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OBSERVATIONS ON WOODY VEGETATION TYPES IN THE PANTANAL AND AT CORUMBÁ, BRAZIL

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ABSTRACT. Studies of cerrado, cerradão and deciduous (or semideciduous) forest vegetation were made in cordilheiras and capões in the Nhecolândia subarea of the Pantanal, Mato Grosso do Sul, and in the north Pantanal, near Poconé, Mato Grosso. Point-centred quarter transects were used to analyse the vegetation and the results are given in Tables 1–7. The cerradões belong to the mesotrophic type widespread in Central Brazil, while the cerrado is related to this but shows characteristics of cerrado of damper habitats. The forests are similar to the deciduous and semideciduous forests of Central Brazil. Soil analyses show levels of minerals and pH typical of these vegetation types (Table 10). An area of deciduous forest was studied on a calcareous hill at Corumbá, Mato Grosso do Sul (Tables 8 & 9). The vegetation is closely related to the Caatinga of NE Brazil, and the possibility that such vegetation may have been very much more widespread in the past is discussed.

The present communication is based on work carried out during brief visits to Corumbá and to Fazenda Nhumirim, Pantanal de Nhecolândia, Mato Gross do Sul, in late August/early September 1984 and in early October 1985. This rapid survey, however, was only possible because of the knowledge of the vegetation which two of the team (A.P. and V.J.P.) had built up over years of study. In addition, some results from a very brief visit to the north Pantanal with a University of Brasília postgraduate fieldcourse in early October 1986 are also included—here again the background knowledge of one of the authors (C.N. da C.) allowed results to be obtained in little time.

The Pantanal do Mato Grosso (Fig. 1) is a huge, low-lying floodplain, 75–170m in altitude, covering an area of some 140,000km^2 in the basin of the Rio Paraguai. It consists of a mosaic of lakes (some of them saline), permanent swamps, seasonal swamps, and vast extensions of seasonally inundated grassy campos dotted with patches of slightly elevated ground (c.1–2m above the level of the campos) bearing forest or cerrado vegetation. These elevations are not subject to inundation; the larger are called 'cordilheiras' (*paleodiques*) while small isolated woods are called 'capões' (singular 'capão'—from *caa* = forest, *pon* = round, in aborigine Tupi). As pointed out by Prance & Schaller (1982): 'a striking aspect of the Pantanal is its curious combination of mesic and xeric vegetation growing side by side. The reasons for this mixture are the topography and the seasonal climate. Hence patches of *terra firme* experience severe drought during the six month dry season. These areas of higher ground are often interspersed with flooded areas of swamp or aquatic vegetation types'. Rather paradoxically, the climate of the Pantanal is not a very moist one but belongs to Köppens 'Savanna Subtype' (AW) of the Tropical Rain Climate (A); the average

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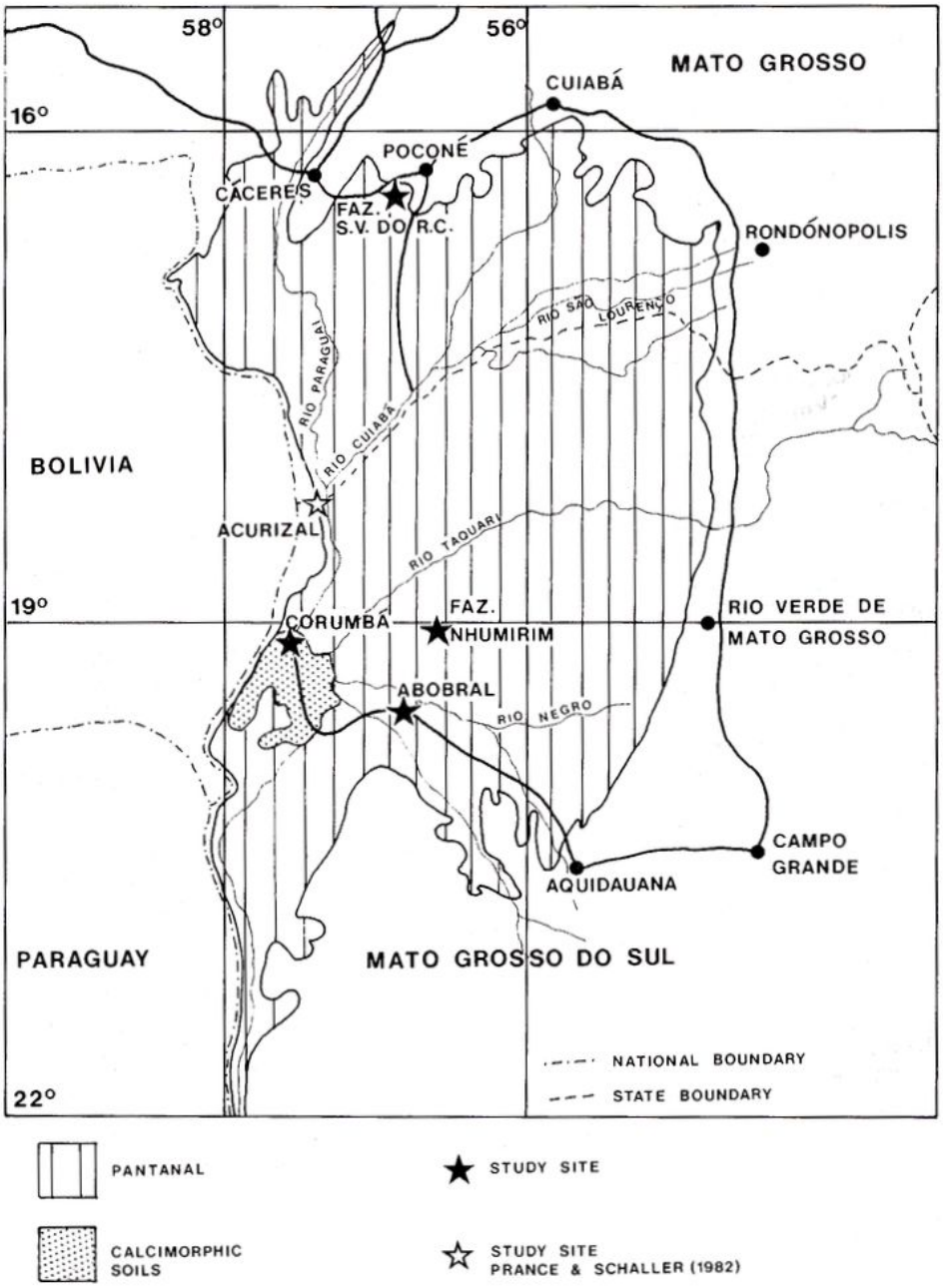

FIG. 1. Map of the Pantanal showing localities mentioned in the text.

annual temperature for Corumbá (MS) is 24·8°C and average annual precipitation 1246mm, while for Cuiabá (MT) the figures are 26.5°C and 1388mm. The inundation of the area is brought about by its extreme flatness (in the c.1320km of the Alto Paraguai passing through the Pantanal there is a fall of only 30m), the great size of the headwater catchment of the Rio Paraguai, and the very seasonal pattern of rainfall.

Prance & Schaller (1982) summarize the remarkably scanty literature on the vegetation of the Pantanal. The flora incorporates elements of the major nearby vegetation types: Cerrado, Chaco and Amazonian forest. Practically all studies have been extensive reconnaissances providing valuable general information but little detailed data; exceptions are Prance & Schaller (1982), who conducted an intensive study of an area in the western Pantanal, and Pott *et al.* (1986), who give a habitat list of 601 species on Fazenda Nhumirim.

Description of the Study Areas

Fazenda Nhumirim is a 4,300ha ranch owned by the Centro de Pesquisa Agropecuária do Pantanal and maintained as a research station. It is situated some 75km SE of Corumbá, Mato Grosso do Sul, at 18°59′S 56°39′W at an altitude of c.89m (Fig. 1). The vegetation is typical of the Nhecolândia subarea of the Pantanal* and consists of a mosaic of physiognomic types, determined by topography and degree of inundation. The principal habitats are: lakes (baias), both permanent and temporary; brackish lakes (salinas), surrounded by semideciduous forests; swamps; campo grasslands; campo de murundu (grassy campo with small hummocks bearing cerrado vegetation); cordilheiras covered in cerradão or semideciduous forest; and 'lixeiro', a type of damp cerrado dominated by shrubs of *Curatella americana* and *Byrsonima orbignyana*. The neighbouring Fazenda Ipanema in which one study area was situated is essentially similar.

The deciduous forest site is in the low calcareous hills which surround Corumbá (19°01′S 57°39′W) and stretch over a considerable area (Fig. 1). The hills are steep-sided with shallow soil and much outcropping of the calcareous rocks belonging to the Bocaina/arara formation (Cunha, 1985). Similar vegetation is also found on the flat ground between the hills but is much more disturbed than on the slopes.

