

**The woody flora and soils of seven Brazilian
Amazonian dry savanna areas**

**A thesis presented for the degree of
Doctor of Philosophy
at the
University of Stirling**

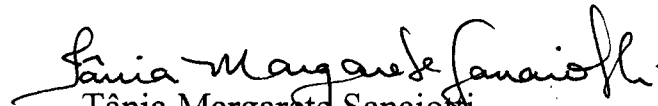
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Declaration

I hereby declare that this thesis has been composed by myself and except where otherwise stated the work contained herein is my own.


Tânia Margarete Sanaiota

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Abstract

This study compares the soils, floristic composition, phytosociological structure and history of seven Brazilian savannas in the Amazon basin: those at Alter do Chão, Amapá, Roraima and SE Humaitá are islands in rain forest; and those at Chapada dos Parecis, Redenção, and Carolina are on the periphery (northern border) of the central Brazilian savannas (the so-called 'cerrado'). A total of 26 transects were sampled by the PCQ method (for trees with dbh \geq 5 cm) and additional tree species were recorded by 'wide patrolling'. A total of 101 species were recorded from the transects and another 43 species were recorded by 'wide patrolling'. *Byrsonima crassifolia*, *B. coccolobifolia*, *Curatella americana*, *Salvertia convallariodora* and *Plathymenia reticulata* occurred in most or all sites, but no species occurred in all transects. The number of species in the isolated savannas decreased with the distance from the central Brazilian core savanna area. Both cluster analysis (based on the Sørensen Similarity Index) and ordination (DCA), showed that the disjunct and non-isolated peripheral areas were in floristically distinct groups. Five surface soil samples (0 - 10 cm) were collected from each of the 26 transects. Two soil cores (up to 4 m depth), one located in the savanna and the other from the nearest forest present, were taken from each study site for carbon isotope analysis. All the sites had acidic soils (pH 4.5 - 5.2) and a wide range of concentrations of aluminium (0.12 - 1.49 meq 100g^{-1}); most of the other soil properties varied significantly within study sites. An ordination (PCA) distinguished the soils from Amapá, Alter do Chão, Redenção and Roraima, but did not distinguish the disjunct sites from non-isolated peripheral ones. The soil $\delta^{13}\text{C}$ values of all the disjunct savannas indicated a vegetation change in the past from C_3 to C_4 plants, showing that forest (or at least a vegetation with few C_4 plants) formerly covered these sites. ^{14}C dating indicated that the disjunct savannas are of relatively recent origin, e.g. Humaitá was dated at about 2,000 years BP, and hence that they are not remnants of a more widespread Pleistocene savanna in the Amazon.

Resumo

Este estudo compara os solos, a composição florística, a fitossociologia e a história de sete savanas situadas na bacia Amazônica brasileira: Alter do Chão, Amapá, Roraima e sudeste de Humaitá são ilhas isoladas dentro de floresta de terra firme; enquanto Chapada dos Parecis, Redenção e Carolina estão na periferia da distribuição do cerrado. Um total de 26 transectos foram amostrados pelo método de ponto-quadrante (árvores com $dap \geq 5$ cm) e através de reconhecimento geral. Um total de 101 espécies foram amostradas pelos transectos e outras 43 foram registradas somente pelas listas de reconhecimento. *Byrsonima crassifolia*, *B. coccolobifolia*, *Curatella americana*, *Salvertia convallariodora* e *Plathymenia reticulata* foram encontradas na maioria das regiões estudadas mas não em todos os transectos. O número de espécies encontrado para cada savana isolada diminuiu com o aumento de sua distância em relação a área central do cerrado. As análises de agrupamento (baseada no índice de similaridade de Sørensen) e ordenações (DCA) separaram em grupos florísticos distintos as savanas da periferia das isoladas. Cinco amostras de solo superficial (0 - 10 cm) foram coletadas para cada um dos 26 transectos. Duas tradagens (até 4 m de profundidade), uma na savana e outra na mata de terra firme mais próxima foram feitas para cada uma das sete áreas de estudo para análises isotópicas. Todas as áreas possuem solos ácidos (pH 4,5 - 5,2) e com concentrações de alumínio muito variadas (0,12 - 1,49 meq 100g⁻¹); a maioria das outras propriedades do solo variaram significativamente entre os transectos. A análise de ordenação (PCA) distinguiu os solos do Amapá, Alter do Chão, Redenção e Roraima, porém não os separou entre áreas isoladas e da periferia. Os valores de $\delta^{13}C$ de todas as áreas isoladas indicam que a vegetação mudou no passado de plantas do tipo C₃ para C₄, inferindo que uma floresta (ou uma vegetação densa com poucas plantas C₄) cobriu aquelas áreas. A datação de carbono indicou que as savanas isoladas são de origem relativamente recente, e.g. Humaitá foi datada em 2.000 anos A.P., sugerindo que elas não são relíquias de uma possível vegetação de savana de ampla distribuição na Amazônia durante o Pleistoceno.

Chapter 1.

General introduction

The concept of savanna used in this study follows Sarmiento (1984) who modified the usage of Beard (1953) to give a more precise definition of the tropical savanna ecosystem:

“a type of ecosystem of the warm (lowland) tropics dominated by a herbaceous cover consisting mostly of bunches of grasses and sedges that are more than 30 cm in height at the time of maximum activity. The herbaceous cover shows a clear seasonality in its development, with a period of low activity related to water stress. Fire in these systems is a recurring natural factor, and fires may also be started by people once a year. The savanna may include woody species (shrubs, trees, palm trees), but they never form a continuous cover that parallels the grassy one”.

Neotropical savanna ecosystems can be classified on characteristics of seasonality (Sarmiento & Monasterio 1975):

1. Semi-seasonal savannas occur under weak seasonal variation, with one and sometimes two very short dry seasons producing a slight water stress. They form disjunct patches in areas otherwise covered by rainforests.
2. Seasonal savannas, which are the most widespread, are characterised by rather long periods of water deficiency.
3. Hyperseasonal savannas are subjected to alternate periods of water shortage and waterlogging during each annual cycle. They occur in areas which are poorly drained for much of the year.

4. Marshy savannas that experience long periods of water excess. They occur in wet sites on valley sides or tableland margins throughout the region.

In addition to this ecological system, Sarmiento (1983) also classified neotropical savannas on structural characteristics according to their position on the gradient from open treeless grassland to closed woodland.

A variety of terms equivalent to the seasonal savannas of the present study are used in different parts of South America and these are listed in Table 1.1.

This study investigates seven seasonal savannas in the Brazilian Amazon. Four are islands in rain forest and three are on the periphery (northern border) of the central Brazilian savannas (the cerrado). Chapter 2 characterizes the study sites, including climate, soils and vegetation. Chapter 3 assesses the nutrient status and physical soil characteristics for all the sites. Chapter 4 examines the floristic composition and analyzes the similarities among the sites. Chapter 5 uses isotope techniques and organic matter carbon dating to investigate the vegetational history of the sites.

species of South American savannas corresponding to the seasonal savannas in the present study.

Region and local name	Characteristic species
SURINAME	
Dry savanna ¹	<i>Bombax flaviflorum</i> , <i>Clusia fockeana</i> , <i>C. nemorosa</i> , <i>Conomorpha magnoliifolia</i> , <i>Humiria floribunda</i> , <i>Licania incana</i> , <i>Matayba opanea</i> , <i>Ocotea schomburgkiana</i> , <i>Pagamea guianensi</i> .
Dry savanna forest ¹	<i>Cupania scorbiculata</i> , <i>Dimorphandra conjugata</i> , <i>Loxopterygium sacotii</i> , <i>Licania incana</i> , <i>Ocotea glomerata</i> , <i>Ormosia</i> , <i>Swartzia bannia</i> .
Dry savanna wood ¹	<i>Dimorphandra conjugata</i> , <i>Humiria floribunda</i> , <i>Inga lateriflora</i> , <i>Ormosia costulata</i> , <i>Pagamea capitata</i> , <i>Retiniphyllum schomburgkii</i> , <i>Swartzia bannia</i> , <i>Ternstroemia punctata</i> .
GUAYANA	
Open wooded savanna ²	
Campo cerrado	<i>Byrsonima coccolobifolia</i> , <i>B. coriacea</i> , <i>B. crassifolia</i> , <i>Bowdichia virgilioides</i> , <i>Curatella americana</i> , <i>Pavonia speciosa</i> , <i>Plumeria inodora</i> .
Campo coberto	<i>Antonia ovata</i> , <i>Byrsonima coccolobifolia</i> , <i>B. coriacea</i> , <i>B. crassifolia</i> , <i>Curatella americana</i> , <i>Plumeria inodora</i> , <i>Randia formosa</i> .
VENEZUELA	
Dry savannas ³	
Sabana cerrada (low, spaced trees)	<i>Byrsonima crassifolia</i> , <i>Bowdichia virgilioides</i> , <i>Curatella americana</i>
Sabana boscosa (parkland)	
Amazonian-type savannas ⁴	<i>Archytaea</i> , <i>Cyrilla racemiflora</i> , <i>Clusia</i> , <i>Duguetia</i> , <i>Humiria balsamifera</i> , <i>Ocotea</i> , <i>Qualea</i> , <i>Ramatoulla</i> , <i>Rhodognaphalopsis</i> , <i>Pentamerista</i> , <i>Terminalia</i> .
Llanos-type savannas ⁴	<i>Byrsonima crassifolia</i> , <i>Bowdichia virgilioides</i> , <i>Casearia sylvestris</i> , <i>C. ulmifolia</i> , <i>Chaunochiton angustifolium</i> , <i>Curatella americana</i> , <i>Hirtella racemosa</i> , <i>Jacaranda</i> sp., <i>Platycarpum orinocense</i> , <i>Roupala montan</i> , <i>Xylopia aromatica</i> .
COLOMBIA	
Macaireo rufescentis-Bonetietum martianae ⁵	<i>Bonnetia martiana</i> , <i>Macairea rufescens</i> .
Dimorphandra cuprea-Ilex divaricata ⁵	<i>Dimorphandra cuprea</i> , <i>D. vermicosa</i> , <i>Ocotea esmeraldana</i> , <i>Ormosia macrophylla</i> , <i>Schizaea incurvata</i> .
BOLIVIA	
Arboleda ⁶ , Pampa arbolada ⁷	<i>Curatella americana</i> , <i>Tabebuia suberosa</i> ,
Chaparral ⁶	<i>Acacia</i> , <i>Cassia</i> , <i>Mimosa</i> .
BRAZIL: AMAZON	
Campo cerrado ⁸	<i>Byrsonima crassifolia</i> , <i>Curatella americana</i> .
Coberto, campo alto, campina de caimbé ⁹	<i>Aegiphila lhotzkyana</i> , <i>Curatella americana</i> , <i>Pithecellobium cochleatum</i> , <i>Plumeria</i> sp.
Chapada, tabuleiro, carrasco ¹⁰	<i>Callisthene fasciculata</i> , <i>Caryocar cuneatum</i> , <i>Dimorphandra gardneriana</i> , <i>Parkia platycephala</i> , <i>Platonia insignis</i> , <i>Salvertia convallariodora</i> .
Teso ¹¹	<i>Byrsonima crassifolia</i> , <i>Curatella americana</i> , <i>Hancornia speciosa</i> , <i>Salvertia convallariodora</i> .
Campos de terra firme ¹²	<i>Antonia ovata</i> , <i>Bowdichia virgilioides</i> , <i>Byrsonima crassifolia</i> , <i>Caryocar microcarpum</i> , <i>Cassia moschata</i> , <i>Curatella americana</i> , <i>Hancornia speciosa</i> , <i>Himatanthus articulatus</i> , <i>Humiria balsamifera</i> , <i>Piptademia macrocarpa</i> , <i>Roupala complicata</i> , <i>Salvertia convallariodora</i> , <i>Tabebuia caraiba</i> , <i>Xylopia aromatica</i> .
BRAZIL: CENTRAL	
Campo cerrado ^{13,14,15}	<i>Anacardium pumilum</i> , <i>Andira humilis</i> , <i>Annona crassiflora</i> , <i>A. coriacea</i> , <i>A. dioica</i> , <i>Aspidosperma tomentosum</i> , <i>Byrsonima coccolobifolia</i> , <i>Byrsonima verbascifolia</i> , <i>Caryocar brasiliense</i> .
Cerrado <i>sensu stricto</i> ^{13,14,15}	<i>Connarus suberosus</i> , <i>Curatella americana</i> , <i>Dalbergia violacea</i> .
Savana arbórea densa ¹⁶	<i>Didymopanax vinosum</i> , <i>D. macrocarpum</i> , <i>Dimorphandra mollis</i> .
Savana arbórea aberta ¹⁶	<i>Diospyros hispida</i> , <i>Erythroxylum suberosum</i> , <i>Hancornia speciosa</i> .
Savana parque ¹⁶	<i>Kielmeyera coriacea</i> , <i>Ouratea spectabilis</i> , <i>Palicourea rigida</i> , <i>Pisonia olfersiana</i> , <i>Piptocarpha rotundifolia</i> , <i>Plathymenia reticulata</i> , <i>Qualea parviflora</i> , <i>Salvertia convallariodora</i> , <i>Sclerolobium aureum</i> , <i>Tabebuia ochracea</i> , <i>Tocoyena formosa</i> , <i>Vochysia elliptica</i> , <i>V. rufa</i> .

¹ Heyligers 1963, ² Eden 1964, ³ Sarmiento & Monasterio 1969, ⁴ Huber 1982, ⁵ Duirevoorden & Lipps 1995, ⁶ Denevan 1966.

⁷ Killeen 1990, ⁸ Takeuchi 1960, ⁹ Andrade-Lima 1960, ¹⁰ Eiten 1994, ¹¹ Huber 1898 and Bastos 1984, ¹² Braga 1979, ¹³ Ratter & Dargie 1992, ¹⁴ Ribeiro *et al.* 1983, ¹⁵ Ferri 1983, ¹⁶ Veloso *et al.* 1991.

Chapter 2.

Study sites

This study was carried out in seven sites in Brazilian Amazonia. The sites at Amapá, Alter do Chão, Roraima and South-east Humaitá are isolated savannas surrounded by rain forest; whilst those at the Chapada dos Parecis, Redenção and Carolina have contact with the large (core) area of Central Brazilian savannas (Fig. 2.1).

LOCATION

The latitudes and longitudes for each site are in Table 2.1, with detailed descriptions given below. The Highway nomenclature follows Quatro Rodas (1993), where BR means national highway, with other letters (e.g. PA, MT) specifying the state highways.

Amapá -Three survey sites were located along BR 156, the first transect (**T3**) 27 km N of Macapá, the second (**T1**) 45 km N of Macapá, opposite the entrance of the EMBRAPA-CPAF experimental station, and the third (**T2**) 4 km N of the Ferreira Gomes bridge (Fig. 2.2).

Table 2.1. Coordinates of all survey sites for each study area.

