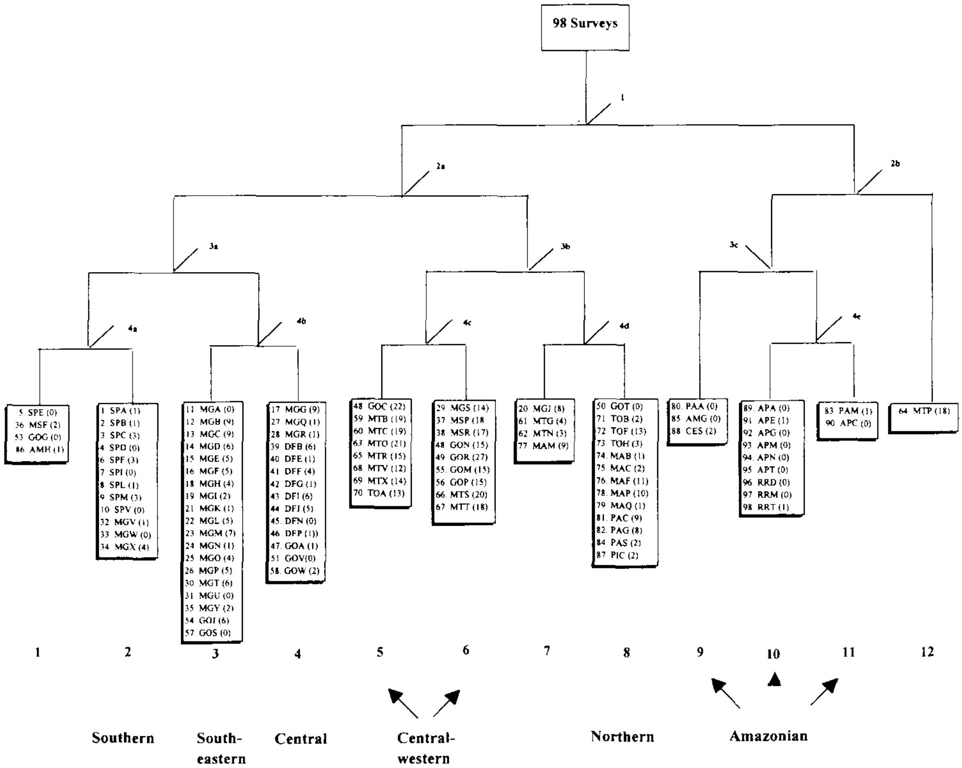

FIG. 2. Site hierarchy derived from TWINSPAN data analysis. Site codes as in Table 1. Figures in parentheses after site code represent the number of mesotrophic soil indicator species for that location. The figures below are the group numbers discussed in the text.

lacking any unicate species. Forty-six species are recorded for the Humaitá site of which nine are unicates.

Group 2: This is a geographically very natural group consisting of all 10 São Paulo sites included in the analysis, apart from the anomalous 5 SPE in Group 1, and three sites from the Rio Grande region of southern Minas Gerais, close to the São Paulo border (Carvalho, 1987). A further (fifth) level of division separates the Minas from the São Paulo sites. All of the sites show low occurrences of mesotrophic indicator species.

Group 3: Like the previous, this forms a clearly natural group. It consists of 17 sites from Minas Gerais, covering most of the latitudinal and longitudinal range of the state, and two in the southern part of Goiás. The number of mesotrophic indicator species in most of the sites is relatively low.

Group 4: This again is a very natural group. It consists of 13 sites from the Federal District, Minas Gerais and Goiás. As in the previous groups, the number of mesotrophic species in most of the sites is relatively low.

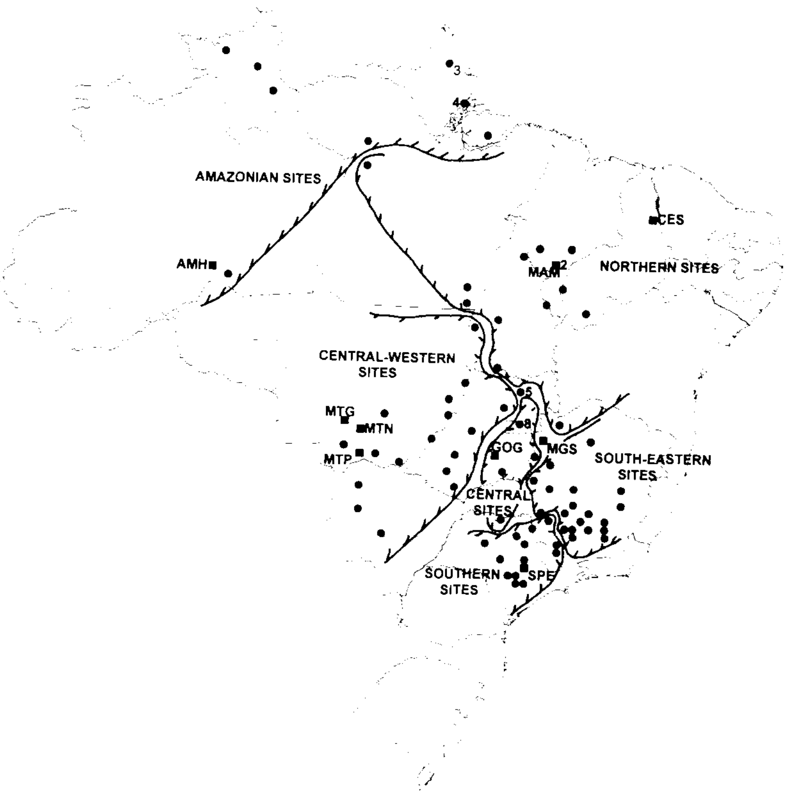

FIG. 3. Map showing the geographical pattern of the groups defined by TWINSPAN. Southern sites are group 2; southeastern, 3; central, 4; central-western, 5 & 6; northern, 8; disjunct Amazonian, 9–11. Where two or more sites are in close proximity they are represented by a single dot with a figure denoting the number of sites. 'Misclassified' sites are indicated by solid squares and code-letters.

Groups 5 & 6: These contain the sites rich in mesotrophic indicator species and have a strong floristic affinity despite the level of division separating them. They are from the states of Goiás, Mato Grosso, Mato Grosso do Sul, Tocantins on the Mato Grosso border (Ilha do Bananal) and, in one case, northern Minas Gerais (Sagarana).

Group 7: This consists of two sites from Cuiabá, Mato Grosso, one from Januária, northern Minas Gerais, and one from Carolina, Maranhão, all of which have relatively small numbers of species. The Carolina site has the highest mesotrophic index recorded in the study (nine mesotrophic species out of 22 recorded = 0.41) and the index is also very high for Januária (0.21).