The north Pantanal study area is situated on Fazenda São Vicente do Rio Claro, a large ranch in the Pantanal do Poconé, some 25km S of Poconé, Mato Grosso (16°16′S 56°38′W) (Fig. 1). The area consists of great expanses of seasonally inundated grassy campo with scattered areas of slightly elevated ground bearing cerradão or semideciduous forest. These areas are sometimes quite extensive cordilheiras while others are small capões. Around the elevations there are often areas of 'lixeiro' made up of the same species as at Fazenda Nhumirim.

Methods

The vegetation was studied by means of point-centred quarter (PCQ) transects, as described by Mueller-Dombois & Ellenberg (1974), and by general observation and collecting. On most transects the nearest trees or

* The subdivisions of the Pantanal follow Adamoli (1982).

shrubs at each point of both ⩾10cm and ⩾30cm circumference at breast height (cbh) were measured; this allowed figures to be calculated for the two size classes. Total basal area, absolute and relative density, absolute and relative dominance, absolute and relative frequency and importance value index (rel. dens. + rel. dom. + rel. freq.) were calculated for each species; only order of importance value, absolute density and absolute dominance are given in Tables 2–5, 7 and 9 but the other parameters are available for anyone interested and are lodged at E.

Voucher specimens of many of the species are lodged in the herbaria of the Centro de Pesquisa Agropecuária do Pantanal and Royal Botanic Garden, Edinburgh (E), with some duplicates at UFMT, UB and K. A list of all species recorded is given in the Appendix.

Cerrado and Cerradão

Cerrado and more particularly cerradão vegetation is common on the smaller and lower cordilheiras and 'islets' on Fazenda Nhumirim and the neighbouring Fazenda Ipanema. Observations were made of cerradão in three localities and more open cerrado in another. Notes on the individual areas are given below and results are presented in Tables 1–4. In addition data are given for an area of cerradão at Fazenda São Vicente do Rio Claro (Tables 1 and 5).

Fazenda Ipanema: cerradão

The area consists of a cordilheira covered in cerradão with the taller trees about 13m and producing a broken canopy. A list of the tree and shrub species is given in Table 1, while Table 2 shows the species ⩾30cm cbh occurring on a PCQ transect. A number of the species recorded, such as *Curatella americana* and *Simarouba versicolor*, are commonest close to the campo margin of the cordilheira—such species are marked with 'm' in Table 1. The ground vegetation is dominated by *Bromelia balansae* which in places produces an almost complete cover with fiercely spiny leaves to 1.5m tall, making penetration on foot extremely difficult.

Fazenda Nhumirim: cerradão at the edge of Bahia Suja

In this locality the cerradão is very dense with the tallest trees approximately 10m in height. Our examination of the vegetation was much more rapid than in the other localities and no quantitative observations were made. The species recorded are listed in Table 1.

Fazenda Nhumirim: cerradão on the track to Salina Grande

This is an area of low, relatively dense, cerradão on a large cordilheira with signs of old disturbance (logging). The tallest trees are c.12m tall, and specimens of *Magonia pubescens* of about 8m were particularly common. During our visit in October the majority of the taller trees, with the notable exception of *Dipteryx alata*, were either leafless or with only a sparse covering of leaves—in the rainy season there is a continuous leafy crown cover. In

general, ground vegetation is very sparse, especially under *Magonia pubescens*, although in some areas there are fair quantities of *Bromelia balansae*. In places the cerradão runs into deciduous forest with many 'Acuri' palms (*Attalea phalerata*). A list of tree and shrub species is given in Table 1, and Table 3 shows the species ⩾10cm cbh and ⩾30cm cbh occurring on a PCQ transect; care was taken in siting the transect to avoid areas of transition to the deciduous forest which occurs on the cordilheira.

TABLE 1

Tree and larger shrub species of the cerrado and cerradão sites.

m = marginal

		Faz. Nhumirim			
	Faz. Ipanema	**Bahia Suja**	**Salina Grande**	**Cerrado**	**Faz. S.V. do Rio Claro (MT)**
Acosmium subelegans					X
Acrocomia totai	X	X	X	X	
Agonandra brasiliensis	X			X	
Alchornea discolor				X	
Alibertia sessilis	X		X	X	
A. sp.	X	X	X	X	
Anadenanthera colubrina var. cebil		X			X
Andira cuyabensis				X	
A. paniculata				X	
Annona cf. tomentosa					X
Aspidosperma subincanum					X
A. tomentosum	X				
Astronium fraxinifolium	X	X	X	X	X
A. urundeuva			X		X
Attalea phalerata		X	X		
Bambusa (Guadua) sp.			X		
Banisteriopsis pubipetala	X			X	
Bauhinia mollis					X
B. rufa				X	
Bowdichia virgilioides	X			X	
Brosimum gaudichaudii			X		
Buchenavia tomentosa	X			X	
Byrsonima coccolobifolia	X	X	X	X	
B. crassifolia	X			X	
B. orbignyana				X	
B. verbascifolia				X	
Callisthene fasciculata					X
Calycophyllum multiflorum					X
Caryocar brasiliense	X	X	X	X	
Casearia decandra			X		
C. sylvestris var. lingua	X	X	X	X	
Cecropia pachystachya	X[m]			X	
Celtis pubescens		X			
Chomelia obtusa	X	X	X	X	X
Chrysophyllum marginatum subsp. marginatum	X		X	X	
Connarus suberosus subsp. fulvus				X	
Copaifera martii	X	X	X		
Cordia glabrata	X		X		X
Couepia grandiflora	X	X		X	
Curatella americana	X[m]	X	X	X	X
Davilla elliptica	X		X	X	
Dilodendron bipinnatum			X		X

TABLE 1 (cont.)

	Faz. Ipanema	Faz. Nhumirim			Faz. S.V. do Rio Claro (MT)
		Bahia Suja	Salina Grande	Cerrado	
Diospyros hispida		X		X	
Dipteryx alata	X		X	X	X
Diptychandra aurantiaca subsp. aurantiaca		X	X	X	
Duguetia furfuracea				X	
Enterolobium contortisiliquum			X		
Eriotheca gracilipes	X		X		
Eugenia sp. R5061	X	X	X	X	
Fagara sp. aff. hassleriana	X	X	X	X	
F. cf. rhoifolia			X		X
F. chiloperone			X		
Ficus sp.				X	
Guazuma ulmifolia			X		
Guettarda viburnoides	X		X		
Hancornia speciosa		X			
Himatanthus obovatus			X		
Hymenaea stigonocarpa	X	X	X	X	X
Jacaranda cuspidifolia	X				X
Kielmeyera coriacea	X				
Lafoensia pacari	X	X	X		
Licania minutiflora				X	
Linociera hassleriana			X		X
Luehea paniculata					X
L. sp.	X		X	X	X
Machaerium acutifolium?			X		
M. hirtum					X
Magonia pubescens		X	X		X
Mouriri elliptica	X			X	
Myrcia sp.				X	
Ocotea suaveolens	X		X	X	
Ouratea hexasperma?		X			
Pouteria ramiflora	X			X	
Protium heptaphyllum	X	X	X	X	
Pseudobombax longiflorum	X			X	
P. marginatum	X		X		
P. tomentosum					X
P. sp.				X	
Pterogyne nitens				X	
Qualea grandiflora	X		X		
Q. parviflora	X				
Rhamnidium elaeocarpum	X		X		
Rourea induta	X			X	
Sclerolobium aureum				X	
Simaba sp.		X			
Simarouba versicolor	X[m]			X	
Sorocea sprucei subsp. saxicola				X	
Sterculia striata			X		
Strychnos pseudoquina				X	
Stryphnodendron adstringens	X				
Swartzia sp. ('Justa conta')			X		
Syagrus flexuosa	X				
Tabebuia impetiginosa			X	X	X
T. caraiba	X	X	X	X	X
T. ochracea	X		X		
T. roseo-alba			X		

TABLE 1 (cont.)

	Faz. Nhumirim			
	Faz. Ipanema	**Bahia Suja**	**Salina Grande**	**Cerrado**	**Faz. S.V. do Rio Claro (MT)**
Terminalia argentea	X		X	X	X
Tocoyena formosa		X	X	X	
Trichilia elegans subsp. elegans		X			
Unonopsis lindmannii			X		
Vatairea macrocarpa	X			X	
Vitex cymosa		X		X	
Ximenia americana var. americana			X		
Myrtaceae sp.				X	
Myrtaceae sp. ('Goiabinha')					X
Indet.					X
Indet. 3				X	

TABLE 2

Point-centred quarter transect in cerradão at Fazenda Ipanema with species in order of Importance value.