Transect Number	Location
(Ap) Amapá state	
T1	00° 14'N, 51° 03'W
T2	00° 27'N, 51° 05'W
T3	00° 54'N, 51° 11'W
(Alt) Alter do Chão, Pará	
T4	02° 30'S, 54° 56'W
T5	02° 31'S, 54° 56'W
T6	02° 28'S, 54° 54'W
T7	02° 32'S, 54° 54'W
(RR) Roraima state	
T8	03° 38'N, 60° 58'W
T9	03° 21'N, 60° 52'W
T10	04° 53'N, 60° 54'W
T11	02° 54'N, 60° 32'W
(Hu) SE Humaitá, Amazonas	
T12	08° 28'S, 61° 43'W
T13	08° 30'S, 61° 38'W
T14	08° 35'S, 61° 25'W
T15	08° 35'S, 61° 23'W
(CP) Chapada dos Parecis, Mato Grosso	
T16	14° 20'S, 58° 02'W
T17	14° 20'S, 58° 06'W
T18	14° 00'S, 58° 16'W
(Re) Redenção, Pará	
T19	08° 12'S, 50° 02'W
T20	08° 18'S, 50° 02'W
T21	08° 16'S, 50° 02'W
T22	08° 08'S, 49° 54'W
(C) Carolina, Maranhão	
T23	07° 11'S, 47° 25'W
T24	07° 07'S, 47° 25'W
T25	07° 02'S, 47° 27'W
T26	06° 57'S, 47° 28'W

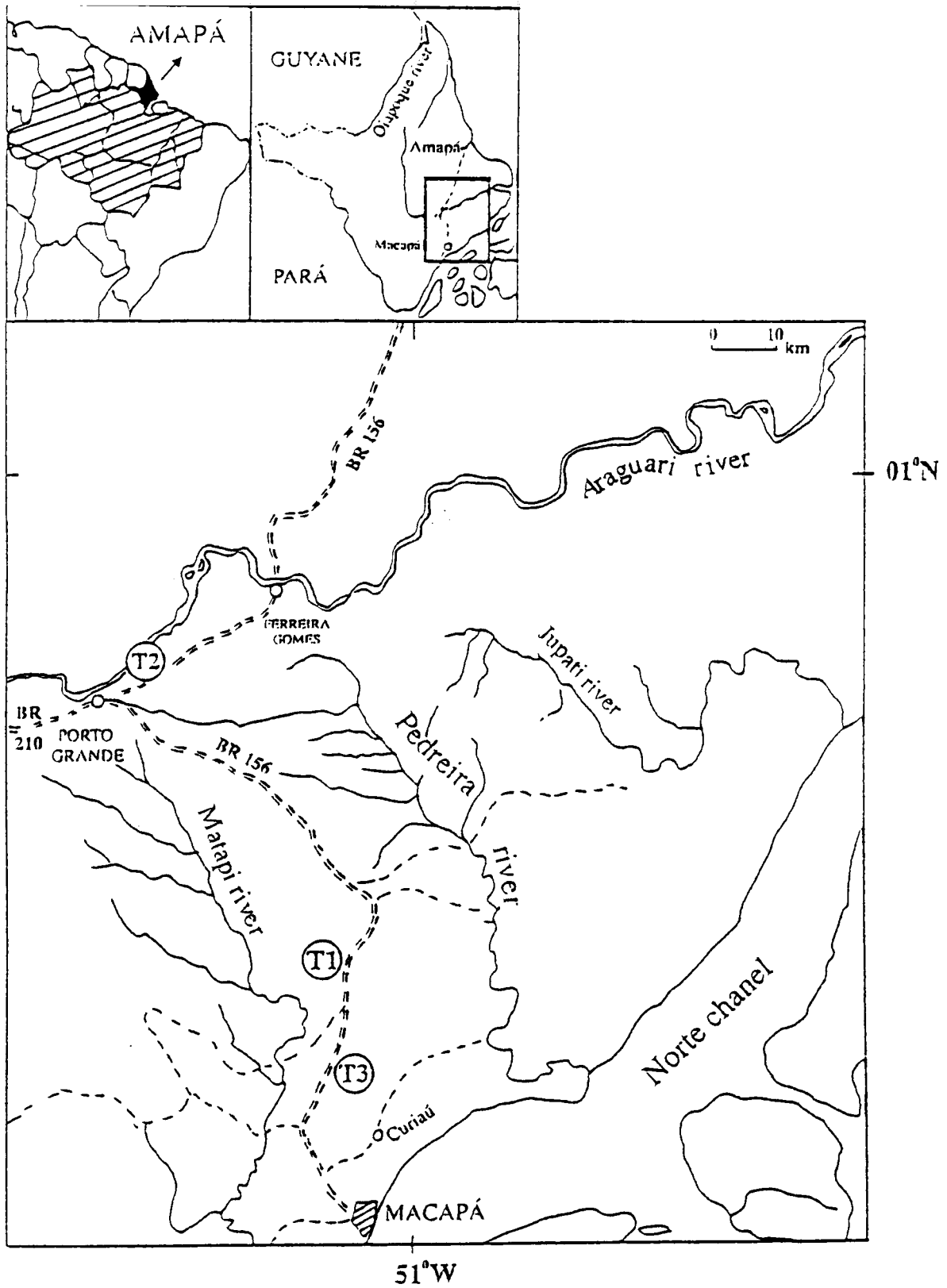


Fig. 2.2. Map of the Amazon Basin showing the state of Amapá (above) and the location of the three transects (below).

Alter do Chão - Four transects were located near the village of Alter do Chão towards the city of Santarém, state of Pará. Two transects (**T4** and **T5**), located 3 km apart, were near the eastern margin of Lake Verde. The third transect (**T6**) was 15 km E of Alter do Chão on the PA 457, then taking the road to Ponta de Pedra and about 3 km before the village, while the fourth transect (**T7**) was located 7 km from Alter do Chão on the same road (Fig. 2.3).

Roraima - Four transects were located in the state of Roraima. The first transect (**T8**) was located 98 km N of Boa Vista on the BR 174, 2 km E along a small side road (ramal). The second transect (**T9**) lay 55 km N of the Caumé river along the BR 174. Transect **T10** was situated 128 km N of Boa Vista on the RR 400 some 10 km E of its junction with the BR 174, and (**T11**) was located some 27 km from Boa Vista on the RR 321 to the Água Boa de Cima stream, 3 km past the bridge (Fig. 2.4).

South-east Humaitá - Four transects were made along the road to Bodocó and Igarapé Preto which crosses the isolated patch of savanna located south of the Transamazônica highway (BR 230) about 150 km E of the city of Humaitá. The first transect (**T12**) was 67-69 km south of the junction with the BR 230, the second (**T13**) 80 km south, the third (**T15**) at 110 km S of Bodocó and the fourth (**T14**) some 4 km E of Bodocó on the road to Igarapé Preto (Fig. 2.5).

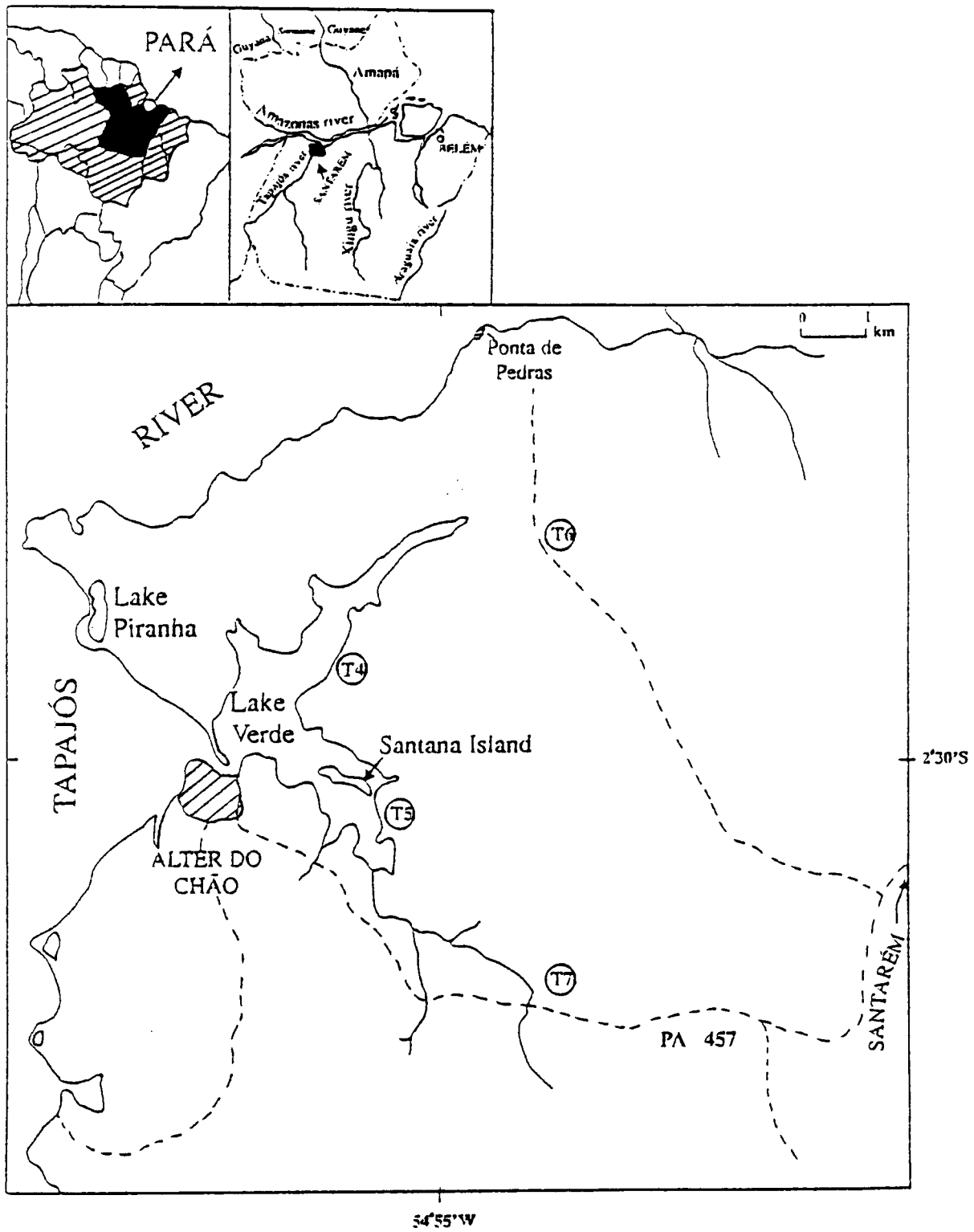


Fig. 2.3. Map of the Amazon Basin showing the state of Pará (above) and the location of the four transects near Alter do Chão (below).

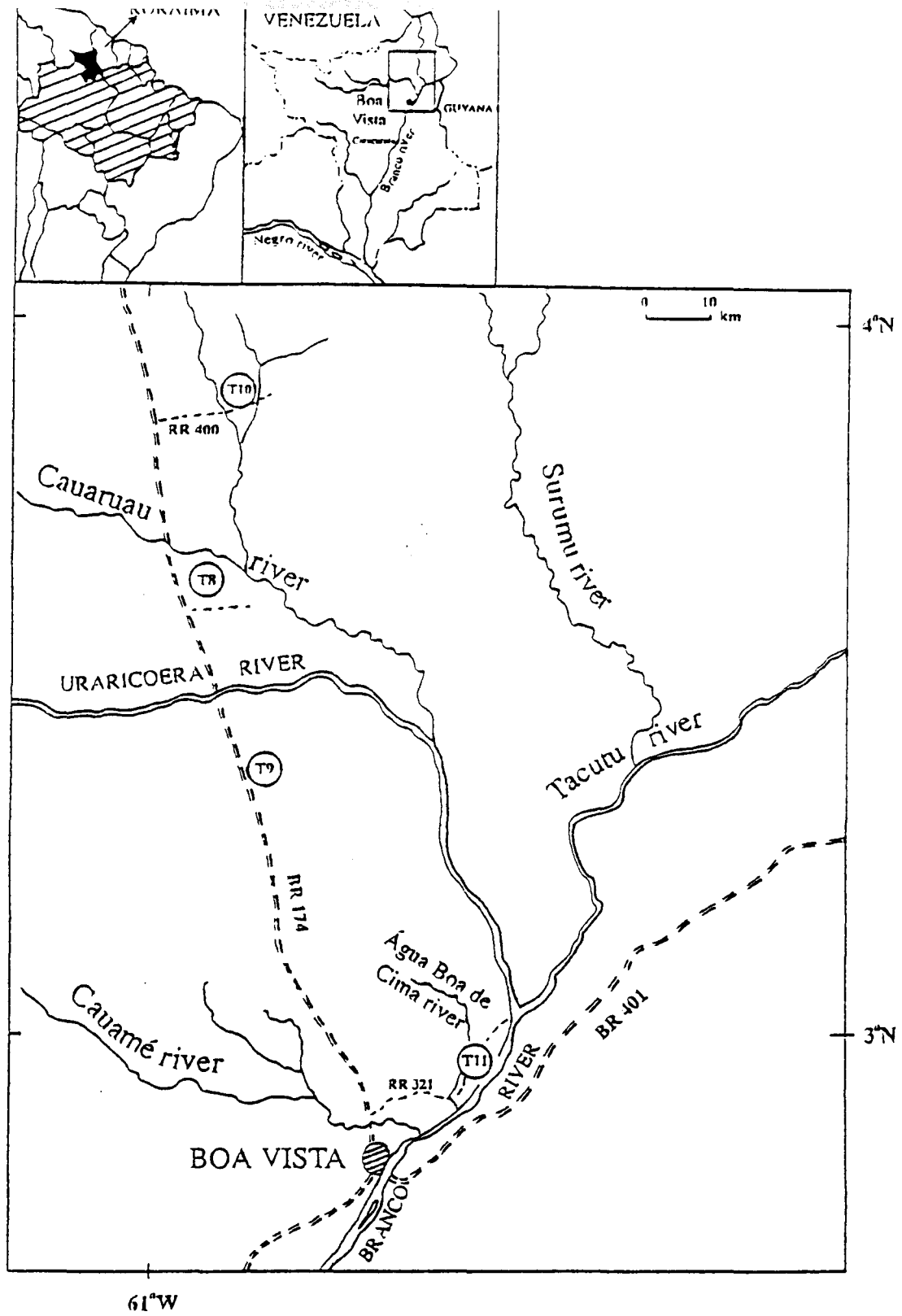


Fig. 2.4. Map of the Amazon Basin showing the state of Roraima (above) and the location of the four transects (below).

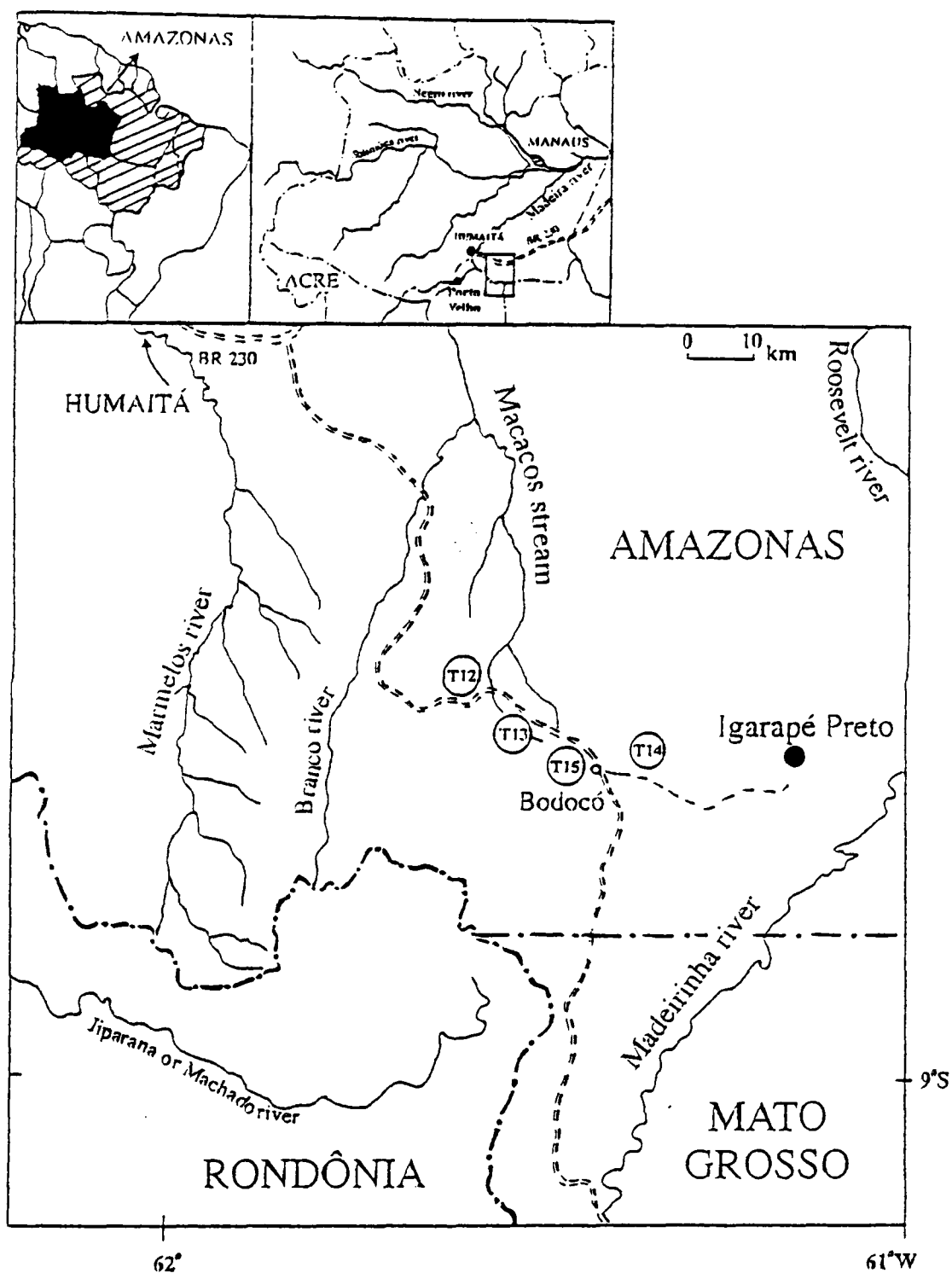


Fig. 2.5. Map of the Amazon Basin showing the state of Amazonas (above) and the location of the four transects (below).

Chapada dos Parecis - Three transects were made in non-cultivated areas inside a farm called “Grupo Itamarati Norte”, in the state of Mato Grosso. The first (T16) and the second (T17) transects were only 2 km apart, on the MT 170, 3 km N of its junction with the BR 364. The third (T18) lay on a small unclassified road 2 km E of the MT 170 9 km from its crossing with the BR 364 (Fig. 2.6).

Redenção - Four transects were made near the city of Redenção, state of Pará. Three (T19 - T21) were south of the city (at 21 km, 30 km and 28 km respectively), the last of these was in the Fazenda Chocolate ranch. The fourth transect (T22) was 18 km east of the city on the PA 287 to Conceição do Araguaia (Fig. 2.7).