Group 8: This is another geographically natural group, as can be seen on the maps (Figs 1, 3). It has a northern distribution in the states of Maranhão, Piauí, Tocantins and Pará, but includes a single site from Goiás (56 GOP). The disjunct cerrado at

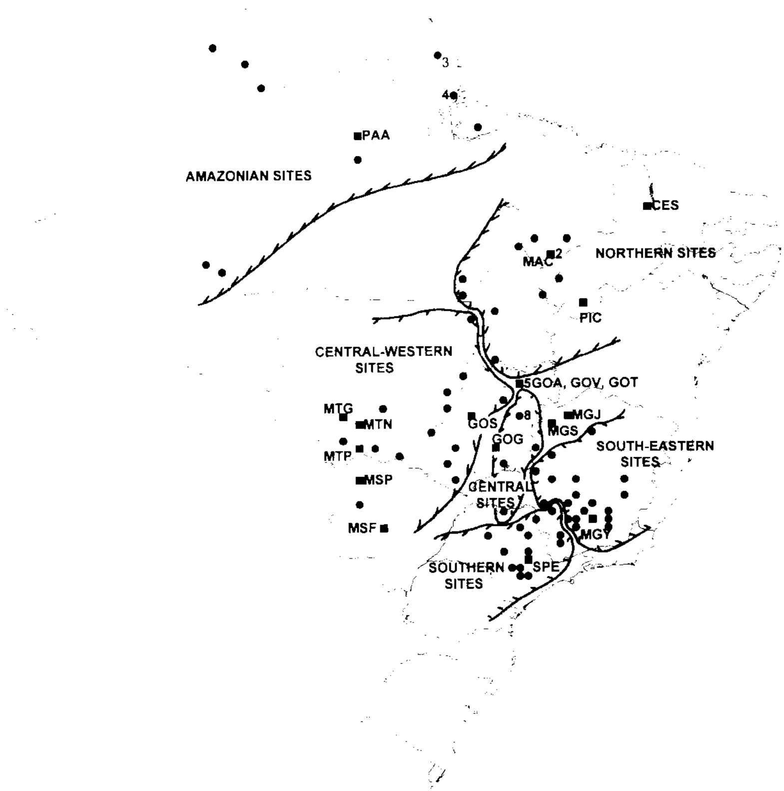

FIG. 4. Map showing the geographical pattern of the groups defined by UPGMA. Where two or more sites are in close proximity they are represented by a single dot with a figure denoting the number of sites present. 'Misclassified' sites are indicated by a solid squares and code-letters.

Alter do Chão, Pará, which is comparatively species-rich in terms of isolated Amazonian sites, is included in this group but separates from the other sites at the next (fifth) level of division.

Groups 9, 10 & 11: With the exception of an anomalous site in Ceará falling into Group 9, these are all species-poor Amazonian savannas, the majority situated north of the River Amazon.

Group 12: This consists of one site only, Poconé in the Mato Grosso Pantanal (64 MTP). It was separated from all the other 'core area' sites by the uppermost dichotomy in the classification, and seems to be misclassified. In the original analysis of 26 areas by Ratter & Dargie (1992) it was grouped with another Pantanal site from Mato Grosso do Sul (38 MSR) and another Mato Grosso site (67 MTT), all of which were regarded as misclassified. These three sites all have high numbers of mesotrophic soil indicator species and, intuitively, it was thought they should be correctly placed amongst the groups showing this character. This has, in fact, happened in the present analysis for both MSR and MTT which are now classified in Group 6. MTP, however, remains literally 'out on a limb', classified on the branch of the disjunct Amazonian sites.

Classification pattern summary. Various features emerge from the interpretation of the classification hierarchy. The first is a strong geographical pattern of grouping (see Figs 2, 3) with southern sites (Group 2, São Paulo and southern Minas Gerais), southeastern sites (Group 3, largely Minas Gerais), central sites (Group 4, Federal District, Goiás and parts of Minas Gerais), central-western sites (Groups 5 & 6, largely Mato Grosso, Goiás and Mato Grosso do Sul) and northern sites (Group 8, Maranhão, Tocantins, Piauí and Pará), as well as the disjunct group of Amazonian savannas (Groups 9–11). The second is the distinction of groups with largely dystrophic soils (Groups 1–4 and, to some extent, 7 and 8) from those with more mesotrophic soils (Groups 5 & 6), as judged by the presence of indicator species, backed up in many cases by soil analyses. Such soil differences often over-ride spatial proximity, producing strong beta-diversity (Whittaker, 1967) in a small geographical area, as shown for example by the separation of the dystrophic (Group 4) and mesotrophic sites (Group 6) from the Chapada dos Veadeiros, Goiás. More minor features indicate a number of under-recorded sites in Group 1, and at least one grossly misclassified site (64, Mato Grosso, Poconé, Group 12).

2. Agglomerative hierarchical classification (UPGMA)

Analyses were made using (i) the same data matrix as for TWINSPAN and DCA, and (ii) the full data matrix of 534 species. The former uses a slightly modified Sørensen Coefficient of Community since unicate species (occurring at only a single site) are excluded. Both of these analyses showed a high level of correspondence and produced the same recognizable patterns as in TWINSPAN, but that derived from the matrix minus unicates was undoubtedly superior in terms of geographical fit and other factors. The explanation of this is perhaps that addition of unicates produces irrelevant 'noise': many of them are undoubtedly 'rogues', including, for instance, non-cerrado species from bordering vegetation types (gallery forests, etc.), misidentifications, unrecognized synonyms, etc. The analysis reported here is therefore that based on the data matrix with unicates excluded. There seems to be little point in publishing the other and giving details of the minutiae by which the two differ; however, these data are available from the authors.

Most patterns already indicated by TWINSPAN appear in the UPGMA dendrogram (Fig. 5), the map (Fig. 4) and the Minimal Spanning Tree (Fig. 6); in fact the correspondence between the two approaches is extremely close, as demonstrated by the two maps (Figs 3, 4). This close agreement of the results derived from the two methods coincides with the findings of Oliveira-Filho & Ratter (1995) in a similar study of species distribution patterns in Central Brazilian forests. The main features of the classification and differences between it and TWINSPAN are dealt with below.