29 points, 15m apart. Trees and shrubs ⩾30cm circumference at breast height.

Mean distance between individuals 4.57m. Absolute density (individuals/ha) = 479.

n = no. of individuals on transect; ba = basal area (cm^2).

	n	**Abs. dens.** (individ./ha)	**Abs. dom.** (total ba/ha)
1. Caryocar brasiliense	15	62·0	39480·3
2. Mouriri elliptica	12	50·0	9185·0
3. Vatairea macrocarpa	8	33·0	15318·2
4. Dipteryx alata	7	29·0	12862·5
5. Terminalia argentea	7	29·0	10466·3
6. Tabebuia caraiba	8	33·0	8139·4
7. Buchenavia tomentosa	8	33·0	5725·8
8. Astronium fraxinifolium	6	25·0	12091·4
9. Bowdichia virgilioides	4	16·5	8532·6
10. Byrsonima crassifolia	5	21·0	4648·7
11. Eriotheca gracilipes	2	8·3	8958·0
12. Tabebuia ochracea	3	12·4	3418·0
13. Curatella americana	3	12·4	3234·2
14. Ocotea suaveolens	3	12·4	4530·2
15. Couepia grandiflora	3	12·4	3950·4
16. Cecropia pachystachya	2	8·3	4173·8
17. Qualea parviflora	3	12·4	2402·9
18. Byrsonima coccolobifolia	3	12·4	2170·3
19. Qualea grandiflora	2	8·3	2827·0
20. Agonandra brasiliensis	2	8·3	2060·9
21. Chomelia obtusa	2	8·3	762·0
22. Hymenaea stigonocarpa	1	4·1	3285·4
23. Fagara cf. hassleriana	1	4·1	1143·6
24. Pouteria ramiflora	1	4·1	821·5
25. Aspidosperma tomentosum	1	4·1	725·6
26. Acrocomia totai	1	4·1	579·4
27. Luehea sp.	1	4·1	525·8
28. Roures induta	1	4·1	357·7
29. Alibertia sessilis	1	4·1	315·5

TABLE 3

Point-centred quarter transect in cerradão near Salina Grande, Fazenda Nhumirim.

25 points, 10m apart. Trees and shrubs measured to two qualifying girths at each point: ⩾10cm and ⩾30cm.

Species in order of ⩾30cm Importance value; all figures for ⩾10cm are given in brackets.

Mean distance between individuals: ⩾30cm, 3.95m; ⩾10cm, 2.13m. Absolute density (individuals/ha): ⩾30cm, 642; ⩾10cm, 2198.

n = no. of individuals on transect; ba = basal area (cm^2).

⩾30cm	⩾10cm		n	Abs dens. (individ./ha)	Abs. dom. (total ba/ha)
1	(1)	Magonia pubescens	20 (20)	128·4 (439·6)	16936·0 (42375·2)
2	(3)	Tabebuia ochracea	13 (8)	83·5 (175·8)	12372·6 (17553·2)
3	(5)	Terminalia argentea	10 (4)	64·2 (87·9)	10035·1 (8594·2)
4		Tabebuia impetiginosa	6	38·5	17662·1
5	(7)	Machaerium acutifolium?	9 (5)	57·8 (109·9)	7105·7 (5099·4)
6	(16)	Lafoensia pacari	8 (2)	51·4 (44·0)	5688·1 (1189·2)
7	(6)	Guazuma ulmifolia	5 (3)	32·1 (65·9)	5933·4 (10603·2)
8		Tabebuia roseo-alba	5	32·1	5087·2
9	(4)	Diptychandra aurantiaca	4 (6)	25·7 (131·9)	3995·8 (6594·0)
10	(13)	Protium heptaphyllum	3 (3)	19·3 (65·9)	1299·4 (956·1)
11	(19)	Attalea phalerata	1 (1)	6·4 (22·0)	4045·2 (1470·5)
12		Dipteryx alata	2	12·8	1484·3
13	(14)	Astronium fraxinifolium	2 (2)	12·8 (44·0)	982·3 (2945·3)
14	(8)	Enterolobium contortisiliquum	1 (1)	6·4 (22·0)	2292·6 (7849·1)
15	(21)	Sterculia striata	1 (1)	6·4 (22·0)	1963·2 (846·2)
16		Acrocomia totai	1	6·4	1838·7
17		Astronium urundeuva	1	6·4	1489·4
18		Tabebuia caraiba	1	6·4	1328·3
19		Luehea sp.	1	6·4	1328·3
20	(27)	Byrsonima coccolobifolia	1 (1)	6·4 (22·0)	900·7 (294·5)
21		Cordia glabrata	1	6·4	661·9
22	(11)	Rhamnidium elaeocarpum	1 (3)	6·4 (65·9)	556·0 (1569·4)
23	(2)	Casearia sylvestris	1 (19)	6·4 (417·6)	556·0 (9647·0)
24	(12)	Chrysophyllum marginatum	1 (3)	6·4 (65·9)	523·2 (1723·2)
25	(18)	Linociera hassleriana	1 (1)	6·4 (22·0)	459·7 (1573·8)
—	(9)	Guettarda viburnoides	(3)	(65·9)	(1729·8)
—	(10)	Alibertia sessilis	(3)	(65·9)	(1576·0)
—	(15)	Swartzia sp.	(2)	(44·0)	(1013·3)
—	(17)	Casearia decandra	(2)	(44·0)	(1024·3)
—	(20)	Ocotea suaveolens	(1)	(22·0)	(1092·4)
—	(22)	Unonopsis lindmannii	(1)	(22·0)	(630·8)
—	(23)	Fagara cf. hassleriana	(1)	(22·0)	(505·5)
—	(24)	Eriotheca gracilipes	(1)	(22·0)	(505·5)
—	(25)	Tocoyena formosa	(1)	(22·0)	(448·4)
—	(26)	Chomelia obtusa	(1)	(22·0)	(393·4)
—	(28)	Ximenia americana	(1)	(22·0)	(175·8)

Fazenda Nhumirim: cerrado

The study site is a small, low cordilheira broken up by tongues of campo (alternatively it could be described as an archipelago of small, raised islands). Most of the trees were 4–6m tall and produce only a very broken crown cover. The low vegetation includes a tussocky ground cover of grasses. The trees and shrubs observed are listed in Table 1, while Table 4 shows those ⩾10cm cbh and ⩾30cm cbh occurring on a PCQ transect.

TABLE 4

Point-centred quarter transect in cerrado on Fazenda Nhumirim.

25 points, 15m apart. Trees and shrubs measured to two qualifying girths at each point: ⩾10cm and ⩾30cm.

Species in order of ⩾30cm Importance value; all figures for ⩾10cm are given in brackets.

Mean distance between individuals: ⩾30cm, 4·69m; ⩾10cm, 3·44. Absolute density (individuals/ha): ⩾30cm, 454; ⩾10cm, 844.

n = no. of individuals on transect; ba = basal area (cm²).