Carolina - Four transects were located north of the city of Carolina, state of Maranhão, along the BR 010. The first transect (T23) at 18 km, (T24) at 26.5 km, (T25) at 38 km and (T26) at 48 km, all towards the city of Estreito (Fig. 2.8).

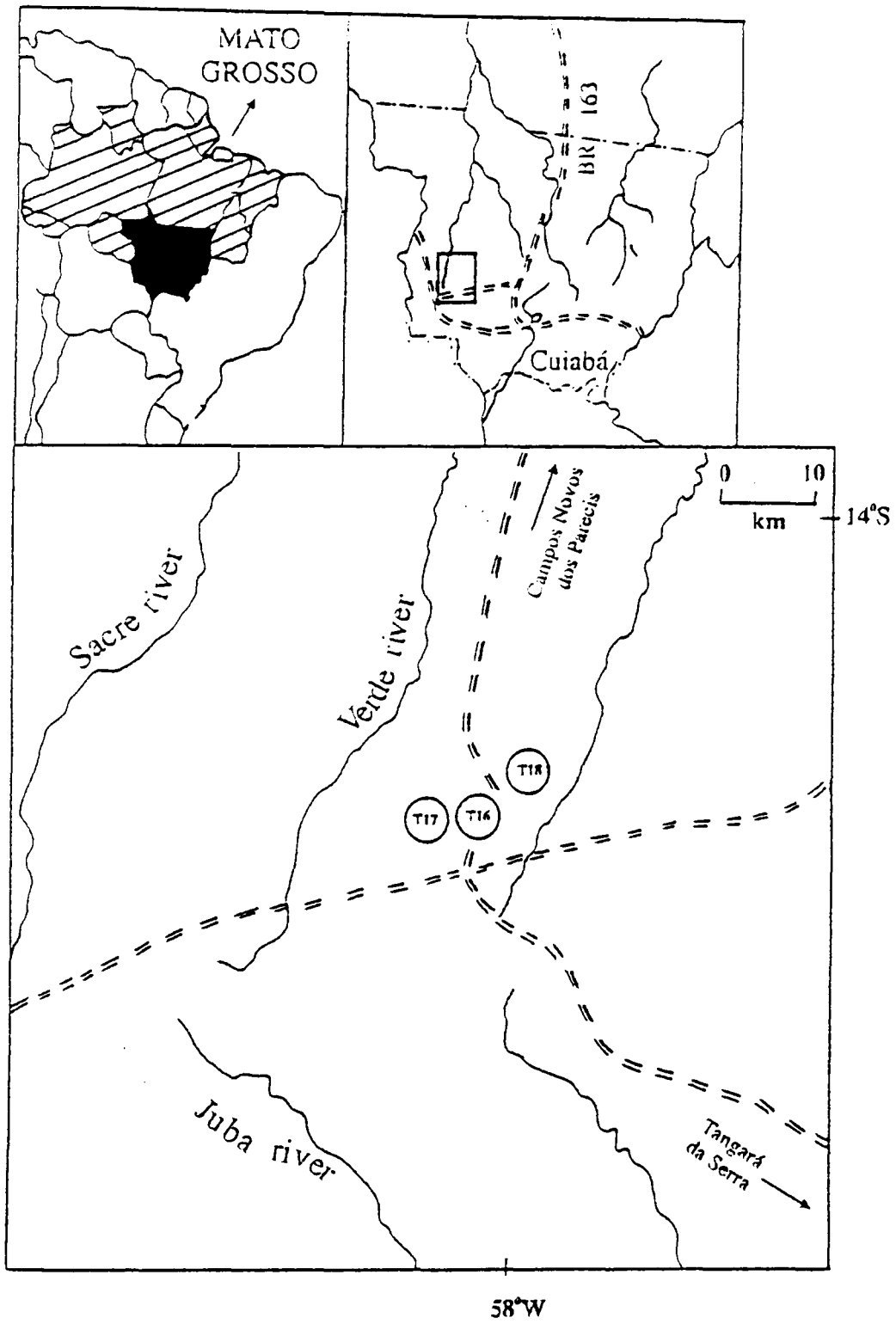


Fig. 2.6. Map of the Amazon Basin showing the state of Mato Grosso (above) and the location of the three transects in the Chapada dos Parecis (below).

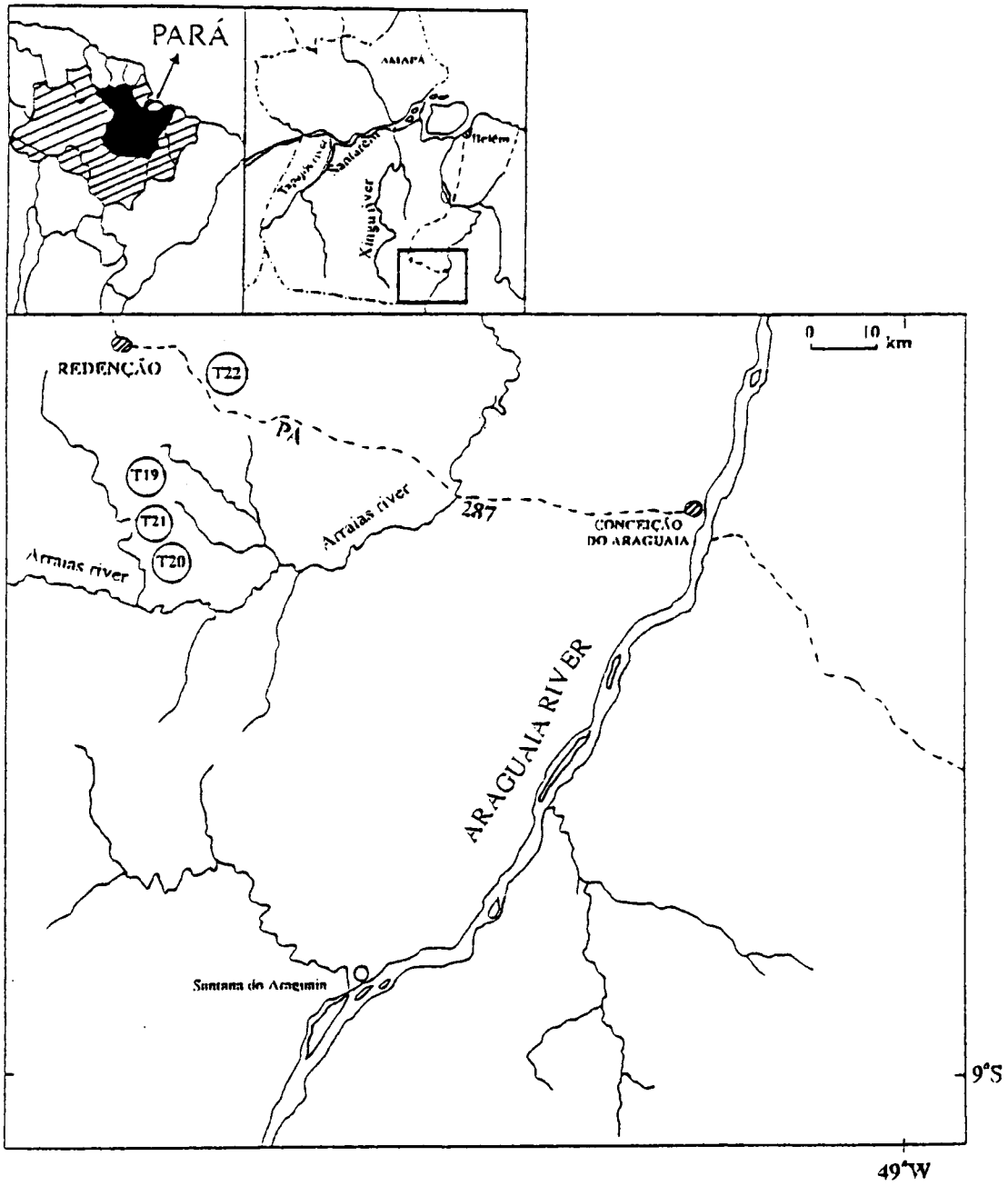


Fig. 2.7. Map of the Amazon Basin showing the state of Pará (above) and the location of the four transects near Redenção (below).

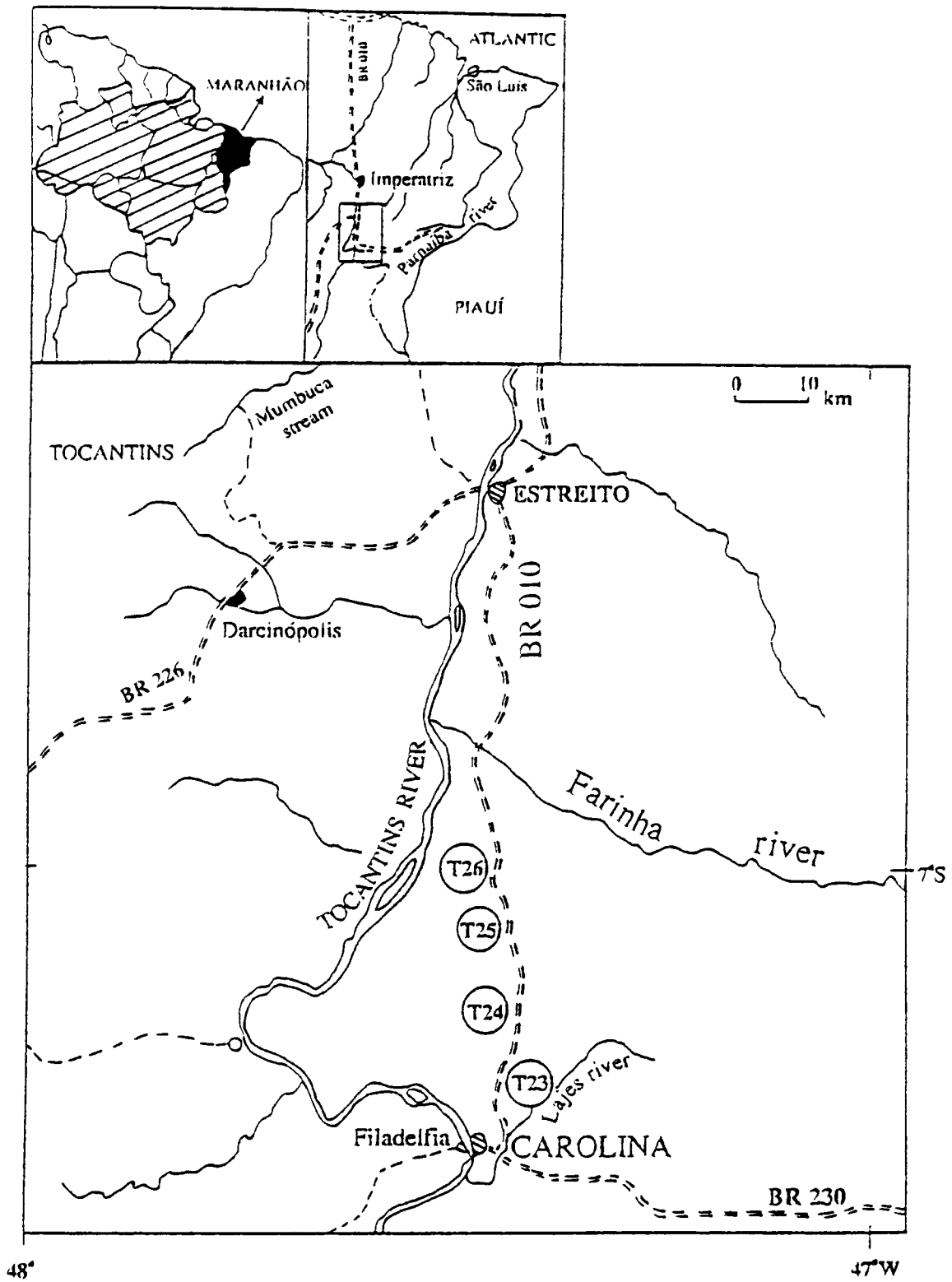


Fig. 2.8. Map of the Amazon Basin showing the state of Maranhão (above) and the location of the four transects north of Carolina (below).

CLIMATE

Summarizing climatic types for all the study sites, Roraima is Tropical hot subhumid, Amapá, Alter do Chão, Humaitá, Chapada dos Parecis, Redenção and Carolina are Equatorial hot humid (Nimer 1989).

Temperature

Roraima and Amapá have the highest mean monthly temperatures, above 26°C, all other sites have between 24° and 26°C. Mean monthly temperatures for up to 30 years are shown in Table 2.2.

Rainfall

Annual rainfall for up to 30 years in the Roraima and Carolina areas was 1,500 to 1,750 mm; Alter do Chão, Chapada dos Parecis and Redenção have between 1,750 and 2,000 mm; and Amapá and SE Humaitá have 2,750 mm.

The rainy season for the most southerly sites at SE Humaitá, Chapada dos Parecis, Redenção and Carolina is from October to April; at Alter do Chão and Amapá, the rainy season is from December to May. Figure 2.9 shows monthly rainfall figures for Amapá, Roraima, Chapada dos Parecis, Redenção and Carolina averaged over the same period as for the temperature figures in Table 2.2.

Table 2.2. Mean monthly temperatures (°C) (with the ranges of the mean minima and mean maxima, in parentheses) for all study sites. Data provided by DNMET (1992), RADAM (1975), Airport of Santarém (PA), Grupo Itamarati Norte (MT) and DNAEE (DF).

	Amapá 1968-90	Alter do Chão 1985-91	Roraima 1977-93	SE Humaitá 1966-81	Chapada dos Parecis 1962-90	Redenção 1966-90	Carolina 1976-90
January	26.0 (23.0-29.7)	25.7 (23.4-30)	27.8 (19-36.1)	28.5 (23-34)	24.0 (20.4-32.3)	25.1 (20.2-31.2)	25.2 (21.9-30.1)
February	25.7 (23.1-29.2)	25.5 (22.3-30)	28.0 (20.2-37.6)	27.5 (23-32)	27.0 (21.2-31.6)	25.2 (20.3-31.1)	25.3 (22.0-30.3)
March	25.7 (23.2-29.3)	25.6 (23.6-28.4)	28.4 (19.2-38.2)	28.5 (24-33)	24.3 (20.4-31.4)	25.4 (20.5-31.3)	25.4 (22.2-30.3)
April	25.9 (23.5-29.5)	25.7 (24.4-28.9)	28.2 (20-37.4)	28.5 (24-35)	27.7 (19.1-33.6)	25.8 (20.8-31.9)	25.9 (22.3-31.2)
May	26.1 (23.5-30)	25.7 (24.4-28.9)	27.0 (19-36.2)	29.5 (24-35)	24.4 (19.1-31.5)	26.1 (20.3-33)	26.2 (21.5-32.3)
June	26.2 (23.2-30.3)	25.5 (23.9-28.7)	26.2 (18.6-34.3)	28.5 (23-34)	25.4 (15.1-32.1)	25.5 (18.3-33.6)	26.1 (20-33.2)
July	26.1 (22.9-30.6)	25.6 (23.4-29.6)	26.1 (17.6-35)	28.5 (22-35)	24.5 (16.4-32.8)	25.4 (17.7-34.3)	26.4 (19.5-33.2)
August	26.8 (23.3-31.5)	26.2 (24.4-30)	26.7 (21-34.8)	28 (20-36)	24.7 (19.1-34.9)	26.1 (17.9-35.2)	27.5 (20.6-33.8)
September	27.5 (23.4-32.1)	26.8 (25.5-29.7)	28.2 (20-36.4)	27 (22-34)	25.3 (19.5-32.5)	26.4 (19.7-34.2)	27.8 (22.3-34.2)
October	27.9 (23.5-32.6)	27 (24.7-29.8)	28.8 (20.6-36.8)	28.5 (23-34)	24.5 (20.8-32.8)	26.0 (20.8-32.7)	26.6 (22.2-32.1)
November	27.7 (23.5-32.3)	26.8 (24.5-30.6)	28.6 (21.2-36.2)	27.5 (23-32)	25.0 (21.8-32.9)	25.8 (20.5-32.1)	25.9 (22.1-31.0)
December	27.0 (23.4-31.4)	26.5 (23.8-30.5)	28.3 (21.2-36.6)	28.5 (24-33)	25.5 (19.9-32.9)	25.3 (20.3-31.5)	25.4 (21.8-30.4)