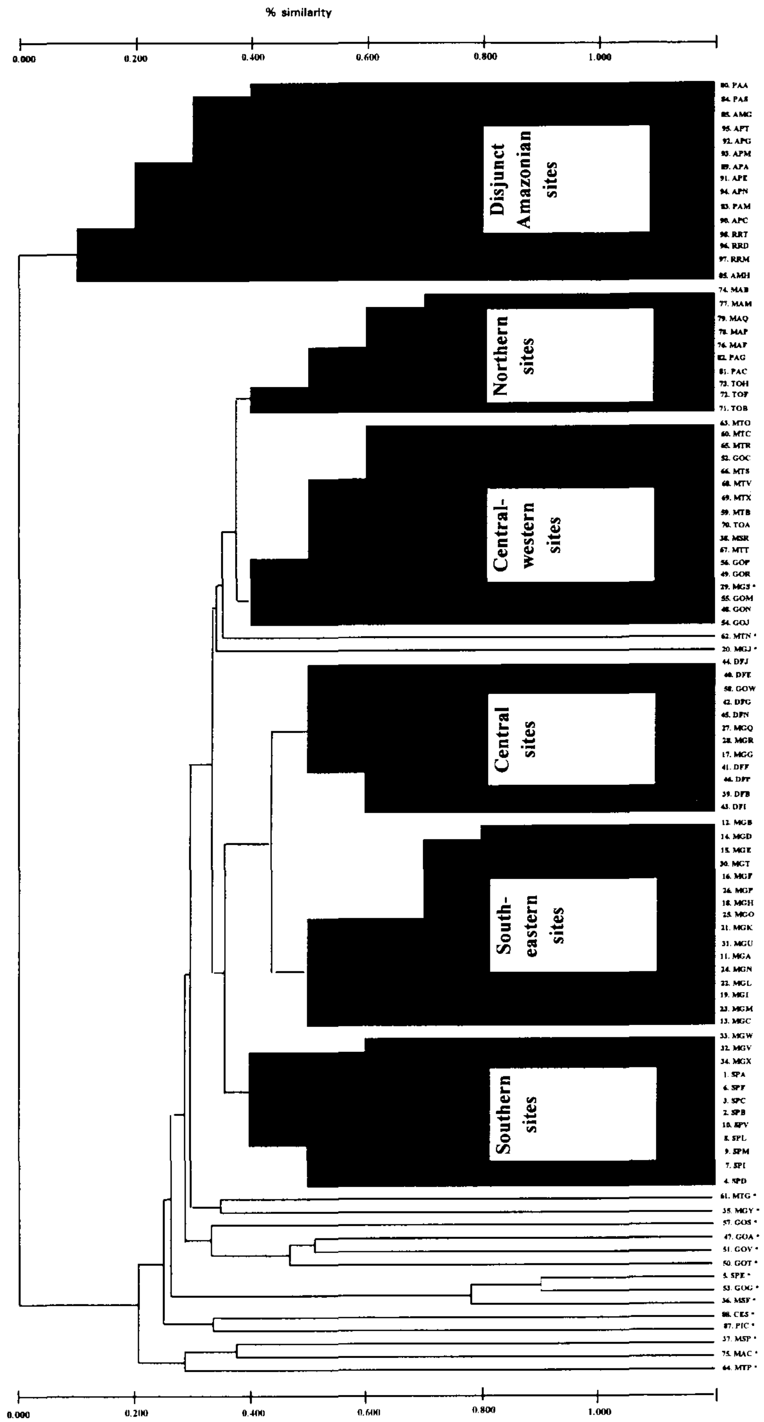

FIG. 5. Similarity dendrogram yielded by UPGMA, using Sørensen Coefficients of Community. Site codes as in Table 1. 'Misclassified' sites indicated by asterisks.

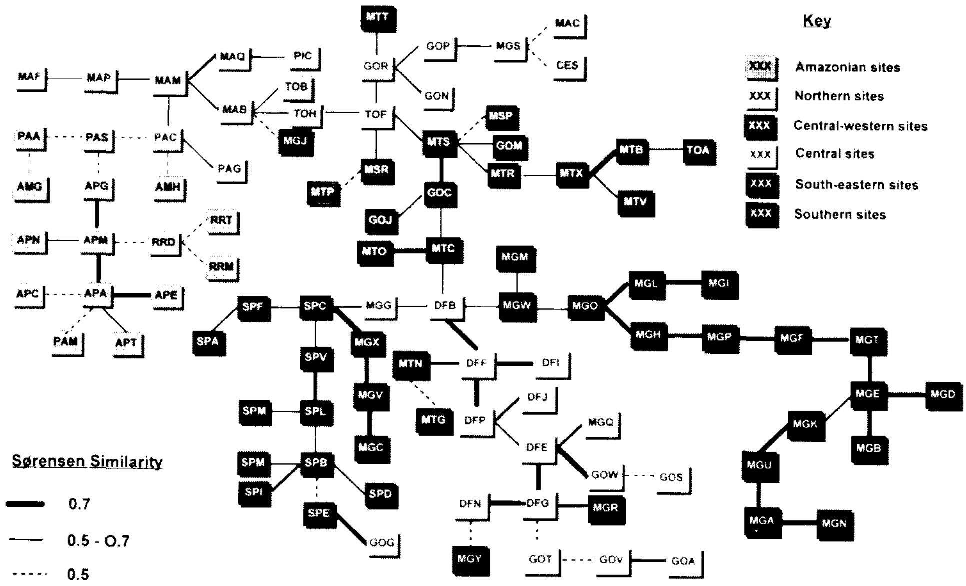

FIG. 6. Minimal spanning tree of Sørensen Coefficients of Community. Site codes as in Table 1 but without numbers.

The southern sites (Fig. 5) coincide exactly with TWINSPAN Group 2, comprising nine sites from São Paulo and three sites from Minas Gerais close to the São Paulo border.

The central sites correspond to Group 4 of TWINSPAN, while the southeastern consist of Group 3 with one Minas site (35 MGY) and the two Goiás sites (54 GOJ and 57 GOS) removed. The southeastern group as defined by UPGMA consists of 16 sites covering most of the state of Minas Gerais.

The central-western sites of Fig. 5 correspond to Groups 5 and 6 of TWINSPAN Fig. 2, consisting of sites rich in mesotrophic indicator species and showing a strong geographic relationship. Site 50 GOJ (Goiás, Jataí) has now been classified within this group, nearest to its closest neighbour, 51 GOM (Goiás, between Caiapônia and Mineiros), lying only 80km distant. By TWINSPAN 50 GOJ was placed in Group 3 with another site from Goiás and two from Minas Gerais. The TWINSPAN classification could be defended but certainly that provided by UPGMA is more natural.

The northern sites of Fig. 5 consist of Group 8 of TWINSPAN but with the removal of the single Piauí site (87 PIC) and the aberrant Goiás 56 GOT. The group as defined by UPGMA is now confined to Maranhão, Tocantins and Pará.