⩾30cm	⩾10cm		n	Abs dens. (individ./ha)	Abs. dom. (total ba/ha)
1	(1)	Curatella americana	26 (17)	118·0 (143·5)	36270·0 (39851·2)
2	(3)	Fagara sp.	15 (9)	68·1 (76·0)	8980·6 (6123·2)
3	(16)	Hymenaea stigonocarpa	5 (2)	22·7 (16·9)	16112·9 (3556·6)
4	(2)	Mouriri elliptica	8 (10)	36·3 (84·4)	6696·1 (8103·2)
5	(4)	Caryocar brasiliense	4 (4)	18·2 (33·8)	15668·5 (7808·7)
6	(8)	Tabebuia caraiba	5 (4)	22·7 (33·8)	4719·8 (3948·2)
7	(5)	Acrocomia totai	4 (4)	18·2 (33·8)	3752·3 (6975·7)
8	(11)	Byrsonima coccolobifolia	4 (3)	18·2 (25·3)	4468·7 (5017·6)
9	(12)	Buchenavia tomentosa	3 (2)	13·6 (16·9)	5819·4 (6413·6)
10	(6)	Tabebuia impetiginosa	3 (3)	13·6 (25·3)	5707·7 (10610·8)
11	(10)	Couepia grandiflora	4 (4)	18·2 (33·8)	1754·7 (2124·4)
12	(14)	Cecropia pachystachya	2 (1)	9·1 (8·4)	4481·9 (7686·3)
13	(9)	Dipteryx alata	2 (3)	9·1 (25·3)	3288·3 (6195·0)
14	—	Byrsonima crassifolia	2	9·1	1641·2
15	(13)	Chrysophyllum marginatum	1 (1)	4·5 (8·4)	4530·0 (8421·4)
16	(9)	Andira paniculata	2 (2)	9·1 (16·9)	1439·2 (1209·5)
17	—	Sorocea sprucei subsp. saxicola	1	4·5	4212·2
18	—	Ocotea suaveolens	1	4·5	2031·2
19	(15)	Diptychandra aurantiaca	1 (2)	4·5 (16·9)	1924·5 (4031·8)
20	(24)	Banisteriopsis pubipetala	2 (2)	9·1 (16·9)	429·5 (798·4)
21	—	Simarouba versicolor	1	4·5	1300·3
22	(25)	Vitex cymosa	1 (1)	4·5 (8·4)	1014·2 (1885·5)
23	(26)	Terminalia argentea	1 (1)	4·5 (8·4)	832·2 (1547·1)
24	—	Astronium fraxinifolium	1	4·5	521·6
25	(21)	Diospyros hispida	1 (2)	4·5 (16·9)	43·6 (282·7)
—	(7)	Pterogyne nitens	(4)	(33·8)	(4080·7)
—	(17)	Duguetia furfuracea	(3)	(25·3)	(248·1)
—	(18)	Bauhinia rufa	(3)	(25·3)	(902·2)
—	(20)	Agonandra brasiliensis	(2)	(16·9)	(533·4)
—	(22)	Myrtaceae	(2)	(16·9)	(253·2)
—	(23)	Alibertia sessilis	(2)	(16·9)	(150·6)
—	(27)	Rourea induta	(1)	(8·4)	(454·1)
—	(28)	Connarus suberosus subsp. fulvus	(1)	(8·4)	(324·9)
—	(29)	Strychnos pseudoquina	(1)	(8·4)	(268·4)
—	(30)	Chomelia obtusa	(1)	(8·4)	(172·2)
—	(31)	Casearia sylvestris	(1)	(8·4)	(151·1)
—	(32=)	Indet. 3	(1)	(8·4)	(81·0)
—	(32=)	Tocoyena formosa	(1)	(8·4)	(81·0)

Fazenda São Vicente do Rio Claro: cerradão

The area is a cordilheira, some 250m wide and of considerably greater length, covered with dense cerradão. The trees are 8m or more tall and produce a continuous canopy. There is much *Bromelia balansae* in the ground vegetation, lianas are frequent, and *Chomelia obtusa* and *Calliandra*

TABLE 5

Point-centred quarter transect in cerradão at Fazenda São Vicente do Rio Claro (MT) with species in order of Importance value.

50 points, 10m apart. Trees and shrubs ⩾30cm circumference at breast height.

Mean distance between individual 3·22m. Absolute density (individuals/ha) = 956.

n = no. of individuals on transect; ba = basal area (cm^2).

	n	Abs. dens. (individ./ha)	Abs. dom. (total ba/ha)
1. Machaerium hirtum	50	240	44486
2. Astronium urundeuva	44	211	41332
3. Cordia glabrata	28	134	30557
4. Anadenanthera colubrina var. cebil	18	86	23808
5. Magonia pubescens	19	91	9689
6. Astronium fraxinifolium	11	53	9314
7. Callisthene fasciculata	11	53	7232
8. Dilodendron bipinnatum	5	24	6686
9. Pseudobombax tomentosum	3	14	6874
10. Tabebuia impetiginosa	2	10	5095
11. T. caraiba	2	10	945
12. Dipteryx alata	1	5	1432
13. Linociera hassleriana	1	5	848
14. Jacaranda cuspidifolia	1	5	805
15. Indet.	1	5	545
16. Tabebuia sp.	1	5	460
17. Luehea paniculata	1	5	407
18. Bauhinia mollis	1	5	315

TABLE 6

Tree and large shrub species of forest on cordilheiras and capões

	Faz. Nhumirim		Rio Abobral		Faz. S.V. do Rio Claro (MT)
	Salina 2	Salina Grande	Capão 1	Capão 2	Capão
Acrocomia totai	X	X		X	X
Agonandra brasiliensis	X	X			
Anadenanthera colubrina var. cebil	X			X	
A. sp. ('Angico preto')	X	X			
Andira inermis?				X	
Aspidosperma subincanum	X				
A. sp. ('Peroba')	X		X	X	
Astronium fraxinifolium	X	X		X	
A. urundeuva	X	X			
Attalea phalerata	X	X	X	X	X
Bauhinia mollis	X				
Bambusa (Guadua) sp.	X	X			
Casearia decandra	X				
Cecropia pachystachya	X		X		X
Ceiba sp.					X
Celtis pubescens	X		X		
Cereus peruvianus	X				
Chomelia obtusa	X	X			X
Coccoloba sp.	X				
Combretum leprosum	X				X
Copernicia australis	X	X	X		X
Cordia glabrata	X	X			

TABLE 6 (cont.)

	Faz. Nhumirim		Rio Abobral		
	Salina 2	Salina Grande	Capão 1	Capão 2	Faz. S.V. do Rio Claro (MT) Capão
Dilodendron bipinnatum	X		X		
Enterolobium contortisiliquum		X		X	X
Eugenia pyriformis	X				
Fagara chiloperone	X				
F. sp. aff. hassleriana	X	X	X	X	
Ficus spp.	X		X	X	X
Guazuma ulmifolia					X
Hymenaea courbaril var. stilbocarpa					X
Inga sp.	X				
Jacaratia corumbensis	X				
Jatropha vitifolia var. cnicodendron	X				
Linociera hassleriana	X	X	X		
Lippia cf. urticoides	X	X			
Lonchocarpus sp.? ('Sangue de Bugre')					X
Luehea sp.	X	X			X
Ocotea suaveolens	X				
Ouratea castaneaefolia					X
Pithecellobium edwallii	X				
Platypodium elegans	X				
Protium heptaphyllum	X				
Pseudobombax marginatum	X				
Pterogyne nitens	X		X		
Randia armata	X		X		
Rhamnidium elaeocarpum	X	X	X		X
Salacia elliptica	X				
Sapindus saponaria			X	X	
Sapium haematospermum	X				
Spondias lutea					X
Sterculia striata	X	X	X		X
Swartzia sp. ('Justa conta')	X			X	
Tabebuia impetiginosa	X	X	X	X	
T. roseo-alba	X				
Tocoyena formosa	X				
Trema micrantha			X		
Trichilia elegans subsp. elegans	X			X	
Unonopsis lindmannii				X	X
Vitex cymosa	X	X	X	X	X
Xylosma sp.	X	X			
Indet.					X

parviflora are common as small shrubs—the last is particularly characteristic of mesotrophic facies cerradão (Ratter *et al.* 1977). At the margin of the cordilheira is a typical 'lixeiro', i.e. an area of damp cerrado consisting mainly of *Curatella americana* and *Byrsonima orbignyana*. Species occurrence is given in Table 1, and Table 5 records the results of a PCQ transect.

FOREST ON CORDILHEIRAS

A number of forest cordilheira and capão sites were examined, both at Fazenda Nhumirim and on the route between the fazenda and Corumbá. All

TABLE 7

Point-centred quarter transect in forest near Salina 2, Fazenda Nhumirim.

25 points, 15m apart. Trees ⩾30cm in circumference at breast height.

Species in order of Importance value.

Mean distance between individuals 4·18m. Absolute density (individuals/ha) = 573.

n = no. of individuals on transect; ba = basal area (cm^2).

	n	Abs. dens. (individ./ha)	Abs. dom. (total ba/ha)
1. Attalea phalerata	32	183·4	96426·8
2. Tabebuia impetiginosa	8	45·8	29833·8
3. Anadenanthera sp. ('Angico preto')	5	28·7	35103·1
4. Vitex cymosa	6	34·4	10832·0
5. Astronium urundeuva	5	28·7	11816·4
6. A. fraxinifolium	5	28·7	10245·2
7. Protium heptaphyllum	4	22·9	5226·3
8. Rhamnidium elaeocarpum	4	22·9	4263·1
9. Casearia decandra	4	22·9	6841·6
10. Coccoloba sp.	4	22·9	2396·9
11. Agonandra brasiliensis	3	17·2	6229·1
12. Dilodendron bipinnatum	2	11·5	7869·6
13. Aspidosperma tomentosum	3	17·2	4356·6
14. Sterculia striata	1	5·7	9984·0
15. Lippia cf. urticoides	3	17·2	1552·3
16. Pterogyne nitens	1	5·7	5923·7
17. Cordia glabrata	1	5·7	4027·7
18. Chomelia obtusa	1	5·7	1641·1
19. Tabebuia roseo-alba	1	5·7	1329·4
20. Linociera hassleriana	1	5·7	1185·5
21. Luehea sp.	1	5·7	1139·7
22. Tocoyena formosa	1	5·7	803·9
23. Swartzia sp. ('Justa conta')	1	5·7	624·0
24. Platypodium elegans	1	5·7	590·8
25. Bauhinia mollis	1	5·7	558·1
26. Trichilia elegans subsp. elegans	1	5·7	410·3

observations were made in September and early October when most of the trees were leafless. Notes on the individual areas are given below and results are presented in Tables 6 and 7. In addition, for comparison, data are given for a large capão at Fazenda São Vicente do Rio Claro (Table 6).