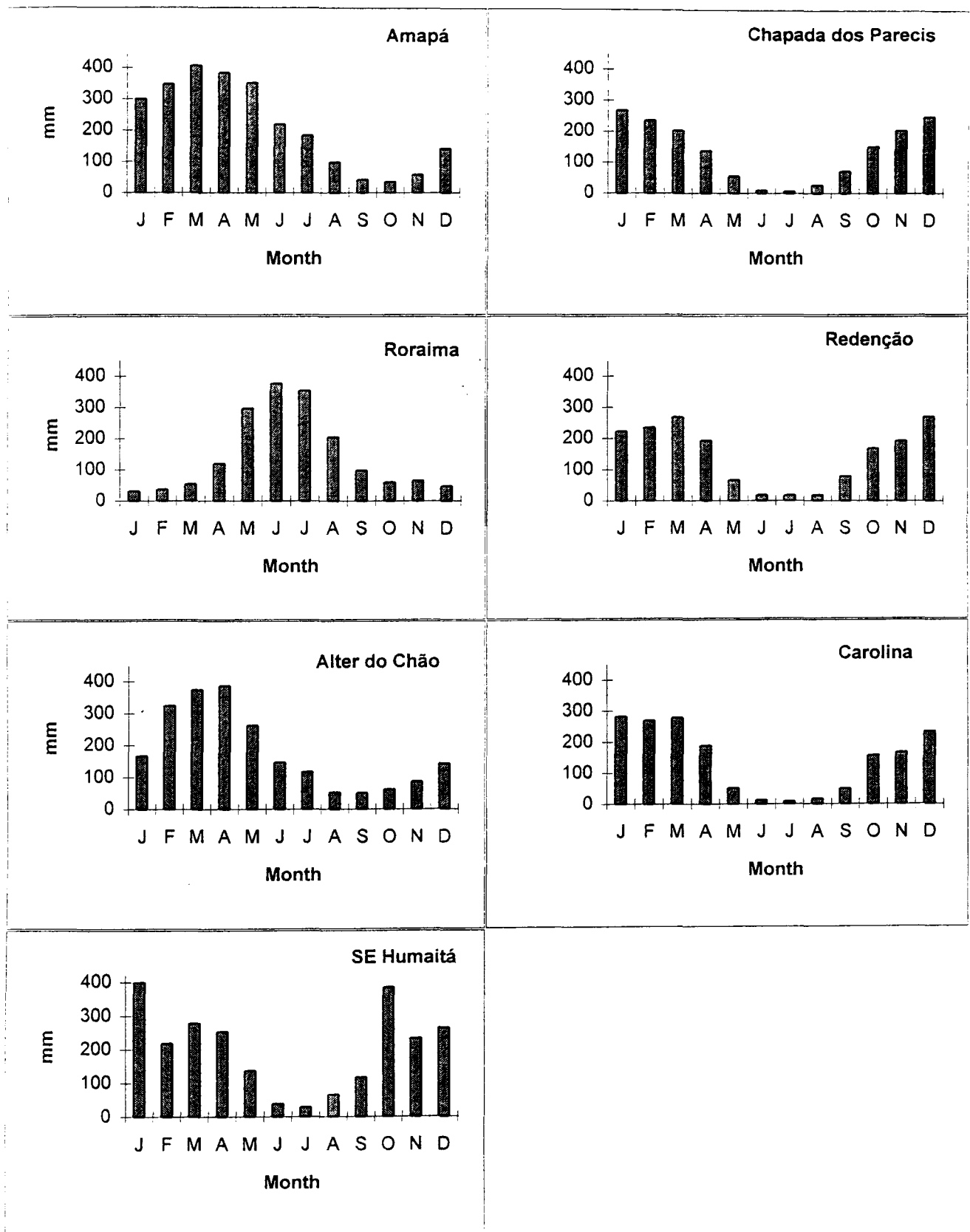


Fig. 2.9. Monthly rainfall (mm) of all the study sites. Data provided by DNMET (1992), RADAM (1975), Airport of Santarém (PA), Grupo Itamarati Norte (MT) and DNAEE (DF).

VEGETATION, SOIL AND GEOLOGY GENERAL OVERVIEW

Amapá - The savanna vegetation here is a long strip stretching north-east along most of the length of the state, and with an area of about 11,000 km² (RADAM 1974). The vegetation type varies from wooded to treeless grasslands and hyperseasonal savannas dominated by tall grasses and sedges (Azevedo 1967). The soils are classified as dystrophic yellow latosols, derived from Tertiary sediments (RADAM 1974)*.

Alter do Chão - The Tapajós river area has several small patches of isolated savanna vegetation. The village of Alter do Chão is near the mouth of the river, and the savannas between Alter do Chão and Santarém cover an area of about 50 km². The vegetation of the region is mainly savanna with scattered trees, but the peninsula in front of the village has areas with large clumps of shrubs and trees and areas of open grassland (Miranda 1993, Sanaiotti & Magnusson 1995). The soils are classified as dystrophic yellow latosols and dystrophic quartz sands, belonging to the Alter do Chão Formation, derived from paleozoic and/or cenozoic sediments (RADAM 1976).

* The soil classifications are from RADAM using the Brazilian system (EMBRAPA 1981), the equivalent terminology following two widely used international systems (FAO/UNESCO 1974, Soil Survey Staff 1975, 1987) is presented in Table 2.3.

Table 2.3. Taxonomic correlations among three major classification systems for soils discussed in relation to the study sites (after Sanchez 1976; Richter & Babbar 1991).

Brazilian ¹	FAO / UNESCO ²	USDA Soil Taxonomy ³
Latossolos Latossolos amarelos	Ferralsols Xantic Ferralsols	Oxisols Ustox / Udox
Solos Podzólicos	Acrisols	Ultisols
Podzóis Regossolos Areias quartzosas	Podzols Arenosols/Regosols Arenisols	Spodosols Psamments / (Entisols) Quartzipsamments
Podzóis gigantes	Arenosols	Albic quartzipsamments
Podzóis Hidromórficos	Arenosols	Tropaquods

¹ EMBRAPA (1981)

² FAO / UNESCO (1974)

³ Soil Survey Staff (1975, 1987)

Roraima - The savannas are located in the north of the state, and extend over the borders into Guyana (Rupununi savannas) and Venezuela (Gran sabana) (Goodland 1966), covering an area of approximately 17,000 km². The savanna areas include both grassland and savana parque RADAM (1975). Other studies in the Rio Branco-Rupununi savannas (Dantas & Rodrigues 1982, Takeuchi 1960) characterized large regions as waterlogged. The soils are classified as yellow latosols and lateritic concretionary soils, belonging to the Boa Vista Formation with Tertiary Pleistocene sediments (RADAM 1975).

SE Humaitá - The area is about 5,000 km² and dominated by savana parque (RADAM 1978) although a large part is waterlogged for part of the year. Two botanical studies (Gottsberger & Morawetz 1986 and Janssen 1986) were made in the savannas near the city. The soils are classified as Hydromorphic alic laterites and Hydromorphic quartz sands, belonging to the Prosperança Formation, derived from Upper Pre-Cambrian to eo-Paleozoic sediments (RADAM 1978).

Chapada dos Parecis - RADAMBRASIL (1982) classified the region as savana arbórea aberta. Previous studies in the region were mainly carried out near the capital, Cuiabá (Guarim Neto *et al.* 1994, Nascimento & Saddi 1992). The soils are classified as dark red and red yellow latosols, and belong to the Planalto dos Parecis Formation, derived from Tertiary sediments (RADAMBRASIL 1982).

Redenção - The area has both savana parque and savana arbórea aberta (RADAMBRASIL 1981). The soils are classified as Litholic red-yellow podzols, belonging to the Xingu Formation and Tocantins Group, derived from the lower-middle Pre-Cambrian (RADAMBRASIL 1981).

Carolina - The area is classified as park savanna (RADAM 1973). However, Eiten (1994) visited nearby study sites and found a wide variety of physiognomies. The soils are classified as quartz sandy and litholic, and belong to the Sambaíba Formation, derived from Triassic sediments (RADAM 1973).

Chapter 3.

Surface soils

INTRODUCTION

Soil mineralogy, organic matter content, charge chemistry and soil structure are fundamental to the understanding of nutrient dynamics (Sollins 1989). Although each factor can be easily measured on its own, no single factor ever acts by itself and interactions are of paramount importance. Some authors, e.g. Goodland (1969), have considered that plants react more to the ratios between factors than to individual factors themselves. In the present study, 11 soil factors which have previously been found to be important in plant nutrition (Alvin & Araujo, 1953, Askew *et al.* 1971, Lopes 1980) were measured in seven Amazonian savanna areas.

Most of the soils studies in Brazilian savannas have been done in Central Brazil. This region has a striking diversity of soil types, although many authors (e.g. Askew *et al.* 1971, Eiten 1972, Furley & Ratter 1988) have characterized most soils as acidic, with a low cation exchange capacity and a high concentration of aluminium. The soil acidity and aluminium are likely to affect the root system directly and inhibit calcium and phosphorus uptake indirectly. These same soil properties have also been reported as the main factors underlying physiognomical and floristic variations of the Central Brazilian savannas (Goodland & Ferri 1979, Lopes & Cox 1977, Ranzani 1971).

The aim of this chapter is to assess the nutrient status and physical characteristics of the soils of the seven savannas areas studied, and to find a combination of soil variables which may account for some of the observed differences between them.

MATERIALS AND METHODS

Four to six surface soil samples (0-10 cm) were collected for each of the 25 floristically surveyed transects described in Chapter 2. Five random positions along the transects were selected for soil collection. The samples were collected with a spade, air-dried, ground and sieved through a 2 mm mesh. Chemical and granulometric analyses were carried out at EMBRAPA-CPAC (The National Agricultural Research Agency, Centre for the Agriculture Research of Cerrado). Soil texture was quantified by the Boyoucos hydrometer method (Day 1965). For the estimation of silt and sand, 20 g of air-dried fine soil were dispersed by 1N NaOH, in 100 ml of distilled water. For the clay fraction the sample was dispersed in distilled water. Classification of particle size was as follows: coarse sand < 2 - 0.2 mm, fine sand < 0.2 - 0.05 mm, silt < 0.05 - 0.002 mm and clay < 0.002 mm. Measurement of pH was with a potentiometer in a 1:2.5 mixture of soil-deionized water. Available P and K were extracted with 0.05N HCl + 0.025N H₂SO₄. Measurement of K was carried out by flame photometry and of P by colorimetry in a phosphomolybdate complex, with ascorbic acid as the reducing agent. Ca + Mg and Al were determined after extraction with 1N KCl. Ca + Mg were measured by titration with EDTA (Disodium dihydrogen ethylenediamine tetraacetate), and Al by titration with NaOH, using a bromothymol indicator. Ca was determined separately using the Calcon

indicator (Black 1976, p.1005). Organic carbon was measured by the Walkley-Black method (Allison *et al.* 1976) and organic matter (OM) was calculated by multiplying the organic carbon by 1.724.

Since the laboratory was not able to provide the total acidity (H + Al) for most samples, it was impossible in this study to estimate cation exchange capacity and percentage of base saturation.

Comparison of the soil properties among savanna sites and transects within sites was carried out by two-way nested ANOVA using a SYSTAT statistic pack (Wilkinson 1990). If significant differences occurred for soil properties, multiple comparisons among sites were performed using Tukey test (Zar 1996). The ordination technique Principal Components Analysis (PCA) was used to analyse nine variables, pH, Al, Ca, Mg, K, P, organic matter (OM), coarse sand (CS) and fine sand (FS), in order to seek geographic patterns among the study sites. PCA was made with the CANOCO program version 3.1 (ter Braak 1988), using the correlation path and with all data log-transformed in order to reduce the variance.

RESULTS AND DISCUSSION

The sites studied vary quite widely in soil texture. They range from clay to sandy, including intermediate classes (by the criteria of Soil Survey Staff 1975, 1987). Alter do Chão and Carolina were the only sites with exclusively sandy soils (< 18% clay; Appendix 3.1, Fig. 3.1); while SE Humaitá varied from sandy to loamy (< 18% to 35% clay); Redenção had from loamy to clay (18% to > 35% clay); the highest variation among

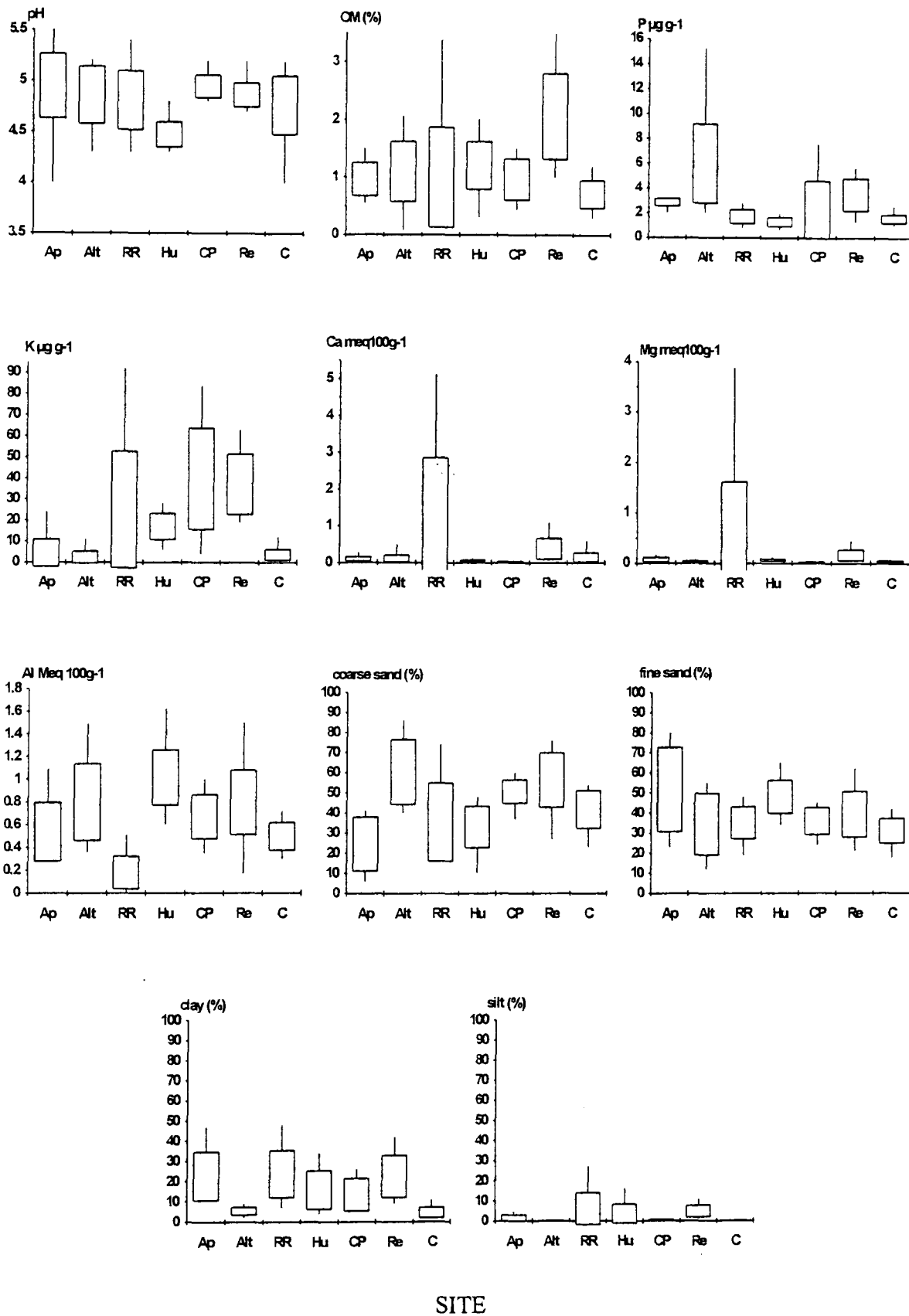


Fig. 3.1. Chemical and textural properties of the soils (0-10 cm) of the seven savanna areas (letter codes as in Table 2.1). Boxes represent the standard deviation and vertical lines the observed range.

transects were found for the northernmost sites (Amapá and Roraima), which varied from sandy to clay soils (< 18% to 60%).

In general all the study sites had acidic soils (4.5 - 5.2, $\text{pH}_{\text{H}_2\text{O}}$) and had moderate concentration levels of aluminium, mostly above 0.3 meq 100 g^{-1} and up to 1.49, the lower limit of alic soil according to Resende *et al.* 1995 (Fig. 3.1). An exception to this is Roraima (0.01 - 0.51 meq 100 g^{-1}). The soils of the Chapada dos Parecis and Redenção were richer in K than the others. Alter do Chão was the richest site in P (0.3 - 15.3 $\mu\text{g g}^{-1}$), while Roraima, SE Humaitá and Carolina were the poorest (0.6 - 7.6 $\mu\text{g g}^{-1}$). The detailed data from all soil analyses are presented in Appendix 3.1. Most soil properties showed significant differences between the different transects of the same study site (Table 3.2), the only exceptions to this were K and Ca. The high variation between transects in the same region demonstrates a high degree of soil heterogeneity. All soil properties were significantly different among sites ($P < 0.000$).