The disjunct Amazonian savannas of the UPGMA classification include all sites placed in Groups 9–11 of TWINSPAN with the addition of the Alter do Chão, Pará (84 PAS) and Humaitá, Amazonas (86 AMH) sites. Obviously the inclusion of the last two sites in this grouping is logical. The inclusion by TWINSPAN of Humaitá in the very anomalous Group 1 seems to have little or no natural basis and can be considered a misclassification, but on the other hand the classification of Alter do Chão in the main Pará, Maranhão and Tocantins group (8) seems to indicate a real affinity. The UPGMA classification also removes the misclassified Ceará site, 88 CES, from the disjunct Amazonian category, where it was placed by TWINSPAN in Group 9, while the very anomalous Mato Grosso Poconé (64 MTP) from the Pantanal is also removed from this branch. The Minimal Spanning Tree (Fig. 6) demonstrates that the similarity indices between these disjunct Amazonian sites are in general much lower than those occurring in the other groupings.

Outside these main natural groupings there remain 16 sites, many of which are anomalous in their classification, and once again these largely correspond in both UPGMA and TWINSPAN. One natural group amongst these consists of three cerrado rupestre sites from the Chapada dos Veadeiros (47 GOA, 57 GOV and 56 GOT) which were rather unnaturally divided between Groups 4 and 8 by TWINSPAN. The three sites of Ferri & Coutinho (1958) in Group 1 of TWINSPAN also remain together in the UPGMA classification. Low species number is a characteristic of some of these sites which are difficult to fit into any groups of natural affinity (see Table 1).

3. Ordination (DCA)

The ordination of the sites on the two principal axes is given by Fig. 7. Fourteen disjunct Amazonian sites and other outliers were not entered in the analysis, since their inclusion caused excessive clumping of the other sites. The results agree closely with those given by TWINSPAN and Sørensen/UPGMA, showing similar groupings of southern, southeastern, central, central-western and northern sites.

It is interesting to see the positions of some of the sites regarded as perhaps misclassified by TWINSPAN. Alter do Chão (84 PAS) is placed in the northern group close to the other Pará sites; this is fairly close to its TWINSPAN classification in which it constitutes a separate group most closely related to the other northern sites. It is striking that the Poconé site (64 MTP), placed so much 'out on a limb' by TWINSPAN, is in the same position here.

DCA does not enforce a dichotomous hierarchy and the correspondence of the groupings produced by it with those from TWINSPAN and Sørensen/UPGMA show that the patterns of the data set are not being obscured by the imposition of a hierarchy in the latter two methods.

GENERAL DISCUSSION AND CONCLUSIONS

The most striking result of this study is the demonstration of a very strong geographical pattern in the distribution of the flora of the cerrado biome. This emerges from all three methods of analysis, which in themselves show a remarkable level of agreement. Such a pattern was indicated by Ratter & Dargie (1992) but the increase in the number of sites compared from 26 to 98 provides much more reliable information.

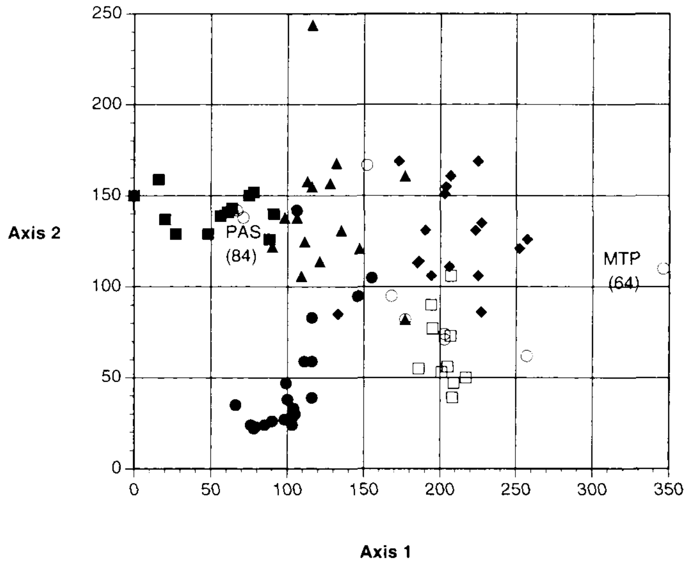

FIG. 7. Ordination of the sites on the first two DCA axes. To avoid excessive clumping of the other sites, some disjunct Amazonian sites and other outliers are not included. These are marked by asterisks in Table 1. The symbols give the geographical groups indicated by TWINSPAN and UPGMA: ■, southern; ● , southeastern; ▲, central; ◆, central-western; □, northern; ○, misclassified. 64 MTP = Poconé, Mato Grosso, and 84 PAS = Alter do Chão, Pará (see text, p. 169).

We do not consider that the patterns so far discovered are sufficient to postulate firm phytogeographic subprovinces within the cerrado region: the terms we have used (southern, southeastern, central, central-western, northern, and disjunct Amazonian) refer to objectively demonstrated groupings, but more information is necessary before they can be defined with rigour. However, the ever-increasing research referred to in the introduction means that there should soon be much more information available for accurate formulation of biogeographic patterns in the cerrado biome. It is particularly interesting that the results of the comparable research of A.A.J.F. Castro (1994a, b) seem largely in accord with our own. In the future, a synthesis of the two studies should provide very valuable conclusions.

Climate, and particularly overall precipitation and length of dry season, are undoubtedly important factors in the distribution of cerrado vegetation. The recent work of L.H.R. de Castro et al. (1994) has demonstrated great variability in these factors and identified at least five precipitation groups within the cerrado region. These groups differ particularly in duration and time of occurrence of the dry season. As would be expected, the groups show a strong geographic pattern and a detailed correlation of them with our phytogeographic data is a priority for future work. Other environmental factors, such as the effect of altitude, are also of great importance and will have to be studied in the future.

A number of other points emerge from, or are emphasized by, this study. For instance, as shown in previous research (e.g. Ratter et al., 1977; Ratter & Dargie, 1992), occurrence of mesotrophic soils in cerrado areas is a factor of great importance, since there is a characteristic flora associated with such soils. A large number of mesotrophic sites, principally from Mato Grosso, Mato Grosso do Sul and Goiás, are grouped together by all three analysis techniques used in this study. Information is also shed on the isolated Amazonian savannas included in the analysis. Of these, only Alter do Chão, Pará (84 PAS) and Humaitá, Amazonas (86 AMS), with 48 and 46 species recorded respectively, really seem to represent disjunct islands of species-rich cerrado. The rest are floristically depauperate areas dominated by a few species, usually of the cerrado flora, and often fall into the category of hydrologic savanna.