Fazenda Nhumirim: forest near Salina 2

The forest lies around the salina (brackish lake with pH 10) which has a marginal fringe of *Copernicia australis* and *Attalea phalerata* palms, indicating the ultrabasic conditions.

A PCQ transect was sited in the forest (Table 7) and more extensive observations were made over a larger area. The taller trees produce a canopy c.17–20m in height. Very few had foliage in the late dry season—exceptions were *Agonandra brasiliensis*, *Cecropia pachystachya*, *Fagara chiloperone*, *F.* sp. aff. *hassleriana*, *Linociera hassleriana*, *Protium heptaphyllum*, *Salacia elliptica* and, of course, the palms. The tree species recorded are given in Table 6; those noted as common or abundant in the more extensive observations were *Agonandra brasiliensis*, *Anadenanthera* sp. ('Angico preto'), *Astronium urundeuva*, *A. fraxinifolium*, *Attalea phalerata*, *Combretum*

leprosum, *Cordia glabrata*, *Dilodendron bipinnatum* and *Sterculia striata*. *Pithecellobium edwallii* ('Mulateira') was very common in the *Copernicia* zone on the banks of the salina. *Attalea phalerata* was very important as an understorey tree, and in places was massed to dominate the understorey completely—producing the so-called 'Acurizais'. A multi-trunked *Coccoloba* sp., tall bamboos (*Bambusa* sp.), and *Chomelia obtusa* are also important in the understorey, while large areas have a dense, almost impenetrable ground layer of *Bromelia balansae* which sometimes reaches 2m in height.

Fazenda Nhumirim: Salina Grande

A very rapid reconnaissance was made of the forest at Salina Grande. It is very similar to that around Salina 2. The most abundant species are recorded in Table 6.

Capões near the Rio Abobral

Rapid surveys were made of two of the numerous capões at the side of the old Corumbá-Campo Grande road (MS 184) in the area near the Rio Abobral. These capões consist of areas of deciduous forest borne on small islands of somewhat elevated ground (to 2m) on a plain of seasonally inundated campo. The substrate is a petrocalcic calcimorphic soil derived from mollusc-shells (Cunha *et al.*, 1985).

The first capão had been largely destroyed to make a cultivated plot but many of the tree-stumps were resprouting and we succeeded in making a list of the woody vegetation (Table 6). The second had also been partially devastated, this time for extraction of the calcareous subsoil for use in the building of the highway across the pantanal. However, the capão was large and still carried an area of relatively undisturbed forest (Table 6). Most of the taller trees were about 13m and completely leafless—the commonest species in this layer were *Anadenanthera colubrina* var. *cebil*, *Astronium fraxinifolium* and figs, while the broad-crowned *Enterolobium contortisiliquum* was also very conspicuous. There was a dense understorey of *Attalea phalerata* palms producing a shade so deep that it prevented development of other vegetation on the ground.

Colonies of Howler monkeys (*Alouatta*) and Capuchins (*Cebus*) were present, indicating that conservation of capões is not only important in terms of vegetation but is vital for the preservation of fauna.

Other observations

We took a brief glance at the vegetation at the headquarters of Fazenda Nhumirim. It represents the remains of typical semideciduous cordilheira forest and the following trees were noted: *Aspidosperma* sp. 'Guatambu', *Anadenanthera colubrina* var. *cebil*, *Astronium urundeuva*, *A. fraxinifolium*, *Cordia glabrata*, *Dipteryx alata*, *Enterolobium contortisiliquum*, *Ficus* sp., *Linociera hassleriana*, *Luehea* sp., *Pseudobombax marginatum*, *Swartzia* sp. ('Justa conta'), *Sterculia striata*, *Tabebuia impetiginosa*, *Vitex cymosa* and the palms *Copernicia australis*, *Attalea phalerata* and *Acrocomia totai*.

We also visited the sawmill where wood was being cut for making houses. The most common logs were of *Tabebuia impetiginosa*, but *Astronium*

urundeuva, *Cordia glabrata*, *Tabebuia caraiba*, *Enterolobium contortisiliquum*, *Aspidosperma subincanum*, *Anadenanthera* spp. and *Dipteryx alata* were also being used. These species provide the majority of valuable timbers in the region—however, this type of logging on a research station is undesirable as it disturbs the balance of the vegetation of the cordilheiras and for this reason has recently been stopped.

Forest at Corumbá

A brief survey was made of the vegetation of the calcareous hills close to the city of Corumbá. This included a PCQ transect (Table 9).

The vegetation is a low deciduous woodland with the canopy varying in height according to locality but generally 6–15m. It resembles exactly the arboreal Caatingas of NE Brazil (see Discussion p. 520) even to the presence of tall 'Mandacaru' cacti (*Cereus*), which are common in the tree layer. Our observations were made at the end of August and in early October; during the former period almost all the trees were leafless, but in October many were decked with new foliage. Since the area is close to habitation there has been a great deal of cutting for firewood and consequently there is much coppice regeneration producing multi-trunked trees; also, as in the Caatingas of NE Brazil, many of the trees (e.g. *Commiphora* (*Bursera*) *leptophloeos*) are of a naturally multi-trunked, tall shrubby form (deliquescent trees). A list of important tree and larger shrub species is given in Table 8. *Jatropha weddeliana* with bright red flowers and a *Pilocereus* sp. were common as low

Table 8

Trees and large shrubs of Caatinga forest near Corumbá.

Acacia glomerosa*
A. paniculata**
Acosmium cardenasii
Allophyllus edulis
Amburana cearensis*
Anadenanthera colubrina var. cebil*
A. sp. ('Angico preto')**
Aspidosperma pyrifolium*
A. subincanum*
A. tomentosum agg.
Astronium urundeuva*
Bauhinia mollis*
Bumelia cf. sartorum
Caesalpinia taubertiana**
Calycophyllum multiflorum
Capparis sp.**
Celtis sp.**
Cereus peruvianus**
Chomelia obtusa
Chorisia sp.**
Coccoloba sp.**
Combretum leprosum*
Commiphora (Bursera) leptophloeos*
Cordia glabrata*
Diplokeleba floribunda
Enterolobium contortisiliquum*
Erythrina cf. mulungu*
Erythroxylum deciduum
E. pelleterianum
E. sp.
Ficus sp.
Helicteres lhotskyana**
Jacaranda sp.
Jacaratia corumbensis
Jatropha vitifolia var. cnicodendron*
Luehea sp.**
Lonchocarpus sp.? R5126
Maclura tinctoria*
Metrodorea mollis*
Pithecellobium saman
Pseudobombax sp.**
Sapindus saponaria
Sapium sp.**
Sebastiana brasiliensis
Simira corumbensis?
Sterculia striata*
Tabebuia avellanedae*
T. caraiba
Vitex cymosa
Nyctaginaceae sp.
Indet. 2
Indet. 3

* Species characteristic of Caatinga
** Genus characteristic of Caatinga

TABLE 9

Point-centred quarter transect in forest at Corumbá, MS.

25 points, 15m apart. Trees and shrubs measured to two qualifying girths at each point: ⩾10cm and ⩾30cm.

Species in order of ⩾30cm Importance value; all figures for ⩾10cm are given in brackets.

Mean distance between individuals: ⩾30cm, 5·02m; ⩾10cm, 2·90m. Absolute density (individuals/ha): ⩾30cm, 397; ⩾10cm, 1188.

n = no. of individuals on transect; ba = basal area (cm²).