The results of the PCA of the soil sites based on nine soil properties are given in Figure 3.2. The PCA diagram shows a clear geographical ordination pattern. The first ordination axis is highly and positively correlated with clay, silt, Ca and Mg and negatively correlated with coarse sand (CS) (Fig. 3.2). Axis II has Al as the highest positively correlated variable, while fine sand (FS) is negatively correlated. Most of the Redenção samples appear together at the top right quarter of the diagram, corresponding to higher concentrations of clay and OM. Chapada dos Parecis and Humaitá overlap in the centre of the diagram. Alter do Chão appears at the top left, coinciding with high percentage of coarse sand, Al and P. Amapá data are distributed from the centre to the bottom of the diagram. Carolina is concentrated at the lower left, coinciding with lower concentrations of

Table 3.2. Soil properties (n=5) from surface soil (0-10 cm) from three transects in each site (codes follow Table 2.1). Values within a row followed by different letters are significantly different, others non-significant (two-way nested Anova, $p \leq 0.05$, multiple comparisons by Tukey test).

	SITES						
	Ap	Alt	RR	Hu	CP	C	Re
pH _{H2O}	4.96 ^a	4.80 ^{ab}	4.68 ^b	4.43 ^c	4.94 ^a	4.88 ^{ab}	4.82 ^{ab}
OM %	0.97 ^{bc}	1.14 ^{bc}	0.62 ^c	1.16 ^b	0.97 ^{bc}	2.33 ^a	0.75 ^{bc}
P $\mu\text{g g}^{-1}$	2.84 ^b	5.89 ^a	1.59 ^b	1.35 ^b	2.27 ^b	2.78 ^b	1.48 ^b
K $\mu\text{g g}^{-1}$	3.40 ^c	2.87 ^c	10.93 ^b	16.67 ^b	39.53 ^a	37.33 ^a	3.93 ^b
Exchangeable cations (meq/100g ⁻¹)							
Ca	0.09 ^b	0.11 ^b	0.98 ^a	0.06 ^b	0.03 ^b	0.35 ^b	0.16 ^b
Mg	0.06 ^b	0.03 ^b	0.05 ^a	0.06 ^b	0.02 ^b	0.15 ^b	0.04 ^b
Al	0.60 ^{bc}	0.82 ^{ab}	0.22 ^d	1.03 ^a	0.67 ^{bc}	0.85 ^{ab}	0.51 ^c
Particle size (%)							
clay	25.5 ^a	5.5 ^c	22.4 ^{ab}	14.8 ^{bc}	13.3 ^{bc}	26.5 ^a	4.9 ^c
CS	23.9 ^d	57.4 ^a	39.4 ^{bc}	33.7 ^{cd}	50.6 ^{ab}	38.4 ^{bcd}	53.3 ^{ab}
FS	48.9 ^a	37.1 ^{ab}	35.9 ^{ab}	48.8 ^a	35.7 ^{ab}	30.3 ^b	41.8 ^{ab}
silt	1.7 ^b	0.7 ^b	2.3 ^{ab}	2.7 ^{ab}	0.3 ^b	4.8 ^a	0.0 ^b

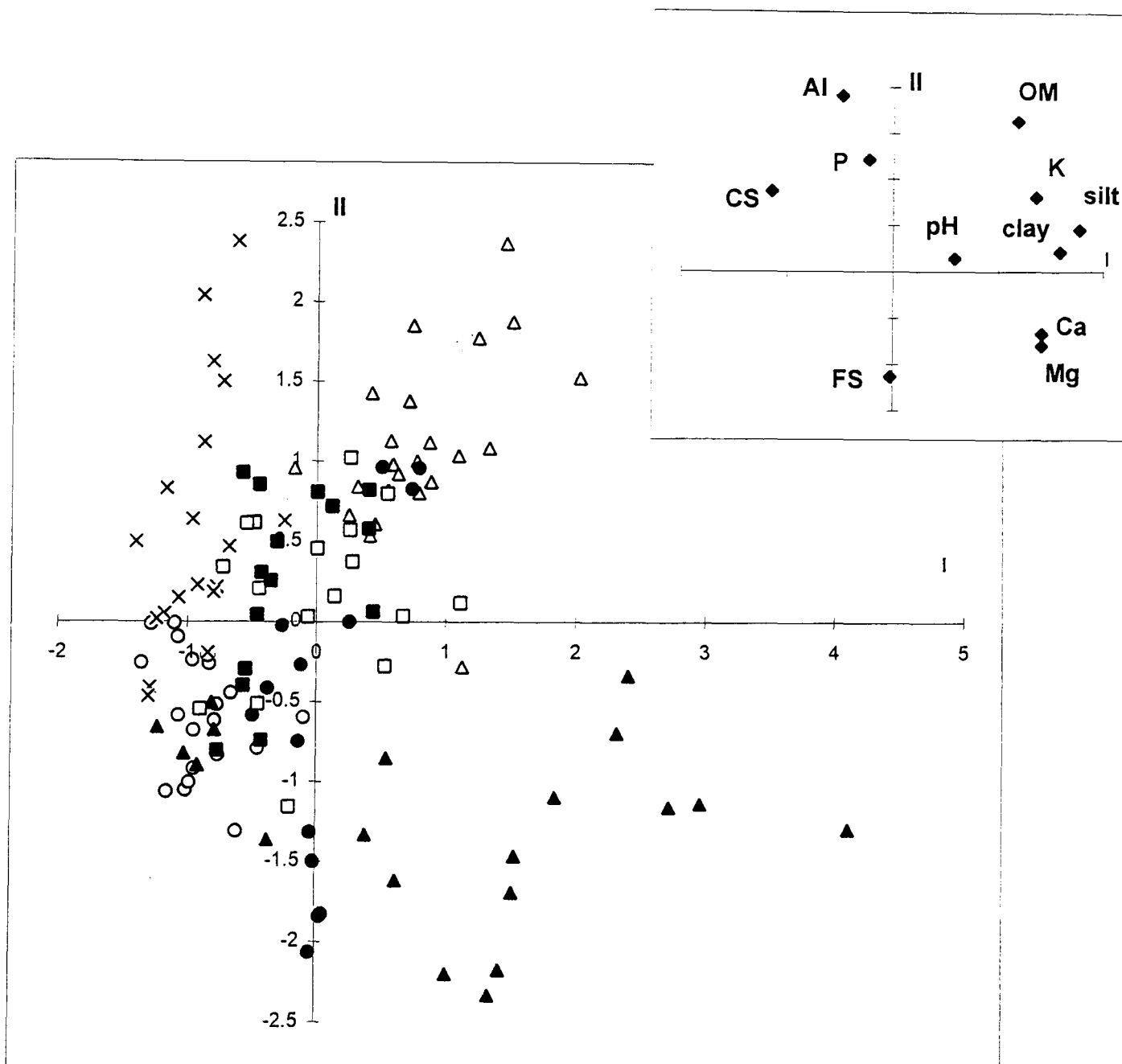


Fig. 3.2. PCA of 128 (0-10 cm) soil samples from the seven study sites measured for nine soil chemical and physical variables. (Δ) Redenção, (\blacksquare) Chapada dos Parecis, (\square) Humaitá, (\blacktriangle) Roraima, (\bullet) Amapá, (\circ) Carolina and (\times) Alter do Chão. The eigenvalues for the four PCA axes were 0.336, 0.172, 0.162 and 0.097, while the cumulative percentage variance of the textural and chemical properties for those axes were respectively 33.6%, 50.8%, 66.9% and 76.7%.

Al. Roraima is concentrated in the lower right, corresponding to high concentrations levels of Ca and Mg.

The results of previous studies carried out in Brazilian Amazonian savannas are summarized in Table 3.3. Soil properties of the areas studied in Amapá were very similar to those obtained for the same region by Souza Filho *et al.* (1992). Dantas & Rodrigues (1982), surveying sites north of Boa Vista, and Eden *et al.* (1991), working near Maracá Island, found soils which were less acidic than those in the present study. The site 180 km SE of Humaitá showed much lower exchangeable Al when compared with samples taken near Humaitá city (Gottsberger & Morawetz 1986, Gross Braun & Andrade Ramos 1959). There were no previous studies near the Chapada dos Parecis which allowed comparisons. However, the data from the Chapada dos Parecis were similar to those about 280 km away near the city of Cuiabá (Guarim Neto *et al.* 1994, Nascimento & Saudi 1992, Oliveira-Filho 1992). Redenção also had no previous study nearby but the soils were similar to those from the Parque Nacional do Araguaia, 240 km south (Ratter 1987). Carolina and Alter do Chão were also previously unstudied and were the poorest in Ca and Mg.

The results of the previous studies carried out in forest and savannas in the Brazilian Amazon are presented in Figure 3.3. Concentrations of Ca, Mg and K in the savanna soils are higher than in those of the lowland evergreen rain forests, and lower for Al and OM. However, the soils of the two vegetation types do not differ significantly in P and pH. Soil nutrients themselves did not explain the occurrence of the islands of savanna inside the rainforest, as also found by Eden (1964) in the Rupununi savannas (British Guiana), where infertile soils support forest as well as savannas. The soil, geology and topography (the last of which affects the water table level) of a given locality must play an important role as

determinant factors, however the factor most important in one site could be outweighed by another in a different area.

Table 3.3. Surface soil sample analysis from previous studies near the present research sites, and from the present investigation.

	Amapá state		Roraima state				SE Humaitá		
	1	x	2	3a	3b	x	4	5	x
depth (cm)	0-20	0-10	0-20	0-10	0-10	0-10	0-10	0-10	0-10
pH _{H2O}	5.5	4.9	5.3	4.9	5.4	4.8	4.2	4.7	4.5
OM %	1.30	1.04	-	1.80	2.15	1.00	1.20	2.38	1.21
P $\mu\text{g g}^{-1}$	0.6	4.69	5.50	0.27	2.80	1.72	t	-	1.29
K $\mu\text{g g}^{-1}$	7.40	3.18	78.00	0.27	0.48	24.95	0.06	0.25	16.88
	Exchangeable cations (meq/100g ⁻¹)								
Ca+Mg	0.40		2.70	0.30	1.50		t	0.56	
Ca		0.11	-	0.22	1.04	1.27	t	0.08	0.06
Mg		0.05	-	0.08	0.46	0.69	t	0.48	0.06
Al	0.50	0.69	1.25	0.48	0.10	0.18	-	3.04	1.02
	Particle size (%)								
clay	20	12	-	-	-	24	28	23	16
sand	69	87	-	-	-	70	46	19	81
CS	55	46	-	-	-	35	0.8	1	33
FS	14	41	-	-	-	35	38	18	48
silt	11	0.6	-	-	-	6	33	57	3

¹ Souza Filho *et al.* (1993), 43 km N of Macapá.

² Dantas & Rodrigues (1982), Surumu, 150 km N of Boa Vista.

³ Eden *et al.* (1991), 130 km northwest of Boa Vista, 3a) Fazenda Patchuli, 3b) Fazenda Pau-roxo.

⁴ Gross Braun & Andrade Ramos (1959), open grassland 5 km from Humaitá towards Lábrea.

⁵ Gottsberger & Morawetz (1986), near the city of Humaitá.

^x This study.

Table 3.3. (cont.)

	Chapada dos Parecis					Redenção	
	6	7a	7b	8	x	9	x
depth (cm)	0-20	0-15	0-15	0-40	0-10	0-15	0-10
pH _{H2O}	5.5	5.3	5.6	5.1	4.9	5.0	4.87
OM %	3.40	0.95	2.12	1.20	0.97	-	2.06
P $\mu\text{g g}^{-1}$	10.0	0.26	0.73	3.30	2.27	2.00	3.51
K $\mu\text{g g}^{-1}$	59.00	0.20	0.21	80.00	96.80	32.0	37.0
	Exchangeable cations (meq/100g ⁻¹)						
Ca+Mg	2.20	-	-	1.70		0.50	0.54
Ca	-	1.05	3.82	-	0.03	-	0.38
Mg	-	0.08	0.56	-	0.02	-	0.16
Al	0.50	0.69	0.23	0.30	0.67	0.50	0.80
	Particle size (%)						
clay	7	-	-	10	13	sand	22
sand	77	-	-	73	87	clay	73
CS	-	-	-	-	51	loam	42
FS	-	-	-	-	36		31
silt	16	-	-	17	0		5

⁶ Oliveira-Filho (1992), 14 km N of Cuiabá.

⁷ Nascimento & Saddi (1992), Coxipó da Ponte, 25 km from Cuiabá, 7a) plot A, 7b) plot B.

⁸ Guarim Neto *et al.* (1994), Nossa Senhora do Guia, 40 km NW of Cuiabá.

⁹ Ratter (1987), Parque Nacional do Araguaia.

^x This study.

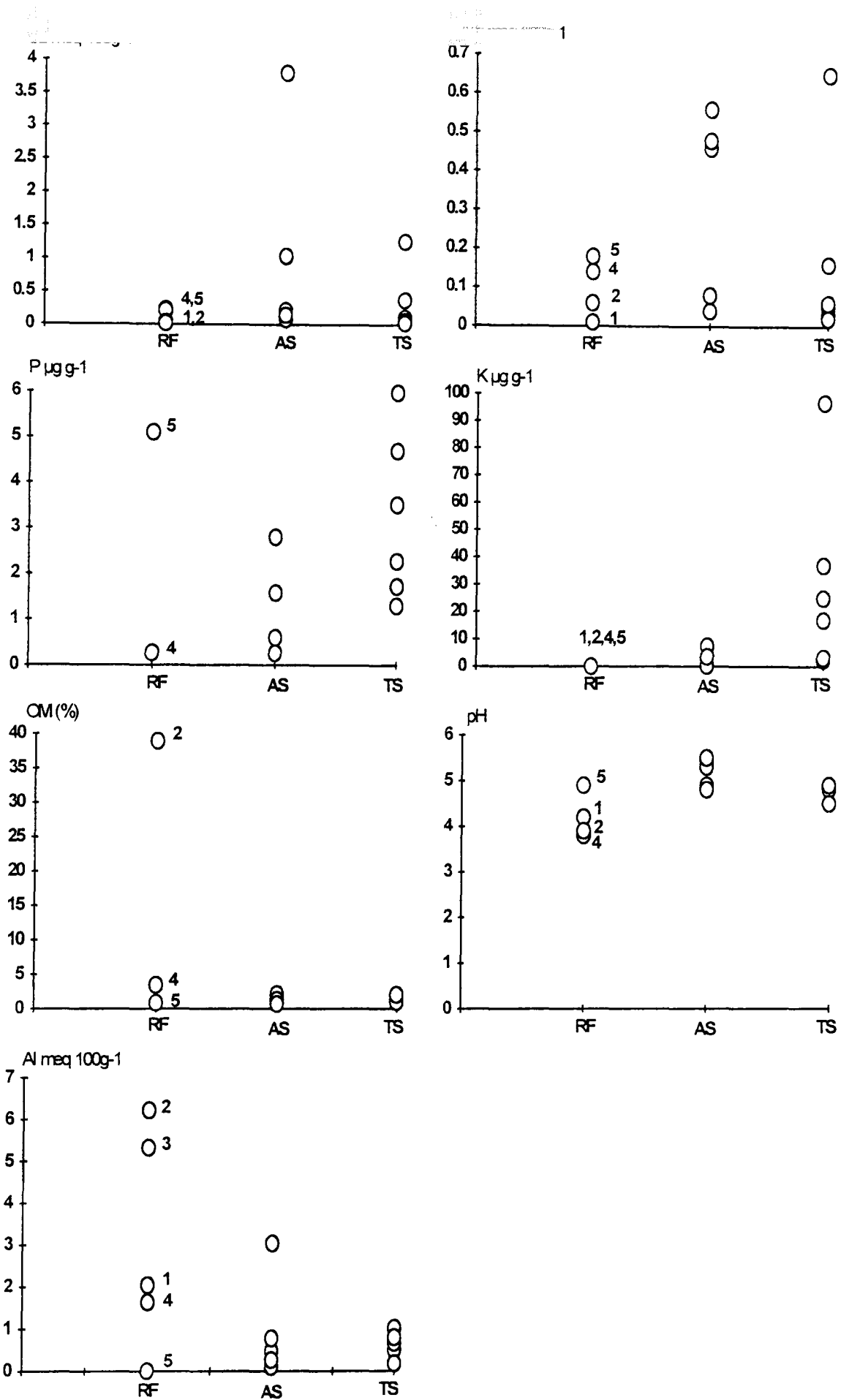


Fig. 3.3 Surface soil sample analyses of various Brazilian (RF) rain forests on acidic soils (pH_{H2O}), ¹ Bravard & Righi 1988, ² Luizão 1995, ³ Nascimento 1994, ⁴ Ranzani 1980, ⁵ Thompson *et al.* 1992, (AS) Amazonian savannas and this study (TS).

Chapter 4.

Floristic and phytosociological comparison of the seven savanna sites

INTRODUCTION

The variety of savanna habitats support a mosaic of plant communities but in most cases the reasons for their diversity are not yet understood. The interpretation of these vegetation patterns through the application of multivariate analysis is recent in landscape ecology, but is becoming a common procedure because of its utility in the search for ecological factors associated with the distribution of vegetation communities. Floristic similarity between two sites should express their ecological relationship or resemblance while dissimilarities point to their differences.