ACKNOWLEDGEMENTS

The authors are very grateful to a large number of people whose contribution to our work was of fundamental importance. A great deal of the data on which the study is based came from as yet unpublished surveys of the Biogeography of the Cerrados and the Biodiversity of the Cerrados projects in which at least two dozen people participated. Amongst the leading contributors to these projects were Profs Jeanine Felfili, Manoel C.D. da Silva, Carolyn Proença, Alba Rezende, Paulo E. da Silva and Sra Cássia Munhoz of the University of Brasília and Bruno Walter (CENARGEM/EMBRAPA). Tânia Sanaiotti (INPA, Manaus) played a very important part in the surveys in Maranhão, Tocantins, Pará and Amapá. Srs Joaquim Fonsêca, Valdir de Lima, José Paixão, João dos Santos and Nelson País (of CPAC) and Edson Cardoso, Newton Oliveira and Marco Silva (of the University of Brasília) carried out a great deal of the fieldwork of the expeditions; we particularly wish to acknowledge their expertise in field identification of plants and the cheerful competence with which they accomplished the myriad logistic tasks. Dr João Ferraz (INPA, Depto de Silvicultura) took official responsibility and arranged the permit for our 1993 fieldwork in Amazônia Legal. Prof. Ary T. Oliveira Filho (Federal University of Lavras, Minas Gerais) and Dr T.C.D. Dargie (independent consultant) gave invaluable encouragement, advice and help with the techniques of analysis. We thank Prof. Alberto Jorge de Castro (Federal University of Piauí) for stimulating discussions and the invitation to present part of our results at the XVII Reunião Nordestina de Botânica.

The Baring Foundation provided a Research Fellowship for Sam Bridgewater and for some months to Ruth Atkinson. Much of the work, both in the field and the UK, including support of Ruth Atkinson, was funded by the European Community financial contribution B92/4-3040/9304.

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Received 30 October 1995; accepted 26 February 1996

APPENDIX 1

Species used in the analyses (present at two or more localities). The figures give the number of sites at which species occur. Species indicating richer (mesotrophic) soils are in bold.

***Acacia paniculata* Willd.** 8
Acosmium dasycarpum (Vogel) Yakovlev 59
A. subelegans (Mohl) Yakovlev 19
***Acrocomia aculeata* (Jacq.) Lodd. ex Mart.** (=*A. sclerocarpa* Mart.) 12
Aegiphila lhotskyana Cham. 34
A. paraguariensis Briq. 4
A. verticillata Vell. 2
Agonandra brasiliensis Miers 33
Alchornea triplinerva Müll.Arg. 2
Alibertia concolor (Cham.) K.Schum. 4
A. edulis (L.Rich.) A.Rich. 28
A. elliptica (Cham.) K.Schum. 2
A. macrophylla K.Schum. 3
A. obtusa Cham. 2
A. sessilis (Cham.) K.Schum. 14
A. verrucosa Moore 2
Amaioua guianensis Aubl. 2
Anacardium occidentale L. 24 (=*A. microcarpum* Ducke)
***Anadenanthera colubrina* (Vell.) Brenan** 9
***A. peregrina* Speg.** 15
Andira cordata Arroyo ex R.T.Pennington 2
A. cuiabensis Benth. 17
A. inermis Kunth 4
A. vermifuga Mart. 24
Annona coriacea Mart. 41
A. crassiflora Mart. 51
A. paludosa Aubl. 5
Antonia ovata Pohl 17
Apeiba tibourbou Aubl. 9
Aspidosperma macrocarpon Mart. 29
A. multiflorum A.DC. 6
A. nobile Müll.Arg. 8
A. olivaceum Müll.Arg. 2
A. parvifolium A.DC. 3
***A. subincanum* Mart.** 14
A. tomentosum Mart. (=*A. dasycarpon* A.DC.) 41
***Astronium fraxinifolium* Schott** 51
***A. urundeuva* Engl.** 18
Attalea speciosa Mart. ex Spreng. (=*Orbignya phalerata* Mart.) 2
Austroplenckia populnea (Reiss.) Lundell. 36

Banisteriopsis dracunculifolia DC. 7
B. latifolia (A.Juss.) Cuatrec. 10
B. pubipetala (A.Juss.) Cuatrec. 3
***Bauhinia cupulata* Benth.** 2
B. forficata Link. 5
B. holophylla Steud. 7
B. rufa (Bong.) Steud. 18
B. tenella Benth. 2
Blepharocalyx salicifolius (Kunth) Berg (=*B. suaveolens* (Cambess.) Burret) 9
Bowdichia virgilioides Kunth (=*B. major* Mart.) 75

Bredmeyera altissima A.W.Benn. 4
Brosimum gaudichaudii Trécul 52
***Buchenavia tomentosa* Eichler** 10
Butia leiospatha (Mart.) Becc. 8
Byrsonima basiloba A.Juss. 10
B. coccolobifolia Kunth 70
B. coriacea DC. 3
B. crassa Nied. 32
B. crassifolia (L.) Kunth 39
B. cydoniifolia A.Juss. 3
B. fagifolia Nied. 2
B. guillerminiana A.Juss. 2
B. intermedia A.Juss. 17
B. orbignyana A.Juss. 2
B. pachyphylla A.Juss. 7
B. verbascifolia Rich. ex A.Juss. 54

***Callisthene fasciculata* (C.K.Spreng.) Mart.** 23
C. major Mart. 13
Calophyllum brasiliense Cambess. 4
***Calycophyllum multiflorum* Griseb.** 2
Campomanesia adamantium (Cambess.) Berg (= *C. cambessedeana* Berg) 2
C. eugenioides Blume 5
C. pubescens (DC.) Berg 21
Cardiopetalum calophyllum Schltdl. 10
Caryocar brasiliense Cambess. 65
C. coriaceum Wittm. 6
Casearia arborea Urb. 6
C. decandra Jacq. 3
C. grandiflora Cambess. 16
***C. rupestris* Eichler** 2
C. sylvestris Sw. 47
Cecropia pachystachya Trécul 7
Cenostigma macrophyllum Tul. 2
Chaetocarpus echinocarpus (Baill.) Ducke 3
Chamaecrista orbiculata (Benth.) Irwin & Barneby 2
Cheiloclinium cognatum (Miers) A.C.Sm. 2
Chomelia obtusa Cham. & Schltdl. 2
C. ribesioides Benth. 12
Chrysophyllum marginatum Radlk. 4
Coccoloba mollis Casar. 3
Cochlospermum regium (Schrank) Pilg. 20
***Combretum duarteanum* Cambess.** 4
***C. leprosum* Mart.** 6
Connarus suberosus Planch. 59
Copaifera langsdorfii Desf. 50
C. martii Hayne 6
Cordia alliodora (Ruíz & Pav.) Oken 4
***C. glabrata* (Mart.) A.DC.** 6
C. insignis Cham. 5
C. sellowiana Cham. 2
***C. trichotoma* (Vell.) Arrab.** 7
Couepia grandiflora (Mart. & Zucc.) Benth. 38
Coussarea hydrangeaefolia Benth. & Hook.f. 5
Curatella americana L. 70
Cybianthus detergens Mart. 9
Cybistax antisyphilitica Mart. 32