⩾30cm	⩾10cm		n	Abs dens. (individ./ha)	Abs. dom. (total ba/ha)
1	(1)	Tabebuia impetiginosa	16 (17)	63·5 (202·0)	15926·9 (46851·2)
2	(2)	Anadenanthera sp. ('Angico preto')	17 (17)	67·5 (202·0)	8942·0 (17170·2)
3	(4)	Jatropha vitifolia var. cnicodendron	10 (5)	39·7 (59·4)	8658·2 (14399·8)
4	(12)	Acosmium cardenasii	8 (3)	31·8 (35·6)	6755·4 (1701·6)
5	(6)	Commiphora leptophloeos	4 (3)	15·9 (35·6)	6150·3 (11415·5)
6	(13)	Astronium urundeuva	5 (1)	19·9 (35·6)	5167·4 (5602·6)
7	(3)	Aspidosperma tomentosum agg + A. pyrifolium	6 (11)	23·8 (130·7)	3016·4 (8558·3)
8	(14)	Ceiba sp.	6 (2)	23·8 (23·8)	2368·1 (1524·2)
9	(9)	Ficus sp.	2 (1)	7·9 (11·9)	8210·8 (11853·9)
10	(11)	Calycophyllum multiflorum	6 (3)	23·8 (35·6)	3692·1 (3979·8)
11	(7)	Amburana cearensis	2 (1)	7·9 (11·9)	4870·8 (13608·5)
12	(22)	Cereus peruvianus	2 (1)	7·9 (11·9)	2161·7 (3289·6)
13	(23)	Cordia glabrata	2 (1)	7·9 (11·9)	1258·5 (2177·6)
14	(21)	Erythroxylum sp.	2 (2)	7·9 (23·8)	1240·6 (349·3)
15	(10)	Anadenanthera colubrina var. cebil	2 (3)	7·9 (35·6)	1124·3 (3227·8)
16	(17)	Enterolobium contortisiliquum	2 (2)	7·9 (23·8)	740·4 (614·2)
17	(24)	Sterculia striata	1 (1)	4·0 (11·9)	1460·2 (2177·6)
18	(25)	Indet. 2	1 (1)	4·0 (11·9)	432·3 (794·8)
19	(15)	Jacaratia corumbensis	1 (2)	4·0 (23·8)	409·3 (1498·1)
20	(16)	Acacia glomerosa + A. paniculata	1 (2)	4·0 (23·8)	365·2 (1228·4)
21	(5)	Simira corumbensis?	1 (7)	4·0 (83·2)	365·2 (2108·7)
22	(18)	Metrodorea mollis	1 (2)	4·0 (23·8)	343·8 (553·6)
23	(20)	Allophyllus edulis	1 (2)	4·0 (23·8)	181·8 (367·1)
24	—	Chomelia obtusa	1	4·0	71·1
—	(8)	Sebastiana brasiliensis	(4)	(47·5)	(1374·5)
—	(19)	Maclura tinctoria	(2)	(23·8)	(472·8)
—	(26)	Nyctaginaceae sp.	(1)	(11·9)	(500·2)
—	(27)	Pseudobombax sp.	(1)	(11·9)	(500·2)
—	(28)	Sapindus saponaria	(1)	(11·9)	(457·4)
—	(29)	Indet. 3	(1)	(11·9)	(417·0)

shrubs, while *Bromelia balansae*, the aroid *Taccarum weddelianum*, *Talinum crassifolium* and an *Anemia* species were noted as common herbs, as were dried-up carpets of a *Selaginella* sp. which would turn green again with the coming of the rains.

The soil is shallow, with much outcropping limestone, and is obviously very calcareous; analyses for a hill neighbouring the one on which we worked are given in Table 10. Large areas of forest are being destroyed as the

limestone is being extracted for the cement industry and the construction of roads and houses.

DISCUSSION

Cerradão and cerrado

The three cerradão areas examined at Nhecolândia and that near Poconé contain many of the indicator species of mesotrophic facies cerradão (Ratter *et al.* 1973, 1977—termed *Magonia pubescens/Callisthene fasciculata* cerradão in the former publication) and clearly belong to that cerrado category. The indicators are:

Acrocomia totai
Anadenanthera colubrina var. cebil**
Aspidosperma subincanum**
Astronium fraxinifolium*
A. urundeuva*
Bauhinia mollis*
Callisthene fasciculata
Cordia glabrata*
Dilodendron bipinnatum*
Dipteryx alata
Enterolobium contortisiliquum**
Guazuma ulmifolia*
Guettarda viburnoides
Jacaranda cuspidifolia
Luehea sp.
Magonia pubescens
Pseudobombax tomentosum
Sterculia striata**
Tabebuia impetiginosa**
Terminalia argentea
Vitex cymosa**

The species marked with an asterisk are equally common in deciduous forest and mesotrophic facies cerradão, while we regard those marked with two asterisks as generally more common in forest than cerradão. The close relationship of these two communities and the commonality of many of their species is discussed by Ratter *et al.* (1977, 1978).

Occurrence of mesotrophic indicators is in accord with the levels of calcium and magnesium known to occur generally in the surface soil of the Pantanal cordilheiras (see Table 10 for analyses from Nhecolândia and the cerradão at Fazenda São Vicente do Rio Claro, MT). The abundance of the important mesotrophic indicator species *Callisthene fasciculata* in the Poconé cerradão is in contrast to the Nhecolândia sites where the species is absent.

Some of the indicator species (e.g. *Acrocomia totai*, *Astronium fraxinifolium*, *Dipteryx alata* and *Luehea* sp.) were also present in the cerrado site

TABLE 10

Analytical data for surface horizon of soils (a & c, 0–30cm; b, 0–10cm)

	Ca me/100g	Mg me/100g	K me/100g	P 10^{-6}	pH in H_2O
(a) Pantanal of Nhecolândia					
Cordilheira (cerradão and forest)	6·7–9·0	2·6–8·9	0·9–1·8	10–12	—
Degraded cordilheira (cerrado, campo cerrado)	1·0–2·4	0·4–1·2	0·4–1·0	1–2	—
(b) Cerradão, Fazenda S.V. do Rio Claro, MT	3·3	1·7	0·4	5	6·1
(c) Calcareous hills with Caatinga forest, Corumbá	19·7	5·0	0·23	96	7·5

(a) Adapted from Cunha (1981); (b) original data; (c) Cunha (1985).

TABLE 11

Occurrence of mesotrophic indicator species on cerrado and cerradão sites. Based on individuals ⩾30cm cbh.

	No. of indicator species	No. of indicator spp. as % of total number of spp.	ba of indicator spp. as % of total ba	No. of trees of indicator spp. per ha as % of total trees/ha
Faz. Nhumirim, cerrado	6	24·0	3·1	12·0
Faz. Ipanema, cerradão	5	17·2	21·1	19·0
Salina Grande, cerradão	14	56·0	63·5	54·0
Faz. S.V. do Rio Claro, cerradão	13 (15)*	72·2 (83·3)	75·2 (98·9)	72·4 (98·4)

* Figure in brackets includes *Machaerium hirta* and *Linociera hassleriana* as indicator species. These two species probably do indicate mesotrophic soil conditions but there is not enough evidence available to be conclusive.

but those demanding higher calcium levels, such as *Magonia pubescens*, *Dilodendron bipinnatum*, *Guazuma ulmifolia* and *Sterculia striata*, were absent. In fact by far the most important species in terms of basal area, number of individuals and importance value in the cerrado site was *Curatella americana*, whose occurrence is probably more closely related to water table levels than to other soil characteristics. The number of indicator species, their basal area and relative density as a percentage of the total at the Nhecolândia sites for which detailed analyses were made is given in Table 11. Such figures probably reflect accurately the pH, calcium and magnesium levels of the surface layers of the soil—with Salina Grande (where the cerradão runs into deciduous forest) by far the highest and the cerrado site the lowest. The same data are also given for the Poconé cerrado. Table 12 gives Sørensen similarity indices and association indices for all the sites.

The absence or rarity of a number of characteristic Planalto species from the cerrados of Nhecolândia is interesting. The most striking examples are the general paucity of Myrtaceae, Vochysiaceae (represented only by rare individuals of *Qualea grandiflora* and *Q. parviflora*—apart from in some areas of very poor sandy soils), and the almost complete absence of that

TABLE 12

Comparison of cerrado and cerradão sites using Sørensen similarity index[1] and, in brackets, association index.[2]

	Faz. Ipanema cerradão	Salina Grande cerradão	Faz. S.V. do Rio Claro cerradão	Faz. Acurizal cerrado (Prance & Schaller, 1982)
Faz. Nhu. cerrado	0·59 (0·64)	0·41 (0·41)	0·28 (0·38)	0·32 (0·50)
Faz. Ipanema cerradão		0·52 (0·56)	0·39 (0·42)	0·46 (0·64)
Salina Grande cerradão			0·36 (0·50)	0·23 (0·36)
Faz. S.V. do Rio Claro cerradão				0·33 (0·36)

[1] $\frac{2 \times \text{No. of spp. in common}}{\text{No. of spp. at locality A} + \text{no. at locality B}}$ (Sørensen, 1948).

[2] $\frac{\text{No. of spp. in common}}{\text{Minimum no. of spp. at either locality}}$ (Dice, 1945).

striking tree of Central Brazil, *Pterodon pubescens*. On the other hand, a number of more sourthern species, such as *Linociera hassleriana*, *Calycophyllum multiflorum* and *Machaerium hirtum* are present.