A number of phytosociological comparisons of specific localities have been published for the central Brazilian savannas (Felfili & Silva Júnior 1993, Goodland 1969, Oliveira-Filho & Martins 1986, Ratter *et al.* 1988, Silva Júnior *et al.* 1987). Large scale floristic comparisons using published species lists (Oliveira-Filho & Martins 1991, Ratter & Dargie 1992, Ratter *et al.* 1996), show a remarkable heterogeneity of woody plant communities within particular regions or over the whole of the savanna.

Studies on floristic composition have been carried out on several Brazilian Amazonian savannas: at Amapá (Azevedo 1967, Ledoux 1968, 1969, Magnanini 1952), Campos do Ariramba and Monte Alegre (Egler 1960, Andrade-Lima 1958), and Roraima

(Bastos 1984, Dantas & Rodrigues 1982, Takeuchi 1960). However, only a few studies of Amazonian savannas such as those at Humaitá (Gottsberger & Morawetz 1986, Janssen 1986), Alter do Chão (Miranda 1993), and Roraima (Milliken & Ratter 1989) have included quantitative information. Kubitzki (1979) and Eiten (1984) have stated that there is a gradient of species richness from Central Brazil to the north but no previous studies have been made using the same sampling method to allow appropriate comparisons between savannas within and outside Amazonia.

In this chapter a qualitative and quantitative comparison is carried out using an agglomerative cluster analysis and an ordination analysis to assess the similarity and floristic links between seven seasonal Amazonian savannas: four disjunct areas, isolated by rain forest at Amapá, Alter do Chão, Roraima and SE Humaitá, and three representing northern extensions of the core area of the central Brazilian savannas, located on the southern borders of the Amazon basin at Chapada dos Parecis, Redenção and Carolina.

MATERIALS AND METHODS

Floristic inventory

The Point-Centred-Quarter (PCQ) method (Cottam & Curtis 1956, Mueller-Dombois & Ellenberg 1974)¹ was used to survey trees with a diameter at breast height (1.3

¹ In this plotless method the points are sited along a transect line, and the area around the points is divided into four quarters and in each the distance to the nearest individual its circumference, height and identity are recorded.

m) of ≥ 5 cm (girth ≥ 15.71 cm). This method was chosen because it allowed quick sampling of wide areas. I restricted the sampling to seasonal and semi-seasonal savannas and subjectively chose areas with the following characteristics: (i) presence of trees with a height range of 2 - 10 m; (ii) apparent physiognomic homogeneity; (iii) location in areas which did not suffer seasonal flooding; and (iv) altitude of less than 200 m above sea level.

Three or four transects of 20 points (giving 80 individual trees) were run at each site. The sample points were on average 30 m apart. The transects had no constant direction and were always located to avoid vegetation gradients. For convenience most of the transects were divided into two parallel half transects (50 m apart) of 10 points each. The distances between transects within each of the seven geographical areas varied from 2 km to 80 km. Diameter/girth was measured with a plastic tape or with a caliper. Tree height up to 5 m was measured with a graduated pole, while taller trees were measured with a Haga height gauge.

Complementary general observation and additional species recording ('wide patrolling') were carried out in the transect areas in order to include rare species, which are recorded in the total species lists for each site. Voucher specimens were lodged at the herbaria of the Instituto Nacional de Pesquisas da Amazônia (INPA) (National Institute for Amazonian Research), the Universidade de Brasília (UB) (University of Brasília), the Royal Botanic Garden of Edinburgh (E), and, in some cases, the Royal Botanic Gardens Kew (K), Museu Paraense Emílio Goeldi (MPEG), Centro Zoobotânico de Macapá (HAMAB), University of Campinas (UNICAMP), and Museu Integrado de Boa Vista .

Phytosociological analysis

The data analysis was carried out using the FITOPAC 2 package designed for PC computers by Prof. George Shepherd (Departamento de Botânica, Universidade Estadual de Campinas, São Paulo, Brasil).

The following were calculated:

$$\text{Absolute density (ADe)} = \frac{\text{number of individuals of a species}}{(\text{average distance})^2 \times \text{total number of individuals of all species}}$$

$$\text{Relative density (RDe)} = \frac{\text{number of individuals of a species}}{\text{total number of individuals of all species}} \times 100$$

$$\text{Relative dominance (RDo)} = \frac{\text{total basal area of a species}}{\text{total basal area of all species}} \times 100$$

$$\text{Relative frequency (RF)} = \frac{\text{frequency of the species}}{\text{sum of frequencies of all species}} \times 100$$

$$\text{Total absolute density (TADe)} = \frac{1}{(\text{average distance})^2}$$

$$\text{Total average dominance (expressed as BA)} = \frac{\text{total basal area of all species}}{(\text{average distance})^2 \times \text{total number of individuals of all species}}$$

Indices of diversity (Shannon Index (H')) and equability (Pielou's evenness Index (J)) follow Zar (1996).

Classification and ordination analysis

The floristic information from 26 transects was organized in three matrices: the first, a presence/absence matrix for tree species recorded by the PCQ method, the second, an Absolute Density (**ADe**) matrix of the same species and the third a presence/absence matrix for the total tree species recorded by the ‘wide patrolling’ method at each transect locality.

Two techniques of multivariate analyses were carried out with all three matrices in order to seek patterns of similarity between the floras and plant communities of the isolated savanna areas and the non-isolated ones (part of central Brazilian distribution). The first was an agglomerative hierarchical classification by UPGMA (Unweighted Pair Groups Method using Arithmetic Averages) (Kent & Coker 1992). The similarities between transects and sites were calculated using Sorensen’s Index:

$$\text{Sørensen's Index} = 2C / A + B$$

where A = total number of species in community a, B = total number of species in community b, and C = number of species shared by the two communities.

The second multivariate analysis was an ordination by Detrended Correspondence Analysis (DCA) (Hill 1979) using the CANOCO package version 3.1 (Ter Braak 1988). **ADe** values were log-transformed prior to entering the analyses.

RESULTS

Species composition and phytosociology

A summary of the phytosociological data for all transects is given in Table 4.1. The lowest average tree densities were found in the most northern savannas, Amapá (108 ha^{-1}) and Roraima (155 ha^{-1}). Although the transects of Alter do Chão and Redenção were similar in their high tree density (363 ha^{-1} and 367 ha^{-1}) they differed greatly in their basal area, with Redenção having a large number of small trees (Average BA= $1.8 \text{ m}^2/\text{ha}$) while Alter do Chão had an average of $5 \text{ m}^2/\text{ha}$.

A total of 101 species was recorded for all 26 transects by the PCQ method, and another 43 species were added to the total list by 'wide patrolling' (Appendix 4.1). A species list with all collection numbers and herbarium location of vouchers is given in Appendix 4.2.

In Amapá 12 species were recorded from 200 individuals measured. *Byrsonima crassifolia* was the most abundant species in all transects followed by *Himatanthus articulatus* and *B. coccolobifolia* in two of the transects (T1-T2), while in the third (T3) *H. articulatus* was not present and *B. crassifolia* accounted for no less than 70% of RDe and 73.1% of basal area, with *B. coccolobifolia* and *Ouratea hexasperma* as the second and third species (Table 4.2).

Alter do Chão had 16 species in 320 individuals measured. *Salvertia convallariodora* and *Byrsonima crassifolia* were the most abundant, with each accounting for about 10% of the density in all transects (T4-T7) (Table 4.3).

Table 4.1. Phytosociological information for all transects. N= number of individuals, NS= number of species, H'=Shannon Index, J=Pielou's evenness Index, AH= average height, BA= basal area (total average dominance).

Transect		Area (ha)	N	NS	H'	J	AH (m)	BA (m ² /ha)	TADe ha
Amapá	T1	0.376	80	10	1.85	0.80	4.0	2.98	212.4
	T2	1.288	80	7	1.38	0.70	4.5	1.47	62.1
	T3	0.805	40	6	1.04	0.60	3.8	0.54	49.7
Alter do	T5	0.252	80	12	2.07	0.83	5.4	5.93	318.1
	T4	0.144	80	11	2.07	0.86	4.7	7.04	556.0
Chão	T6	0.322	80	11	1.99	0.83	5.6	4.16	248.8
	T7	0.243	80	11	1.96	0.82	4.6	4.61	329.3
Roraima	T10	0.991	80	6	1.21	0.68	3.4	1.19	80.8
	T9	0.804	80	5	1.28	0.80	3.5	1.44	99.5
	T8	0.251	40	3	0.80	0.72	3.1	2.61	159.5
	T11	0.284	80	5	1.13	0.70	3.0	2.74	281.5
Humaitá	T12	0.129	40	16	2.41	0.87	4.8	2.61	309.6
	T13	0.524	80	23	2.82	0.90	4.9	1.45	152.6
	T14	0.336	80	9	1.43	0.65	4.6	1.62	238.1
	T15	0.153	40	5	1.45	0.90	4.9	2.02	260.7
Chapada dos	T16	0.411	80	20	2.60	0.87	3.1	2.37	194.5
	T17	0.24	80	20	2.50	0.84	3.3	3.27	333.8
Parecis	T18	0.727	80	18	2.15	0.75	3.2	1.81	110.0
Redenção	T19	0.2	80	28	2.98	0.90	4.9	5.85	399.1
	T20	0.168	60	29	3.06	0.91	4.1	0.37	358.0
	T21	0.251	100	31	2.97	0.86	4.7	0.68	397.7
	T22	0.256	80	32	3.16	0.91	4.9	0.52	312.6
Carolina	T23	0.419	80	25	2.81	0.87	5.7	3.14	191.1
	T24	0.459	80	17	2.31	0.82	4.8	2.64	174.3
	T25	0.374	80	19	2.34	0.80	5.8	2.82	213.9
	T26	0.572	80	26	2.86	0.88	5.2	2.82	139.8

Table 4.2. Species of trees ≥ 5 cm dbh occurring in three transects in the State of Amapá. (N) number of individuals, (P) number of points in the transect, (BA) total basal area, (RDe) relative density, (RF) relative frequency and (RDo) relative dominance.

Species	N	P	BA (m ²)	RDe (%)	RF (%)	RDo (%)
T1						
<i>Byrsonima crassifolia</i>	28	16	0.365	35.0	29.1	32.6
<i>Ouratea hexasperma</i>	15	12	0.228	18.8	21.8	20.4
<i>Byrsonima coccolobifolia</i>	12	8	0.133	15.0	14.6	11.9
<i>Himatanthus articulatus</i>	11	8	0.212	13.8	14.6	18.9
<i>Hirtella ciliata</i>	3	2	0.059	3.8	3.6	5.3
<i>Roupala montana</i>	3	2	0.030	3.8	3.6	2.7
<i>Tocoyena formosa</i>	3	2	0.021	3.8	3.6	1.9
<i>Curatella americana</i>	2	2	0.034	2.5	3.6	3.0
<i>Bowdichia virgilioides</i>	2	2	0.020	2.5	3.6	1.8
<i>Anacardium occidentale</i>	1	1	0.016	1.3	1.8	1.5
T2						
<i>Byrsonima crassifolia</i>	34	17	0.584	42.5	35.4	30.9
<i>Himatanthus articulatus</i>	26	15	0.781	32.5	31.3	41.3
<i>Byrsonima coccolobifolia</i>	11	8	0.198	13.8	16.7	10.5
<i>Anacardium occidentale</i>	5	4	0.246	6.3	8.3	13.0
<i>Curatella americana</i>	2	2	0.026	2.5	4.2	1.4
<i>Ouratea hexasperma</i>	1	1	0.050	1.3	2.1	2.7
<i>Maprounea guianensis</i>	1	1	0.006	1.3	2.1	0.3
T3						
<i>Byrsonima crassifolia</i>	28	10	0.319	70.0	45.5	73.1
<i>Byrsonima coccolobifolia</i>	5	5	0.060	12.5	22.7	13.7
<i>Ouratea hexasperma</i>	3	3	0.046	7.5	13.6	10.5
<i>Salvertia convallariodora</i>	2	2	0.007	5.0	9.1	1.5
<i>Curatella americana</i>	1	1	0.003	2.5	4.6	0.6
<i>Bowdichia virgilioides</i>	1	1	0.002	2.5	4.6	0.5

transects in Alter do Chão.

(N) number of individuals, (P) number of points in the transect, (BA) total basal area, (RDe) relative density, (RF) relative frequency and (RDo) relative dominance.

	Species	N	P	BA (m ²)	RDe (%)	RF (%)	RDo (%)
T4	<i>Byrsonima crassifolia</i>	21	14	0.244	26.3	23.0	16.3
	<i>Salvertia convallariodora</i>	15	12	0.394	18.8	19.7	26.4
	<i>Himatanthus articulatus</i>	14	10	0.217	17.5	16.4	14.5
	<i>Pouteria ramiflora</i>	7	6	0.264	8.8	9.8	17.7
	<i>Byrsonima coccolobifolia</i>	6	5	0.071	7.5	8.2	4.8
	<i>Vatairea macrocarpa</i>	6	5	0.047	7.5	8.2	3.2
	<i>Lafoesia pacari</i>	4	3	0.038	5.0	4.9	2.6
	<i>Sclerolobium paniculatum</i>	2	1	0.107	2.5	1.6	7.2
	<i>Anacardium occidentale</i>	2	2	0.038	2.5	3.3	2.5
	<i>Bowdichia virgilioides</i>	1	1	0.061	1.3	1.6	4.1
	<i>Myrcia cf. obtusa</i>	1	1	0.006	1.3	1.6	0.4
	<i>Tocoyena formosa</i>	1	1	0.005	1.3	1.6	0.3
T5	<i>Salvertia convallariodora</i>	17	11	0.393	21.3	18.0	38.8
	<i>Qualea grandiflora</i>	15	9	0.143	18.8	14.8	14.1
	<i>Lafoesia pacari</i>	12	9	0.112	15.0	14.8	11.0
	<i>Byrsonima crassifolia</i>	12	11	0.098	15.0	18.0	9.7
	<i>Byrsonima coccolobifolia</i>	8	6	0.054	10.0	9.8	5.3
	<i>Pouteria ramiflora</i>	6	5	0.067	7.5	8.2	6.6
	<i>Vatairea macrocarpa</i>	5	5	0.047	6.3	8.2	4.7
	<i>Bowdichia virgilioides</i>	2	2	0.055	2.5	3.3	5.5
	<i>Tabebuia ochracea</i>	1	1	0.037	1.3	1.6	3.7
	<i>Tocoyena formosa</i>	1	1	0.005	1.3	1.6	0.5
	<i>Anacardium occidentale</i>	1	1	0.003	1.3	1.6	0.3
T6	<i>Byrsonima crassifolia</i>	22	14	0.255	27.5	22.2	19.1
	<i>Salvertia convallariodora</i>	21	15	0.690	26.3	23.8	51.6
	<i>Lafoesia pacari</i>	9	8	0.045	11.3	12.7	3.4
	<i>Pouteria ramiflora</i>	8	6	0.107	10.0	9.5	8.0
	<i>Himatanthus articulatus</i>	5	5	0.133	6.3	7.9	9.9
	<i>Byrsonima coccolobifolia</i>	4	4	0.017	5.0	6.4	1.3
	<i>Vatairea macrocarpa</i>	3	3	0.036	3.8	4.8	2.7
	<i>Tocoyena formosa</i>	3	3	0.013	3.8	4.8	1.0
	<i>Roupala montana</i>	2	2	0.025	2.5	3.2	1.9
	<i>Qualea grandiflora</i>	2	2	0.013	2.5	3.2	1.0
	<i>Hirtella ciliata</i>	1	1	0.002	1.3	1.6	0.2
	T7	<i>Byrsonima crassifolia</i>	29	17	0.243	36.3	29.8
<i>Salvertia convallariodora</i>		12	8	0.225	15.0	14.0	20.1
<i>Pouteria ramiflora</i>		11	9	0.184	13.8	15.8	16.4
<i>Byrsonima coccolobifolia</i>		7	6	0.056	8.8	10.5	5.0
<i>Himatanthus articulatus</i>		6	5	0.091	7.5	8.8	8.1
<i>Anacardium occidentale</i>		4	3	0.080	5.0	5.3	7.1
<i>Bowdichia virgilioides</i>		3	2	0.168	3.8	3.5	15.1
<i>Vatairea macrocarpa</i>		3	3	0.043	3.8	5.3	3.9
<i>Tocoyena formosa</i>		3	2	0.011	3.8	3.5	0.9
<i>Hirtella ciliata</i>		1	1	0.012	1.3	1.8	1.1
<i>Lafoesia pacari</i>		1	1	0.006	1.3	1.8	0.6

The Roraima savannas were the poorest in species ($H' = 0.8$ to 1.28), with only eight species recorded from 280 individuals measured. *Byrsonima crassifolia* was the most abundant in two transects (T8-T9), with *Curatella americana* in the third transect (T10) and *B. coccolobifolia* in the fourth transect (T11) (Table 4.4).