Dalbergia miscolobium Benth. (=*D. violacea* (Vogel) Malme) 47
Daphnopsis fasciculata (Meissn.) Nevling 3
Davilla elliptica A.St.-Hil. 39
D. grandiflora A.St.-Hil. & Tul. 2
Didymopanax distractiflorum Harms 6
D. macrocarpum (Cham. & Schltdl.) Seem. 38
D. vinosum (Cham. & Schltdl.) March. 15
***Dilodendron bipinnatum* Radlk.** 19
Dimorphandra mollis Benth. 64
Diospyros burchellii Hiern 8
D. camporum Warm. 2
D. hispida DC. 37
D. sericea DC. 15
***Dipteryx alata* Vog.** 23
Diptychandra aurantiaca (Mart.) Tul. 4
D. glabra Benth. 2
Duguetia furfuracea (A.St.-Hil.) Benth. & Hook. 20

Emmotum nitens (Benth.) Miers 34
***Enterolobium contortisiliquum* (Vell.) Morong** 7
E. gummiferum J.Macbr. 38
Eremanthus glomerulatus Less. 18
E. goyazensis Sch. Bip. 5
E. mattogrossensis Kuntze 5
Eriotheca gracilipes (Schum.) Robyns 31
E. pubescens (Mart. & Zucc.) Schott. & Endl. 16
Erythroxylum ambiguum Peyr. 4
E. cuneifolium Poepp. ex O.E.Schulz 3
E. deciduum A.St.-Hil. 20
E. suberosum A.St.-Hil. 53
E. tortuosum Mart. 36
Eugenia aurata O.Berg 11
E. bimarginata DC. 9
E. dysenterica DC. 31
E. punicifolia (Kunth) DC. 2
E. uniflora L. 2
Eupatorium squalidum DC. 3
Euplassa inaequalis (Pohl) Engl. 5

Fagara hassleriana Chodat 2
F. rhoifolia (Lam.) Engl. 28
***F. riedeliana* Engl.** (=*F. cinerea* Engl.) 16
Ferdinandusa elliptica Pohl 15

Genipa americana L. 5
Gochnatia barrossii Cabrera 4
G. pulchra Cabrera 4
Gomidesia lindeniana Berg 4
Guatteria sellowiana Schltdl. 3
***Guazuma ulmifolia* Lam.** 31
Guettarda viburnioides Cham. & Schltdl. 24

Hancornia pubescens Nees & Mart. 2
H. speciosa Nees & Mart. 50
Heisteria densifrons Engl. 3
Helicteres corylifolia Nees & Mart. 2
***H. macropetala* A.Juss.** 5
H. sacarolha A.St.-Hil. 4
Heteropteris byrsonimifolia A.Juss. 18
H. tomentosa Hook. & Arn. 2
Himatanthus articulatus (Vahl) Woodson 8
H. bracteatus (A.DC.) Woodson 2
H. obovatus (Müll.Arg.) Woodson 44
Hirtella ciliata Mart. ex Zucc. 9
H. glandulosa Spreng. 19
Humiria balsamifera A.St.Hil. 2
Hymenaea courbaril L. 11
H. stigonocarpa Mart. ex Hayne 65
Hyptidendron canum (Pohl ex Benth.)Harley (= *Hyptis cana* Pohl ex Benth.) 15

Ilex cerasifolia Reissek 4
I. concocarpa Reissek 4

Jacaranda brasiliana Pers. 9
J. caroba (Vell.) DC. 10
***J. cuspidifolia* Mart.** 10

Kielmeyera coriacea (Spreng.) Mart. 64
K. corymbosa Mart. 3
K. grandiflora (Wawra) Saddi 3
K. lathrophyton Saddi 5
K. rosea Mart. 5
K. rubriflora A.St.-Hil. 21
K. speciosa A.St.-Hil. 10

Lacistema aggregatum (Berg) Rusby 5
L. floribundum Miq. 2
Lafoensia densiflora Pohl 6
L. pacari St. Hil. 61
Lamanonia ternata Vell. 2
Leandra involucrata Raddi 2
L. lacunosa Cogn. 3
Licania gardneri Kuntze 3
L. humilis Cham. & Schltdl. 15
L. sclerophylla Mart. ex Hook.f. 2
***Linociera hassleriana* (Chodat) Hassler** 2
Lippia corymbosa Cham. 2
Lithraea molleoides (Vell.) Engl. 5
***Luehea candicans* Mart.** 3
L. divaricata Mart. 8
***L. paniculata* Mart.** 25
***L. speciosa* Willd.** 9
Lychnophora ericoides Mart. 2

Mabea fistulifera Mart. 4
Macairea radula DC. 2
Machaerium acutifolium Vogel 54
***M. angustifolium* Mart. ex Benth.** 3
M. opacum Vogel 25
***M. scleroxylon* Tul. 4**
M. villosum Vogel 3
***Magonia pubescens* A.St.-Hil.** 37
Manihot tripartita Müll.Arg. 3
Maprounea guianensis Aubl. 13
Matayba guianensis Aubl. 23
Mezilaurus crassiramea (Meissn.) Taub. 8
Miconia albicans (Sw.) Triana 42
M. burchellii Triana 5
M. chartacea Triana 2
M. fallax DC. 3
M. ferruginata DC. 15
M. holosericea (L.) DC. 2
M. langsdorfii Cogn. 2
M. ligustroides Naud. 8
M. macrothyrsa Benth. 2
M. nervosa Triana 2
M. pohliana Cogn. 11
M. rubiginosa (Bonpl.) DC. 12
M. sellowiana Naud. 6
M. stenostachya DC. 9
Mimosa clausennii Benth. 9
M. laticifera Rizzini & Mattos 6
M. manidea Barneby 2
M. obovata Benth. 2
Mouriri elliptica Mart. 16
M. pusa Gardner 8
Myrcia albo-tomentosa Cambess. 9
M. canescens Berg 2
M. fallax (Rich.) DC. 2
M. formosiana Cambess. 2
M. intermedia Kiaersk. 2
M. lasiantha DC. 5
M. lingua (Berg) Mattos 8
M. multiflora DC. 2
M. pallens DC. 3
M. pubipetala Miq. 3
M. rostrata DC. 6
M. sellowiana Berg 2
M. superba Berg 2
M. tomentosa (Aubl.) DC. 17
M. uberavensis Berg 6
M. variabilis DC. 7
M. velutina Berg 5