There are many brief references in the literature to cerrados and cerradões in the Pantanal region but they seldom give more than the mention of a few tree species. The work of Prance & Schaller (1982) is an exception since it gives data of all the trees on a 1ha plot of cerrado on Fazenda Acurizal 617°45′S 57°37′W, approx. 140km N of Corumbá) (Fig. 1)—the vegetation, however, is rather different from that at either Nhecolândia or Poconé, since *Qualea parviflora* and *Q. grandiflora* are two of the most important species. As in our areas, typical indicator species of better soils, e.g. *Magonia pubescens* (under its synonym *M. glabrata* St. Hil.), *Astronium* sp. and *Callisthene fasciculata* (absent at Nhecolândia but present at Poconé) occur in the Fazenda Acurizal cerrado. Prance & Schaller's cerrado is most similar to that of Fazenda Ipanema with a Sørensen similarity index for the two sites of 0·46 and an association index of 0·64 (Table 12). Even from brief mentions in the literature it is possible to establish that mesotrophic facies cerradão is widespread in the Pantanal, e.g. Loureiro *et al.* (1982, p. 340–41) mention 'Savana Árborea Densa (cerradão)' with *Magonia pubescens* and *Dipteryx alata*.

Forests of cordilheiras and capões

In the main the floristic composition of the forests of the cordilheiras and capões is very similar to that of the deciduous and semideciduous forests of Central Brazil (see Ratter *et al.*, 1978), and anyone familiar with these forests, say in Goiás, would feel fairly at home at Fazenda Nhumirim. Such features as the great numbers of *Attalea phalerata* and *Acrocomia* palms are also found in the Central Brazilian forests, but the abundant *Copernicia* palms, associated with ultrabasic soils, are missing there. Other trees of the cordilheiras, such as *Linociera hassleriana*, *Fagara chiloperone* and *F.* sp. aff. *hassleriana*, problably represent a more southern element in the flora.

Soil nutrients, particularly calcium, recorded in the surface horizons of the forested cordilheiras are also at the levels typical of deciduous and semideciduous forests in Central Brazil (Table 10, a).

As in the case of cerrado, the literature is full of mentions of deciduous and semideciduous forests in the Pantanal (in fact Amaral & Fonzar (1982) remark that their presence is 'notorious') but generally only very short species lists can be found: this reflects the fact that practically all the studies have been widespread surveys or reconnaissances. In the main these short lists agree well with our observations. Prance & Schaller (1982), in their more detailed study of Fazenda Acurizal, record the species composition of a 1ha plot of semideciduous forest which includes some of the species we observed (e.g. *Astronium fraxinifolium*, *Aspidosperma* spp., *Tabebuia* spp. and *Sterculia striata*).

The capões with *Attalea phalerata* palms are mentioned by various authors, e.g. Loureiro *et al.* (1982), Adamoli (1982), Cunha *et al.* (1985), as are the *Copernicia* palms. The *Copernicia* further emphasizes the relationship with the flora of NE Brazil (see below)—Veloso (1947) points out that *Copernicia australis* Becc. of the Pantanal is a vicariant of *C. cerifera* Mart., the 'Carnaúba' of NE Brazil.

Forest at Corumbá

The majority of the important species occurring in the forest are typical of the very disjunct xeric calcicolous vegetation which has its largest extension in the Caatinga of NE Brazil. Many of the others belong to genera characteristic of the Caatinga and probably represent vicariant species, or true Caatinga species which we have failed to determine because they were collected only in vegetative condition (see Table 9 where Caatinga relationships of species are indicated). Similar vegetation with Caatinga affinities is present on areas of calcareous rocks throughout Central Brazil (Ratter *et al.*, 1978) and even occurs to the south in Rio Grande do Sul and to the north in Venezuela (Rizzini, 1979, p. 219–220). In the same work, Rizzini suggests (p. 326) that this now disjunct vegetation evolved [presumably over a large continuous area] during long dry climatic periods in the Tertiary. Such an explanation seems very plausible as xeric conditions would lead to increasing mineralization of soil surface layers by capillarity, and thus produce over large areas the type of soil high in pH and calcium levels needed by this vegetation. When the climate became more humid, leaching and acidification would occur, leaving calcareous soils (and the associated calcicolous vegetation) only where they could be continuously replenished by weathering parent rock—this would result in the fragmentation of an original enormous extension of Caatinga vegetation into the distribution pattern now seen.

The Caatinga forest at Corumbá often seems to be referred to as Chaco, but in fact is quite different from the true Chaco vegetation of Argentina, Paraguay and Bolivia. True Chaco forest, characterized by presence of *Aspidosperma quebracho-blanco* D. F. K. Schldt., *Caesalpinia melanocarpa* Griseb., *Ruprechtia* sp., *Schinopsis* spp., etc., occurs in localities, often of impeded drainage, quite close to Corumbá; it has also been described further south close to Porto Murtinho (Hueck, 1955). Our observations on Brazilian Chaco forest will be reserved for another publication.

Descriptions by various authors of the forest close to Corumbá reflect this use of the term Chaco. It is classified in EDIBAP (1977–80a) as 'Chaco alto' and in EDIBAP (1977–80b) as the 'Floresta' of the 'Província do Chaco', while in EDIBAP (1979) it is described as 'Floresta alta-rala caducifólia' and its relationship to Chaco is mentioned on p. 195. Loureiro *et al.* (1982, p. 337) use the term 'Savana Estépica Arbórea Densa' and like some other authors they point out the relationship with Caatinga: 'Seus géneros arbóreos são vicariantes homólogos da Estepe (Caatinga)'. Other workers refer to this forest as 'Bosque chaqueña' or 'Mata chaqueña'.

Deciduous forests, characterized by great quantities of *Astronium urundeuva* ('Aroeira'), cover the higher calcareous ground for a conciderable distance around Corumbá (e.g. the railway passes through them until it reaches the Pantanal to the south, then again from near Bodoquena to Miranda). The degree of human disturbance of these forests varies, but there must still be areas far from habitation with little destruction and the creation of a reserve of adequate size in such a place would allow the preservation of an extremely interesting ecosystem. Unless such protection is provided the forests will probably eventually be completely destroyed by timber extraction, agriculture, and limestone-quarrying for the cement industry.

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REFERENCES

ADAMOLI, J. (1982). O Pantanal e suas relações fitogeográficas com os Cerrados. Discussão sobre o conceito de 'Complexo do Pantanal'. *XXXII Congresso Nacional de Botânica—Teresina—PI*: 109–119.

AMARAL, D. L. & FONZAR, B. C. (1982). *Projeto Radambrasil. Levantamento de recursos naturais vol. 26: Folha SD. 21 Cuiabá. Vegetação*: 401–451. Rio de Janeiro.

CUNHA, N. G. DA (1981). Classificação e fertilidade de solos da planície sedimentar do Rio Taquari, Pantanal Matogrossense. *EMBRAPA/UEPAE Circular Técnica* No. 4, 56 pp. Corumbá.

—— (1985). Solos calcimórficos de Corumbá. *EMBRAPA/CPAP, Circular Técnica* No. 18, 34 pp. Corumbá.

——, POTT, A. & GONCALVES, A. R. (1985). Solos calcimórficos da sub-região do Abobral, Pantanal Mato-grossense. *EMBRAPA/CPAP, Circular Técnica* No. 19, 52 pp. Corumbá.

DICE, L. R. (1945). Measures of the amount of ecological association between species. *Ecology* 26: 297–302.

EDIBAP (Estudo de desenvolvimento integrado da Bacia do Alto Paraguai) (1977–80a). *Mapa VII. 1. Bacia do Alto Rio Paraguai, Províncias Fitogeográficas.*

—— (1977–80b). *Mapa VII. 2. Ibid., Vegetação.*

—— (1979). *Relatório de la Fase* vol. 2. *Descrição física e recursos naturais.* 235 pp. Brasília.

HUECK, K. (1955). Bosques Chaquenhos e Extração de Tanino no Brasil. *Revta brasil. Geog.* 17: 343–346.

LOUREIRO, R. L. DE, LIMA, J. P. DE S. & FONZAR, B. C. (1982). *Projeto Radambrasil. Levantamento de recursos naturais vol. 27: folha SE 20. Vegetaçao*: 329–372. Rio de Janeiro.

MUELLER-DOMBOIS, D. & ELLENBERG, H. (1974). *Aims and Methods of Vegetation Ecology*. London, Sydney & Toronto.

POTT, V. J., POTT, A., RATTER, J. A. & VALLS, J. F. M. (1986). Flora da Fazenda Nhumirim, Nhecolândia, Pantanal. Relação preliminar. *Pesquisa em Andamento (EMBRAPA CPAP)* No 5, 26 pp.

PRANCE, G. T. & SCHALLER, G. B. (1982). Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. *Brittonia* 34:228–251.

RATTER, J. A. (1984). *Report of a visit to the UEPAE of EMBRAPA, Corumbá, MS.* Unpubl. report to CPAP/EMBRAPA, Corumbá.