Humaitá had a total of 29 species from 240 individuals measured, the number of species varied greatly among transects. The two transects with the highest number of species differed in their most abundant species, the first (T12) had *Antonia ovata*, *Qualea parviflora* and *Byrsonima crassifolia*, while the other (T13) had *Qualea parviflora*, *Caraipa savannarum* followed by *Byrsonima* aff. *cydoniifolia* and *Byrsonima crassifolia*. The two poorest transects also had a distinct community composition balance, with *Antonia ovata*, *Byrsonima crassifolia* and *Caraipa savannarum* the most abundant in one case (T14) and *Caraipa savannarum*, *Byrsonima crassifolia* and *Antonia ovata* in the other (T15) (Table 4.5).

At the Chapada dos Parecis a total of 37 species were found in 240 individuals measured. The first transect (T18) community had mainly *Mouriri pusa* as the most abundant species, and the second (T17) had *M. pusa*, *Vochysia cinnamomea* and *Miconia rubiginosa*. In the third transect (T16) however, *M. pusa* had only one individual and the species position was taken by *Davilla elliptica*, *Salvertia convallariodora* and *V. cinnamomea* (Table 4.6).

Redenção was the richest in species ($H' = 2.97$ to 3.16), with a total of 58 species recorded from 320 individuals scored. The most important species varied among transects: *Qualea grandiflora* was in this position on two transects, with *Diospyros hispida* as second

Table 4.4. Species of trees ≥ 5 cm dbh occurring in four transects in the State of Roraima. (N) number of individuals, (P) number of points in the transect, (BA) total basal area, (RDe) relative density, (RF) relative frequency and (RDo) relative dominance.

Species	N	P	BA (m ²)	RDe (%)	RF (%)	RDo (%)
T8						
<i>Byrsonima crassifolia</i>	40	19	0.474	50.0	38.8	40.2
<i>Curatella americana</i>	26	18	0.528	32.5	36.7	44.7
<i>Byrsonima coccolobifolia</i>	8	6	0.084	10.0	12.2	7.1
<i>Byrsonima aff. intermedia</i>	3	3	0.070	3.8	6.1	6.0
<i>Psidium myrsinoides</i>	2	2	0.014	2.5	4.1	1.2
<i>Bowdichia virgilioides</i>	1	1	0.010	1.3	2.0	0.9
T9						
<i>Byrsonima crassifolia</i>	35	14	0.343	43.8	35.0	29.6
<i>Roupala montana</i>	20	8	0.264	25.0	20.0	22.8
<i>Curatella americana</i>	19	12	0.486	23.8	30.0	41.8
<i>Byrsonima coccolobifolia</i>	5	5	0.063	6.3	12.5	5.5
<i>Byrsonima aff. intermedia</i>	1	1	0.005	1.3	2.5	0.4
T10						
<i>Curatella americana</i>	26	10	0.530	65.0	47.6	81.1
<i>Byrsonima crassifolia</i>	12	9	0.111	30.0	42.9	16.9
<i>Roupala montana</i>	2	2	0.013	5.0	9.5	2.0
T11						
<i>Byrsonima coccolobifolia</i>	38	19	0.370	47.5	41.3	47.5
<i>Byrsonima crassifolia</i>	31	17	0.309	38.8	37.0	39.7
<i>Bowdichia virgilioides</i>	6	5	0.064	7.5	10.9	8.2
<i>Curatella americana</i>	3	3	0.026	3.8	6.5	3.4
<i>Himathantus aff. fallax</i>	2	2	0.010	2.5	4.4	1.3

Species of trees ≥ 5 cm dbh occurring in four transects in Itumaitá, Brazil. (N) number of individuals, (P) percent of total individuals, (BA) total basal area, (RDe) relative density, (RF) relative frequency and (RDo) relative dominance.

Species	N	P	BA (m ²)	RDe (%)	RF (%)	RDo (%)
T12						
<i>Antonia ovata</i>	8	5	0.055	20.0	16.1	16.2
<i>Qualea parviflora</i>	7	5	0.075	17.5	16.1	22.2
<i>Byrsonima crassifolia</i>	7	4	0.035	17.5	12.9	10.4
<i>Connarus suberosus</i>	3	3	0.010	7.5	9.7	3.0
<i>Byrsonima aff. cydoniifolia</i>	2	2	0.009	5.0	6.5	2.6
<i>Plathymenia reticulata</i>	2	2	0.007	5.0	6.5	2.2
<i>Qualea grandiflora</i>	2	1	0.006	5.0	3.2	1.8
<i>Curatella americana</i>	1	1	0.070	2.5	3.2	20.9
<i>Salvertia convallariodora</i>	1	1	0.024	2.5	3.2	7.1
<i>Laxoplumeria tesmannii</i>	1	1	0.016	2.5	3.2	4.8
<i>Caraipa savannarum</i>	1	1	0.015	2.5	3.2	4.6
<i>Vochysia grandis</i>	1	1	0.005	2.5	3.2	1.5
<i>Ouratea hexasperma</i>	1	1	0.003	2.5	3.2	0.9
<i>Roupala montana</i>	1	1	0.003	2.5	3.2	0.8
<i>Hirtella grandulosa</i>	1	1	0.002	2.5	3.2	0.6
<i>Byrsonima coccolobifolia</i>	1	1	0.002	2.5	3.2	0.6
T13						
<i>Qualea parviflora</i>	10	8	0.064	12.5	11.0	8.5
<i>Caraipa savannarum</i>	9	7	0.094	11.3	9.6	12.4
<i>Byrsonima aff. cydoniifolia</i>	7	6	0.042	8.8	8.2	5.5
<i>Byrsonima crassifolia</i>	7	6	0.035	8.8	8.2	4.6
<i>Vochysia grandis</i>	6	6	0.079	7.5	8.2	10.4
<i>Connarus suberosus</i>	6	6	0.044	7.5	8.2	5.8
<i>Byrsonima coccolobifolia</i>	5	4	0.046	6.3	5.5	6.1
<i>Roupala montana</i>	5	5	0.045	6.3	6.9	5.9
<i>Ouratea hexasperma</i>	5	5	0.030	6.3	6.9	4.0
<i>Hancornia speciosa</i>	3	3	0.014	3.8	4.1	1.8
<i>Antonia ovata</i>	3	3	0.012	3.8	4.1	1.6
<i>Emmotum nitens</i>	2	2	0.054	2.5	2.7	7.1
<i>Simarouba amara</i>	2	2	0.024	2.5	2.7	3.2
<i>Himathantus aff. fallax</i>	1	1	0.047	1.3	1.4	6.2
<i>Salvertia convallariodora</i>	1	1	0.032	1.3	1.4	4.2
<i>Plathymenia reticulata</i>	1	1	0.019	1.3	1.4	2.5
<i>Anacardium giganteum</i>	1	1	0.019	1.3	1.4	2.5
<i>Andira vermifuga</i>	1	1	0.017	1.3	1.4	2.2
<i>Didymopanax distractiflorum</i>	1	1	0.017	1.3	1.4	2.2
<i>Occhocosmus barrae</i>	1	1	0.010	1.3	1.4	1.3
<i>Bowdichia virgilioides</i>	1	1	0.007	1.3	1.4	1.0
<i>Brosimum gaudichaudii</i>	1	1	0.005	1.3	1.4	0.6
<i>Miconia rubiginosa</i>	1	1	0.004	1.3	1.4	0.5
T14						
<i>Antonia ovata</i>	31	16	0.203	38.8	33.3	37.2
<i>Byrsonima crassifolia</i>	30	17	0.214	37.5	35.4	39.2
<i>Caraipa savannarum</i>	9	6	0.078	11.3	12.5	14.3
<i>Roupala montana</i>	5	4	0.032	6.3	8.3	5.8
<i>Occhocosmus barrae</i>	1	1	0.005	1.3	2.1	0.8
<i>Andira cordata</i>	1	1	0.004	1.3	2.1	0.7
<i>Guatteria cf. pohliana</i>	1	1	0.004	1.3	2.1	0.7
<i>Qualea parviflora</i>	1	1	0.004	1.3	2.1	0.6
<i>Emmotum nitens</i>	1	1	0.003	1.3	2.1	0.6
T15						
<i>Caraipa savannarum</i>	12	8	0.138	30.0	30.8	44.6
<i>Byrsonima crassifolia</i>	12	7	0.064	30.0	26.9	20.6
<i>Antonia ovata</i>	10	6	0.076	25.0	23.1	24.4
<i>Byrsonima aff. cydoniifolia</i>	4	3	0.018	10.0	11.5	5.8
<i>Qualea parviflora</i>	2	2	0.014	5.0	7.7	4.6

(N) number of individuals, (P) number of points in the transect, (BA) total basal area, (RDe) relative density, (RF) relative frequency and (RDo) relative dominance.

Species	N	P	BA (m ²)	RDe (%)	RF (%)	RDo (%)
T16						
<i>Davilla elliptica</i>	14	13	0.155	17.5	18.3	15.9
<i>Salvertia convallariodora</i>	11	7	0.144	13.8	9.9	14.7
<i>Vochysia cinnamomea</i>	11	9	0.077	13.8	12.7	7.9
<i>Diptychandra aurantiaca</i>	8	7	0.087	10.0	9.9	8.9
<i>Qualea parviflora</i>	5	5	0.113	6.3	7.0	11.6
<i>Licania humilis</i>	5	5	0.087	6.3	7.0	9.0
<i>Caryocar brasiliense</i>	5	4	0.053	6.3	5.6	5.4
<i>Qualea grandiflora</i>	4	4	0.041	5.0	5.6	4.2
<i>Buchenavia tomentosa</i>	2	2	0.043	2.5	2.8	4.4
<i>Emmotum nitens</i>	2	2	0.039	2.5	2.8	4.0
<i>Tabebuia aurea</i>	2	2	0.029	2.5	2.8	3.0
<i>Ouratea spectabilis</i>	2	2	0.013	2.5	2.8	1.3
<i>Connarus fulvus var. suber</i>	2	2	0.009	2.5	2.8	0.9
<i>Piptocarpha rotundifolia</i>	1	1	0.022	1.3	1.4	2.2
<i>Myrcia</i> sp TMS 414	1	1	0.018	1.3	1.4	1.8
<i>Styrax ferruginea</i>	1	1	0.014	1.3	1.4	1.4
<i>Dimorphandra mollis</i>	1	1	0.010	1.3	1.4	1.0
<i>Mouriri pusa</i>	1	1	0.010	1.3	1.4	1.0
<i>Diospyros hispida</i>	1	1	0.009	1.3	1.4	0.9
<i>Didymopanax</i> sp TMS 405	1	1	0.004	1.3	1.4	0.4
T17						
<i>Mouriri pusa</i>	19	13	0.206	23.8	20.6	26.4
<i>Vochysia cinnamomea</i>	12	9	0.096	15.0	14.3	12.3
<i>Miconia rubiginosa</i>	11	8	0.123	13.8	12.7	15.7
<i>Qualea parviflora</i>	7	6	0.129	8.8	9.5	16.5
<i>Salvertia convallariodora</i>	4	4	0.029	5.0	6.4	3.7
<i>Caryocar brasiliense</i>	4	3	0.013	5.0	4.8	1.6
<i>Byrsonima crassifolia</i>	3	2	0.009	3.8	3.2	1.1
<i>Emmotum nitens</i>	2	2	0.048	2.5	3.2	6.2
<i>Andira vermifuga</i>	2	2	0.024	2.5	3.2	3.0
<i>Qualea grandiflora</i>	2	2	0.019	2.5	3.2	2.4
<i>Myrcia</i> sp TMS 414	2	1	0.018	2.5	1.6	2.3
<i>Byrsonima coccolobifolia</i>	2	2	0.009	2.5	3.2	1.2
<i>Davilla elliptica</i>	2	2	0.007	2.5	3.2	0.9
<i>Xylopia aromatica</i>	2	1	0.005	2.5	1.6	0.6
<i>Bowdichia virgiliodes</i>	1	1	0.018	1.3	1.6	2.3
<i>Plathymenia reticulata</i>	1	1	0.011	1.3	1.6	1.4
<i>Buchenavia tomentosa</i>	1	1	0.008	1.3	1.6	1.0
<i>Annona crassiflora</i>	1	1	0.005	1.3	1.6	0.6
<i>Lafoensia pacari</i>	1	1	0.004	1.3	1.6	0.5
<i>Tabebuia ochracea</i>	1	1	0.003	1.3	1.6	0.4
T18						
<i>Mouriri pusa</i>	33	17	0.767	41.3	28.8	58.3
<i>Tabebuia aurea</i>	9	7	0.124	11.3	11.9	9.4
<i>Hancornia speciosa</i>	9	8	0.048	11.3	13.6	3.7
<i>Salvertia convallariodora</i>	4	3	0.129	5.0	5.1	9.8
<i>Kielmeyera coriacea</i>	4	4	0.024	5.0	6.8	1.8
<i>Ouratea spectabilis</i>	3	3	0.081	3.8	5.1	6.1
<i>Annona crassiflora</i>	3	2	0.012	3.8	3.4	0.9
<i>Davilla elliptica</i>	2	2	0.043	2.5	3.4	3.3
<i>Piptocarpha rotundifolia</i>	2	2	0.027	2.5	3.4	2.1
<i>Licania humilis</i>	2	2	0.015	2.5	3.4	1.1
<i>Dimorphandra mollis</i>	2	2	0.007	2.5	3.4	0.6
<i>Eugenia puniceifolia</i>	1	1	0.015	1.3	1.7	1.1
<i>Tabebuia ochracea</i>	1	1	0.008	1.3	1.7	0.6
<i>Himatanthus obovatus</i>	1	1	0.006	1.3	1.7	0.5
<i>Mouriri elliptica</i>	1	1	0.003	1.3	1.7	0.2
<i>Aspidosperma macrocarpon</i>	1	1	0.003	1.3	1.7	0.2
<i>Diospyros hispida</i>	1	1	0.002	1.3	1.7	0.2
<i>Vochysia rufa</i>	1	1	0.002	1.3	1.7	0.2

species on one (T21) or *Connarus suberosus* on the other (T19), while on the other two (T20) *Lafoensia pacari* with *Syagrus comosa* and (T22) *Curatella americana* with *Physocalymma scaberrimum* were the first and second most important respectively (Table 4.7).

Carolina had a total of 38 species recorded from 320 individuals scored, the number of species and those most important varied among transects. Two transects (T23 and T25) had the most important three species, *Vochysia tucanorum*, *Qualea parviflora* and *Hirtella ciliata* in common, while a third transect (T24) had two of these, *V. tucanorum* and *H. ciliata* with *Dalbergia miscolobium* in third place, and in the fourth transect (T26) the most important species were *Plathymenia reticulata*, *Andira cordata* and *H. ciliata* (Table 4.8).

Fifteen species were recorded only in the SE Humaitá savannas (*Anacardium giganteum*, *Bonyunia antoniifolia*, *Buchenavia capitata*, *Byrsonima* aff. *cydoniifolia*, *Caraipa savannarum*, *Didymopanax distractiflorum*, *Guatteria* cf. *pohliana*, *G. mayapuensis*, *Heisteria ovata*, *H. acuminata*, *Laxoplumeria lesmannii*, *Ochthocosmus barrae*, *Pouteria torta*, *Sapium* sp. and *Vochysia grandis*. Sixteen other species were recorded only for the northern disjunct savannas: *Himathantus fallax* and *Machaerium* sp. (SE Humaitá and Roraima), *Godmania esculifolia*, *Vitex schomburgkiana* and *Byrsonima* aff. *intermedia* (Roraima), *Maprounea guianensis* (SE Humaitá and Amapá), *Rauvolfia pentaphylla*, *Trattinickia rhoifolia*, *Annona paludosa*, *Connarus perottetii*, *Licania longistyla*, *Himatanthus drasticus*, *Mycia cuprea* (Amapá) and *Matayba guianensis*, *Myrcia* cf. *obtusata* and *Swartzia* sp. (Alter do Chão). Sixty-one species were recorded only for the south and southeast of the Amazon (in the northern extension of the core area),.

Table 4.7. Species of trees ≥ 5 cm dbh occurring in four transects in Redenção.
 (N) number of individuals, (P) number of points in the transect, (BA) total basal area,
 (RDe) relative density, (RF) relative frequency and (RDo) relative dominance.