Neea spruceana Heim. 2
N. theifera Oerst. 34

Ocotea acutifolia (Nees.) Mez 2
O. pomaderrioides Mez 2
O. pulchella Mart. 9
O. spixiana (Nees) Mez 4
O. suaveolens Hassl. 2
Ouratea castaneaefolia Engl. 19

O. hexasperma (A.St.-Hil.) Benth. 40
O. spectabilis (Mart.) Endl. 17

Palicourea rigida Kunth 39
Parkia platycephala Benth. 7
***Peltogyne confertiflora* (Hayne) Benth.** 8
Pera glabrata (Schott.) Baill. 15
Phoebe erythropus (Nees, Mart. & Spix) Mez 3
***Physocallyma scaberimmum* Pohl** 11
Piptocarpha rotundifolia (Less.) Baker 41
Pisonia graciliflora Mart. (= *P. subferruginosa* Mart. ex J.A.Schmidt) 8
P. noxia Netto 26
P. psammophila Mart. ex J.A.Schmidt 3
Plathymenia reticulata Benth. 46
Platonia insignis Mart. 3
***Platypodium elegans* Vogel** (= *P. grandiflorum* Benth.) 28
Pouteria ramiflora (Mart.) Radlk. 50
P. torta (Mart.) Radlk. 22
Protium heptaphyllum (Aubl.) E.K.Marchal 19
Prunus brasiliensis (Cham. & Schltdl.) D.Dietr. 2
Pseudobombax longiflorum (Mart. & Zucc.) Robyns 47
***P. marginatum* (A.St.-Hil., A.Juss. & Cambess.) Robyns** 8
***P. tomentosum* (Mart. & Zucc.) Robyns** 19
Psidium araça Raddi 2
P. myrsinoides Berg 7
P. warmingianum Kiaersk 8
Psychotria sessilis Vell. 3
Pterodon polygalaeflora Benth. 12
P. pubescens Benth. 30

Qualea cordata Spreng. 4
Q. dichotoma (Mart.) Warm. 11
Q. grandiflora Mart. 80
Q. multiflora Mart. 53
Q. parviflora Mart. 59

Rapanea ferruginea (Ruiz & Pav.) Mez 8
R. guianensis Aubl. 23
R. lancifolia Mez 4
R. umbellata Mez 9
***Rhamnidium elaeocarpum* Reiss.** 14
Roupala brasiliensis Klotzsch 10
R. gardneri Meissn. 2
R. heterophylla Pohl 3
R. montana Aubl. 61
Rourea induta Planch. 20
Rudgea amazonica Müll.Arg. 3
R. viburnioides (Cham.) Benth. 22

Sacoglottis guianensis Benth. 2
Salacia crassifolia (Mart.) Peyr. 23
S. elliptica G.Don 2
Salvertia convallariodora A.St.-Hil. 52
Sapium marginatum Müll.Arg. 4
Schinus terebinthifolius Raddi 13
Sclerolobium aureum (Tul.) Benth. 39
S. paniculatum Vogel 37
Senna rugosa (G.Don) Irwin & Barneby (= *Cassia rugosa* G.Don) 5
S. silvestris (Vell.) Irwin & Barneby (= *Cassia sylvestris* Vell.) 3
S. uniflora (P.Mill.) Irwin & Barneby (= *Cassia uniflora* Mill.) 2
Simarouba amara Aubl. 5
S. versicolor A.St.-Hil. 37
Siparuna guianensis Aubl. 27
Siphoneugena densiflora Berg 6
Solanum crinitum Lam. 2
S. grandiflorum Desf. 4
S. lycocarpum A.St.-Hil. 24
***Spondias mombin* L.** 2
***Sterculia striata* A.St.-Hil. & Naud.** 11
Strychnos pseudoquina A.St.-Hil. 39
Stryphnodendron adstringens (Mart.) Cov. 43
S. coriaceum Benth. 2
S. obovatum Benth. 4
S. polyphyllum Benth. 3
Styrax camporum Pohl 30
S. ferrugineus Nees & Mart. 33
Swartzia laurifolia Benth. 2
Syagrus comosa (Mart.) Mart. 16
S. flexuosa (Mart.) Becc. 16
Symplocos guianensis Gürke 2
S. lanceolata (Mart.) A.DC. 3
S. nitens (Pohl) Benth. 3
Symplocos rhamnifolia A.DC. 4

Tabebuia aurea Benth. & Hook. (= *T. caraiba* Bureau) 55
***T. impetiginosa* (Mart.) Standl.** (= *T. avellanedae* Lorentz ex Griseb.) 9
T. ochracea (Cham.) Standl. 58
***T. roseoalba* (Ridley) Sandw.** (= *T. odontodiscus* (Bur. & K.Schum.) Toledo) 6
Tapirira guianensis Aubl. 42
Tapura amazonica Poepp. & Endl. 2
***Terminalia argentea* Mart. & Zucc.** 37
T. brasiliensis Eichler 18
T. fagifolia Mart. & Zucc. 12
Tetragastris unifoliolata (Engl.) Cuatrec. 2
Tocoyena brasiliensis Mart. 5
T. formosa (Cham. & Schltdl.) Schum. 57
Triplaris americana R.H.Schomb. 3

Unonopsis lindmannii R.E.Fr. 2

Vanillosmopsis erythropappa (DC.) Sch. Bip. 3
V. pohlii Baker 2

V. polycephala (DC.) Sch. Bip. 6
Vatairea macrocarpa (Benth.) Ducke 40
Vellozia squamata Pohl 6
Vernonia ferruginea Less. 21
V. rubriramea Mart. 2
V. ruficoma Schltdl. ex Mart. 5
Virola sebifera Aubl. 28
V. subsessilis Warb. 2
Vismia cayennensis (Jacq.) Pers. 4
Vitex cymosa Bert. ex Spreng. 4
***V. polygama* Cham.** 7
Vochysia cinnamomea Pohl 7
V. elliptica (C.K.Spreng.) Mart. 25
V. haenkeana Mart. 10
V. rufa (C.K.Spreng.) Mart. 33
V. thyrsoidea Pohl 18
V. tucanorum (C.K.Spreng.) Mart. 17

Weigeltia densiflora Mez (=*Cybianthus densiflorus* Miq.) 2

***Ximenia americana* L.** 4
Xylopia aromatica Lam. 56
X. brasiliensis Spr. 2
X. sericea A.St.-Hil. 15

Zeyheria montana Mart. 36

APPENDIX 2

Species recorded at only one site and therefore excluded from analyses. Those indicating richer (mesotrophic) soils are in bold.