——, RICHARDS, P. W., ARGENT, G. & GIFFORD, D. R. (1973). Observations on the vegetation of northeastern Mato Grosso, I. The woody vegetation types of the Xavantina-Cachimbo Expedition area. *Phil. Trans. R. Soc.* (b) 226:449–492.

——, ASKEW, G. P., MONTGOMERY, R. F. & GIFFORD, D. R. (1977). Observações adicionais sobre o cerradão de solos mesotróficos no Brasil Central. *IV. Simpósio sobre o Cerrado*: 306–316. Universidade de São Paulo.

——, ——, —— & —— (1978). Observations on forests of some mesotrophic soils in central Brazil. *Revta brasil. Bot.* 1:47–58.

RIZZINI, C. T. (1979). *Tratado de Fitogeografia do Brasil.* Vol. 2. 374 pp. São Paulo.

SØRENSEN, T. A. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. *K. dan Vidensk Selsk Biol. Skr.* 5:1–34.

VELOSO, H. P. (1947). Considerações gerais sobre a vegetação do Estado de Mato Grosso. II—Notas prelimares sobre o pantanal e zonas de transição. *Mem. Inst. Oswaldo Cruz* 45:253–272.

WALTER, H. & LIETH, H. (1967). *Klimadiagramm-Weltatlas.* Jena.

APPENDIX

Species recorded in the study areas.

(Collecting numbers given in some cases where specific determination is lacking. R = *Ratter et al.*)

Acacia glomerosa Benth.
A. paniculata Willd.
Acosmium cardenasii Irwin & Kalin Arroyo
A. subelegans (Mohl) Yakovlev
Acrocomia totai Hoehne
Agonandra brasiliensis Miers

Alchornea discolor Poeppig
Alibertia sessilis (Vell.) Schumann
A. sp.
Allophyllus edulis Radlk.
Amburana cearensis (Allemão) A. C. Smith
Anadenanthera colubrina (Vell.) Brenan var. cebil (Griseb.) Altschul
A. sp. 'Angico preto'
Andira cuyabensis Benth.
A. inermis Kunth
A. paniculata Benth.
Anemia sp.
Annona cf. tomentosa R. E. Fries
Aspidosperma pyrifolium Mart.
A. subincanum [Mart. ex] A. DC.
A. tomentosum Mart.
A. sp. 'Guatambu'
A. sp. 'Peroba'
Astronium fraxinifolium Schott.
A. urundeuva (Allemão) Engl.
Attalea phalerata Mart.

Bambusa (Guadua) sp.
Banisteriopsis pubipetala (Adr. Juss.) Cuatrec.
Bauhinia mollis (Bong.) D. Dietr.
B. rufa Steudel
Bowdichia virgilioides Kunth
Bromelia balansae Mez
Brosimum gaudichaudii Trécul
Buchenavia tomentosa Eichler
Bumelia cf. sartorum Mart.
Byrsonima coccolobifolia (Spreng.) Kunth
B. crassifolia (L.) Kunth
B. orbignyana Adr. Juss.
B. verbascifolia (Spreng.) Kunth

Caesalpinia taubertiana S. Moore
Calliandra parviflora Benth.
Callisthene fasciculata (Spreng.) Mart.
Calycophyllum multiflorum Griseb.
Capparis sp. R5415
Caryocar brasiliense Cambess.
Casearia decandra Jacq.
C. sylvestris Sw. var. lingua (Cambess.) Eichl.
Cecropia pachystachya Trécul
Ceiba spp.
Celtis pubescens Kunth
C. sp.
Cereus peruvianus Miller
Chomelia obtusa Cham. & Schlecht.
Chrysophyllum marginatum Radlk. subsp. marginatum
Coccoloba sp.
Combretum leprosum Mart.
Connarus suberosus Planchon subsp. fulvus (Planchon) Forero
Commiphora (Bursera) leptophloeos (Mart.) J. B. Gillett
Copaifera martii Hayne
Copernicia australis Becc.
Cordia glabrata (Mart.) A. DC.
Couepia grandiflora Benth.
Curatella americana L.

Davilla elliptica A. St. Hil.
Dilodendron bipinnatum Radlk.
Diospyros hispida A. DC.
Diplokeleba floribunda N. E. Br.
Dipteryx alata Vog.
Diptychandra aurantiaca (Mart.) Tul. subsp. aurantiaca
Duguetia furfuracea (A. St. Hil.) Benth. & Hook.
Enterolobium contortisiliquum (Vell.) Morong
Eriotheca gracilipes (Schumann) Robyns
Erythrina cf. mulungu [Mart. ex] Benth.
Erythroxylum deciduum A. St. Hil.
E. pelleterianum A. St. Hil.
E. sp.
Eugenia pyriformis Cambess.
E. sp. R5061

Fagara chiloperone (Mart.) Engl.
F. sp. aff. hassleriana Chod.
F. cf. rhoifolia (Lam.) Engl.
Ficus sp.

Guazuma ulmifolia Lam.
Guettarda viburnoides Cham. & Schlecht.

Hancornia speciosa Nees & Mart.
Helicteres lhotskyana (Schott. & Endl.) K. Schum.
Himatanthus obovatus (Muell. Arg.) Woodson
Hymenaea courbaril L. var. stilbocarpa (Hayne) Lee & Langenheim
H. stigonocarpa [Mart. ex] Hayne

Inga sp.

Jacaranda cuspidifolia Mart.
J. sp.
Jacaratia corumbensis Kuntze
Jatropha vitifolia Miller var. cnicodendron (Griseb.) Pax
J. weddelliana Baill.

Kielmeyera coriacea (Spreng.) Mart.

Lafoensia pacari A. St. Hil.
Licania minutiflora (Sagot) Fritsch
Linociera hassleriana (Chod.) Hassler
Lippia cf. urticoides Steudel
Lonchocarpus sp.? 'Sangue de Bugre'
L. sp. R5126
Luehea paniculata Mart.
L. sp. R5098V

Machaerium ?acutifolium J. Vogel
M. hirtum (Vell.) Stellf.
Maclura tinctoria (L.) Engl.
Magonia pubescens A. St. Hil.
Metrodorea mollis Taubert
Mouriri elliptica Mart.
Myrcia sp. R5074

Ocotea suaveolens Hassler
Ouratea castaneaefolia Engl.
O. hexasperma (A. St. Hil.) Benth.?

Pilocereus sp.
Pithecellobium edwallii Hoehne
P. saman Benth.
Platypodium elegans Vog.
Pouteria ramiflora (Mart.) Radlk.
Protium heptaphyllum (Aublet) Marchand
Pseudobombax longiflorum (Mart. & Zucc.) Robyns
P. marginatum (A. St. Hil., Adr. Juss. & Cambess.) Robyns
P. tomentosum (Mart. & Zucc.) Robyns
P. sp.
Pterogyne nitens Tul.
Pterodon pubescens Benth.

Qualea grandiflora Mart.
Q. parviflora Mart.

Randia armata DC.
Rhamnidium elaeocarpum Reiss.
Rourea induta Planchon
Ruprechtia sp.

Salacia elliptica (Mart.) Peyr.
Sapindus saponaria L.
Sapium brasiliense [Spreng. ex] Pax
S. haematospermum Muell. Arg.
S. sp.
Sclerolobium aureum (Tul.) Benth.
Sebastiania brasiliensis Spreng.
Selaginella sp.
Simaba sp.
Simira corumbensis (Standley) Steyermark
Simarouba versicolor A. St. Hil.
Sorocea sprucei (Baillon) J. F. Macbr. subsp. saxicola (Hassler) Berg
Spondias lutea L.
Sterculia striata A. St. Hil. & Naud.
Strychnos pseudoquina A. St. Hil.
Stryphnodendron adstringens (Mart.) Cov.
Swartzia sp. 'Justa conta' R5104V
Syagrus flexuosa (Mart.) Becc.

Tabebuia caraiba (Mart.) Bureau
T. impetiginosa (Mart.) Standley
T. roseo-alba (Ridley) Sandw.
Taccarum weddellianum [Brongn. ex] Schott.
Talinum crassifolium Willd.
Terminalia argentea Mart. & Zucc.
Tocoyena formosa (Cham. & Schlecht.) Schumann
Trema micrantha Blume
Trichilia elegans Adr. Juss. subsp. elegans

Unonopsis lindmannii R. E. Fries

Vatairea macrocarpa (Benth.) Ducke
Vitex cymosa Bert.
Vochysia divergens Pohl

Ximenia americana L. var. americana
Xylosma sp.

Myrtaceae sp.
Myrtaceae sp. 'Goiabinha'
Nyctaginaceae sp.
Indet.
Indet. 2 R5125
Indet. 3