Abuta selloana Eichler
Acanthococos emensis Toledo
Aegiphila amazonica Moldenke
A. sellowiana Cham.
Alchornea discolor Poepp.
A. schomburgkii Klotzsch
***Amburana cearensis* (Allem.) A.C.Sm.**
Annona tomentosa R.E. Fr.
Apuleia leiocarpa J.Macbr.
Aspidosperma camporum Müll.Arg.
A. cylindrocarpum Müll.Arg.
A. populifolium A.DC.
A. pyrifolium Mart.
Attalea exigua Drude
***A. phalerata* Mart.**

Baccharis concinna G.M.Barosso
B. pseudotenuifolia (L.) Teodoro
Barbacenia ignea Mart.
Bauhinia mollis D.Dietr.
B. obtusata Vogel
Bocageopsis multiflora (Mart.) R.E.Fries
Butia paraguayensis (Barb. Rodr.) L.H.Bailey
Byrsonima clausenniana A.Juss.
B. inodora S.Moore
B. leucophlebia Griseb.
B. linguifera Nied.
B. psilandra Griseb.
B. vacciniaefolia A.Juss.

Callisthene microphylla Warm.
C. minor Mart.
Casearia commersoniana Cambess.
Cassia speciosa Kunth
Cecropia concolor Willd.
C. cyrtostachya Miq.
***Ceiba speciosa* (A.St.-Hil.) Gibbs & Semir**
Celtis pubescens (Kunth) Spreng.
Chaunochiton kappleri Ducke
Chomelia parviflora Müll.Arg.
Clethra brasiliensis Cham.& Schltdl.
Clusia sellowii Schltdl.
Combretum discolor Taub.
Commiphora leptophloeos (Mart.) J.B.Gillett (= *Bursera leptophloeos* Mart.)
Connarus perottetii (DC.)Planch. var. *angustifolium* Radlk.
Cordia bicolor DC.
C. piauhiensis Fresen.
Coutarea hexandra K.Schum.
Cupania rubiginosa (Poir.) Radlk.

Dalbergia glandulosa Benth.
Duguetia lanceolata A.St.-Hil.
Eremanthus argenteus Macleish & Schmach.
Erythroxylum pelleterianum A.St.-Hil.
Eschweilera nana (Berg) Miers
Esenbeckia febrifuga A.Juss.
Eugenia cerasiflora Kurz
E. chrysantha Berg
E. daphnites Mart.
E. hyemalis Cambess.
E. livida Berg
E. mugiensis Berg
E. polyphylla Berg
Eupatorium vautherianum DC.

Ficus guianensis Aubl.

Gochnatia polymorpha DC.
Guarea paniculata Wall.
Guapira opposita (Vell.) Reitz
Guatteria coriacea R.E.Fr.
G. nigrescens Mart.
G. silvatica R.E.Fr.

Hirtella racemosa Lam.

Ilex affinis Gardn.

Kielmeyera petiolaris Mart.

Lacistema serrulata Mart.
Lafoensia punicaefolia DC.
Leandra solenifera Cogn.
Licania blackii Prance
L. minutiflora (Sagot) Prance
Lithraea aroeirinha E.J.Marchal ex Warm.

Mabea pohliana Müll.Arg.
M. riedelii Müll.Arg.
Machaerium hirtum (Vell.) Stellfeld
M. lanatum Tul.
M. stipitatum Vog.
Manihot grandiflora Müll.Arg.
Maytenus alaternoides Reissek
M. communis Reissek
Miconia argentea DC.
M. cuspidata Naud.
M. flavescens Cogn. ex Britton
M. ibaguensis Schltdl.
M. irwinii Wurdack
M. tiliaefolia Naud.
Mimosa adenophylla Taub.
Monnina martiana Klotzsch ex A.W.Benn.
Moutabea guianensis Aublet
Myrcia castrensis (Berg) P.Legrand
M. longipes Kiaersk.
M. nigro-punctata DC.
M. rhodeosepala Kiaersk.
M. rorida Kiaersk.
M. rufipes DC.
M. sphaerocarpa DC.
M. splendens (Sw.) DC.
Mysine leuconeura Mart.

Neea macrophylla Poepp. & Endl.
Norantea goyazensis Cambess.

Oenocarpus distichus Mart.
Ouratea cuspidata Engl.

Palicourea marcgravii A.St.-Hil.
Persea pyrifolia Nees & Mart. ex Nees
Pisonia ambigua Heimerl.
Plumeria velutina Müll.Arg.
Protium brasiliense Benth.
Prunus myrtifolia (L.) Urb.
P. sellowii Koehne
Psidium acutangulum DC.
P. aerugineum Berg
P. australe Cambess.
P. guianense Sw.
P. pohliana Berg
P. widgrenianum Berg
Psychotria involucrata Sw.
Pterogyne nitens Tul.

Randia armata DC.
R. densiflora Benth.
Remijia amazonica K.Schum.
Roupala tomentosa Pohl
Rudgea villosa Benth.

***Schinopsis brasiliensis* Engl.**
Schoepfia obliquifolia Turcz.
Schwartzia adamantina (Cambess.) Bedell
Simaba glabra Engl.
Simira hexandra (S. Moore) Steyerm.
Solanum jamaicense Mill.
S. subinerme Jacq.
Sorocea illicifolia Miq.
Strychnos brasiliensis Benth.
Styrax nervosum A.DC.
S. pallida A.DC.
Swartzia grandifolia Bong. ex Benth.
Symplocos pubescens Klotzsch ex Benth.
S. tenuifolia Brand
S. uniflora Bedd.

Talisia subalbens Radlk.
Tibouchina candolleana Cogn.
T. clidemioides Cogn.
Tococa formicaria Mart.
Toulicia tomentosa Radlk.
Trichilia elegans A.Juss.
T. weddelii C.DC.

Vernonia brasiliana (L.) Druce
V. cinerea Less.
Vismia amazonica Ewan
Vitex montividensis Cham.
V. schomburgkiana Schauer
Vochysia gardneri Warm.
V. pruinosa Pohl

Wunderlichia crulsiana Taub.
W. mirabilis Riedel ex Baker