Species	N	P	BA (m ²)	RDe (%)	RF (%)	RDo (%)
T19 <i>Qualea grandiflora</i>	10	6	0.009	16.7	11.3	14.8
<i>Connarus suberosus</i>	7	7	0.005	11.7	13.2	8.7
<i>Dimorphandra mollis</i>	4	3	0.007	6.7	5.7	11.7
<i>Curatella americana</i>	3	3	0.003	5.0	5.7	5.1
<i>Rourea induta</i>	3	2	0.002	5.0	3.8	3.6
<i>Qualea parviflora</i>	3	3	0.002	5.0	5.7	3.1
<i>Caryocar brasiliense</i>	2	2	0.009	3.3	3.8	13.9
<i>Myrcia cf. splendens</i>	2	2	0.005	3.3	3.8	7.7
<i>Ourotea hexasperma</i>	2	2	0.003	3.3	3.8	5.4
<i>Lafoensia pacari</i>	2	1	0.002	3.3	1.9	3.9
<i>Rudgea eriuloba</i> (TMS167)	2	2	0.001	3.3	3.8	2.1
<i>Qualea multiflora</i>	2	2	0.001	3.3	3.8	1.4
<i>Byrsonima crassifolia</i>	2	2	0	3.3	3.8	0.8
<i>Tabebuia aurea</i>	1	1	0.002	1.7	1.9	2.9
<i>Magonia pubescens</i>	1	1	0.001	1.7	1.9	2.2
<i>Sclerolobium aureum</i>	1	1	0.001	1.7	1.9	2.2
<i>Ilimatanthus obovatus</i>	1	1	0.001	1.7	1.9	2.0
<i>Caryocar cuicatum</i>	1	1	0.001	1.7	1.9	1.4
<i>Callisthene fasciculata</i>	1	1	0.001	1.7	1.9	1.4
<i>Syagrus comosa</i>	1	1	0.001	1.7	1.9	0.9
<i>Mouriri elliptica</i>	1	1	0	1.7	1.9	0.8
<i>Vatairea macrocarpa</i>	1	1	0	1.7	1.9	0.7
<i>Agonandra brasiliensis</i>	1	1	0	1.7	1.9	0.6
<i>Diospyros hispida</i>	1	1	0	1.7	1.9	0.6
<i>Byrsonima coccolobifolia</i>	1	1	0	1.7	1.9	0.6
<i>Tocoyena formosa</i>	1	1	0	1.7	1.9	0.5
<i>Brosimum gaudichaudii</i>	1	1	0	1.7	1.9	0.5
<i>Kielmeyera coriacea</i>	1	1	0	1.7	1.9	0.4
<i>Protium heptaphyllum</i>	1	1	0	1.7	1.9	0.3
T20 <i>Lafoensia pacari</i>	11	8	0.155	13.8	11.0	13.2
<i>Syagrus comosa</i>	9	6	0.044	11.3	8.2	3.8
<i>Curatella americana</i>	7	7	0.201	8.8	9.6	17.2
<i>Diospyros hispida</i>	7	7	0.074	8.8	9.6	6.3
<i>Qualea grandiflora</i>	5	5	0.044	6.3	6.9	3.8
<i>Dimorphandra mollis</i>	5	5	0.039	6.3	6.9	3.3
<i>Caryocar brasiliense</i>	4	4	0.346	5.0	5.5	29.5
<i>Byrsonima coccolobifolia</i>	4	3	0.029	5.0	4.1	2.5
<i>Andira vermicifuga</i>	3	3	0.061	3.8	4.1	5.2
<i>Physocalymma scaberrimum</i>	2	2	0.023	2.5	2.7	2.0
<i>Salvertia convallariodora</i>	2	2	0.023	2.5	2.7	2.0
<i>Ourotea castaneaeifolia</i>	2	2	0.021	2.5	2.7	1.3
<i>Pouteria ramiflora</i>	2	2	0.013	2.5	2.7	1.1
<i>Vatairea macrocarpa</i>	2	2	0.008	2.5	2.7	0.7
<i>Connarus suberosus</i>	2	2	0.006	2.5	2.7	0.5
<i>Hancornia speciosa</i>	1	1	0.013	1.3	1.4	1.1
<i>Tabebuia aurea</i>	1	1	0.010	1.3	1.4	0.9
<i>Bowdichia virgilioides</i>	1	1	0.009	1.3	1.4	0.8
<i>Andira cordata</i>	1	1	0.009	1.3	1.4	0.8
<i>Mouriri pusa</i>	1	1	0.007	1.3	1.4	0.6
<i>Guapira sp.</i>	1	1	0.006	1.3	1.4	0.5
<i>Tocoyena formosa</i>	1	1	0.006	1.3	1.4	0.5
<i>Eugenia dysenterica</i>	1	1	0.006	1.3	1.4	0.5
<i>Casipouia sylvestris</i>	1	1	0.005	1.3	1.4	0.5
<i>Myrcia rosulata</i>	1	1	0.005	1.3	1.4	0.4
<i>Mabca sp.</i>	1	1	0.004	1.3	1.4	0.4
<i>Annonia coriacea</i>	1	1	0.004	1.3	1.4	0.3
<i>Annonia crassiflora</i>	1	1	0.002	1.3	1.4	0.2

				area (m2)	RF (%)	RF (%)	RDo (%)
T21	<i>Qualea grandiflora</i>	15	10	0.021	15.0	11.4	12.2
	<i>Diospyros hispida</i>	15	11	0.014	15.0	12.5	8.0
	<i>Caryocar brasiliense</i>	7	7	0.025	7.0	8.0	14.6
	<i>Lalönsia pacari</i>	7	7	0.006	7.0	8.0	3.6
	<i>Curatella americana</i>	6	6	0.028	6.0	6.8	16.6
	<i>Salvertia convallariodora</i>	6	6	0.012	6.0	6.8	7.2
	<i>Conarus suberosus</i>	6	5	0.002	6.0	5.7	1.4
	<i>Plathymenia reticulata</i>	4	3	0.01	4.0	3.4	5.7
	<i>Dimorphandra mollis</i>	4	4	0.003	4.0	4.6	1.8
	<i>Andira cordata</i>	3	3	0.016	3.0	3.4	9.3
	<i>Qualea parviflora</i>	3	3	0.003	3.0	3.4	1.9
	<i>Rudgea erioloba</i> (TMS167)	2	1	0.003	2.0	1.1	1.6
	MYRTACEAE TMS166	2	2	0.002	2.0	2.3	1.1
	<i>Mugunia pubescens</i>	2	2	0.002	2.0	2.3	1.0
	<i>Vatairea macrocarpa</i>	2	2	0.001	2.0	2.3	0.8
	<i>Ferdinandusa ovalis</i>	1	1	0.007	1.0	1.1	3.8
	<i>Byrsosima coccolobifolia</i>	1	1	0.002	1.0	1.1	1.4
	<i>Ouratea hexasperma</i>	1	1	0.002	1.0	1.1	1.3
	<i>Vochysia rufa</i>	1	1	0.002	1.0	1.1	1.0
	<i>Eminotum nitens</i>	1	1	0.001	1.0	1.1	0.8
	<i>Brosimum gaudichaudii</i>	1	1	0.001	1.0	1.1	0.7
	<i>Tocoyena formosa</i>	1	1	0.001	1.0	1.1	0.7
	<i>Caryocar cuneatum</i>	1	1	0.001	1.0	1.1	0.6
	<i>Jacaranda brasiliensis</i>	1	1	0.001	1.0	1.1	0.6
	<i>Dipteryx alata</i>	1	1	0.001	1.0	1.1	0.5
	<i>Mouriri pusa</i>	1	1	0.001	1.0	1.1	0.5
	<i>Tabebuia ochracea</i>	1	1	0.001	1.0	1.1	0.4
	<i>Agonandra brasiliensis</i>	1	1	0.001	1.0	1.1	0.4
	<i>Psidium myrsinoides</i>	1	1	0.001	1.0	1.1	0.4
	<i>Himatanthus obovatus</i>	1	1	0	1.0	1.1	0.1
	<i>Casaria sylvestris</i>	1	1	0	1.0	1.1	0.1
T22	<i>Curatella americana</i>	10	9	0.018	12.5	12.0	13.7
	<i>Physocalymna scaberrimum</i>	8	8	0.011	10.0	10.7	8.0
	<i>Diospyros hispida</i>	6	5	0.012	7.5	6.7	9.0
	<i>Salvertia convallariodora</i>	6	6	0.008	7.5	8.0	5.9
	<i>Ferdinandusa ovalis</i>	4	4	0.009	5.0	5.3	6.5
	<i>Pouteria ramiflora</i>	4	4	0.008	5.0	5.3	5.8
	<i>Eminotum nitens</i>	4	3	0.006	5.0	4.0	4.3
	<i>Andira cordata</i>	3	3	0.009	3.8	4.0	6.7
	<i>Ouratea hexasperma</i>	3	3	0.006	3.8	4.0	4.8
	<i>Syagrus cunosa</i>	3	3	0.002	3.8	4.0	1.6
	<i>Davilla elliptica</i>	3	2	0.001	3.8	2.7	1.0
	<i>Caryocar brasiliense</i>	2	2	0.007	2.5	2.7	5.4
	<i>Qualea grandiflora</i>	2	2	0.003	2.5	2.7	1.9
	<i>Tabebuia ochracea</i>	2	2	0.002	2.5	2.7	1.6
	<i>Dimorphandra mollis</i>	2	1	0.002	2.5	1.3	1.2
	<i>Psidium myrsinoides</i>	2	2	0.001	2.5	2.7	1.0
	<i>Qualea multiflora</i>	1	1	0.01	1.3	1.3	7.6
	<i>Anacardium occidentale</i>	1	1	0.007	1.3	1.3	5.0
	MYRTACEAE TMS166	1	1	0.002	1.3	1.3	1.6
	<i>Qualea parviflora</i>	1	1	0.002	1.3	1.3	1.5
	<i>Stryphnodendron obovatum</i>	1	1	0.001	1.3	1.3	1.1
	<i>Mouriri elliptica</i>	1	1	0.001	1.3	1.3	1.0
	<i>Mouriri pusa</i>	1	1	0.001	1.3	1.3	0.9
	<i>Callisthene fasciculata</i>	1	1	0.001	1.3	1.3	0.6
	<i>Plathymenia reticulata</i>	1	1	0.001	1.3	1.3	0.6
	<i>Erythroxylum suberosum</i>	1	1	0.001	1.3	1.3	0.4
	<i>Byrsosima coccolobifolia</i>	1	1	0.001	1.3	1.3	0.4
	<i>Himatanthus obovatus</i>	1	1	0	1.3	1.3	0.3
	<i>Rudgea erioloba</i> (TMS167)	1	1	0	1.3	1.3	0.2
	<i>Tocoyena formosa</i>	1	1	0	1.3	1.3	0.2
	<i>Caryocar cuneatum</i>	1	1	0	1.3	1.3	0.2
	<i>Conarus suberosus</i>	1	1	0	1.3	1.3	0.2

Table 4.8. Species of trees ≥ 5 cm dbh occurring in four transects in Carolina.
(N) number of individuals, (P) number of points in the transect, (BA) total basal area,
(RDe) relative density, (RF) relative frequency and (RDo) relative dominance.

	Species	N	P	BA (m ²)	RDe (%)	RF (%)	RDo (%)
T23	<i>Vochysia tucanorum</i>	12	11	0.192	15.0	15.5	14.6
	<i>Qualea parviflora</i>	10	8	0.255	12.5	11.3	19.4
	<i>Hirtella ciliata</i>	9	6	0.110	11.3	8.5	8.3
	<i>Kielmeyera coriacea</i>	7	6	0.042	8.8	8.5	3.2
	<i>Pouteria ramiflora</i>	6	6	0.157	7.5	8.5	12.0
	<i>Andira cordata</i>	6	5	0.093	7.5	7.0	7.1
	<i>Psidium myrsinoides</i>	5	5	0.030	6.3	7.0	2.3
	<i>Dimorphandra mollis</i>	3	3	0.037	3.8	4.2	2.8
	<i>Parkia platycephala</i>	2	2	0.113	2.5	2.8	8.6
	<i>Bowdichia virgiliodes</i>	2	2	0.048	2.5	2.8	3.7
	<i>Stryphnodendron coriaceum</i>	2	2	0.031	2.5	2.8	2.4
	<i>Plathymenia reticulata</i>	2	2	0.016	2.5	2.8	1.2
	<i>Agonandra brasiliensis</i>	2	1	0.011	2.5	1.4	0.9
	<i>Dalbergia miscolobium</i>	1	1	0.025	1.3	1.4	1.9
	<i>Byrsonima crassifolia</i>	1	1	0.024	1.3	1.4	1.8
	<i>Hymenaea stigonocarpa</i>	1	1	0.023	1.3	1.4	1.8
	<i>Anacardium occidentale</i>	1	1	0.023	1.3	1.4	1.7
	<i>Himatanthus obovatus</i>	1	1	0.022	1.3	1.4	1.7
	<i>Tabebuia aurea</i>	1	1	0.020	1.3	1.4	1.5
	<i>Qualea grandiflora</i>	1	1	0.015	1.3	1.4	1.2
	<i>Stryphnodendron obovatum</i>	1	1	0.011	1.3	1.4	0.8
	<i>Caryocar cuneatum</i> (tido co	1	1	0.006	1.3	1.4	0.4
	<i>Mouriri pusa</i>	1	1	0.004	1.3	1.4	0.3
	<i>Enterolobium gummiiferum</i>	1	1	0.004	1.3	1.4	0.3
	<i>Eriotheca gracilipes</i>	1	1	0.003	1.3	1.4	0.2
T24	<i>Qualea parviflora</i>	28	16	0.653	35.0	25.8	53.9
	<i>Hirtella ciliata</i>	10	8	0.077	12.5	12.9	6.3
	<i>Dalbergia miscolobium</i>	5	5	0.062	6.3	8.1	5.1
	<i>Byrsonima crassifolia</i>	5	3	0.037	6.3	4.8	3.1
	<i>Pouteria ramiflora</i>	5	4	0.034	6.3	6.5	2.8
	<i>Mouriri elliptica</i>	4	4	0.044	5.0	6.5	3.6
	<i>Dimorphandra mollis</i>	4	4	0.042	5.0	6.5	3.5
	<i>Vochysia tucanorum</i>	3	3	0.078	3.8	4.8	6.5
	<i>Anacardium occidentale</i>	3	3	0.059	3.8	4.8	4.9
	<i>Andira cordata</i>	3	2	0.015	3.8	3.2	1.2
	<i>Himatanthus obovatus</i>	2	2	0.038	2.5	3.2	3.1
	<i>Mouriri pusa</i>	2	2	0.012	2.5	3.2	1.0
	<i>Kielmeyera coriacea</i>	2	2	0.008	2.5	3.2	0.7
	<i>Emmotum nitens</i>	1	1	0.016	1.3	1.6	1.3
	<i>Hancornia speciosa</i>	1	1	0.014	1.3	1.6	1.2
	<i>Parkia platycephala</i>	1	1	0.013	1.3	1.6	1.1
	<i>Stryphnodendron coriaceum</i>	1	1	0.009	1.3	1.6	0.8

Table 4.8. cont.

	Species	N	P	BA (m2)	RDe (%)	RF (%)	RDo (%)
T25	<i>Vochysia tucanorum</i>	25	16	0.528	31.3	24.2	41.3
	<i>Hirtella ciliata</i>	15	11	0.097	18.8	16.7	7.6
	<i>Qualea parviflora</i>	6	6	0.143	7.5	9.1	11.2
	<i>Mouriri elliptica</i>	6	5	0.089	7.5	7.6	7.0
	<i>Mouriri pusa</i>	4	4	0.170	5.0	6.1	13.3
	<i>Plathymenia reticulata</i>	3	3	0.056	3.8	4.6	4.4
	<i>Pouteria ramiflora</i>	3	3	0.020	3.8	4.6	1.6
	<i>Psidium myrsinoides</i>	3	3	0.019	3.8	4.6	1.5
	<i>Andira cordata</i>	2	2	0.022	2.5	3.0	1.7
	<i>Parkia platycephala</i>	2	2	0.021	2.5	3.0	1.6
	<i>Emmotum nitens</i>	2	2	0.012	2.5	3.0	1.0
	<i>Byrsonima crassifolia</i>	2	2	0.007	2.5	3.0	0.6
	<i>Caryocar cuneatum</i>	1	1	0.057	1.3	1.5	4.5
	<i>Himatanthus obovatus</i>	1	1	0.017	1.3	1.5	1.4
	<i>Connarus suberosus</i>	1	1	0.007	1.3	1.5	0.5
	<i>Hancornia speciosa</i>	1	1	0.004	1.3	1.5	0.3
	<i>Dimorphandra mollis</i>	1	1	0.003	1.3	1.5	0.2
	<i>Stryphnodendron coriaceum</i>	1	1	0.002	1.3	1.5	0.2
	<i>Himatanthus articulatus</i>	1	1	0.002	1.3	1.5	0.2
	T26	<i>Plathymenia reticulata</i>	14	11	0.306	17.5	15.5
<i>Andira cordata</i>		10	8	0.110	12.5	11.3	6.8
<i>Hirtella ciliata</i>		9	6	0.236	11.3	8.5	14.6
<i>Ouratea hexasperma</i>		6	6	0.054	7.5	8.5	3.4
<i>Pouteria ramiflora</i>		4	3	0.057	5.0	4.2	3.6
<i>Psidium myrsinoides</i>		4	4	0.016	5.0	5.6	1.0
<i>Caryocar cuneatum</i>		3	3	0.143	3.8	4.2	8.9
<i>Sclerolobium paniculatum</i>		3	3	0.117	3.8	4.2	7.2
<i>Stryphnodendron obovatum</i>		3	3	0.031	3.8	4.2	1.9
<i>Byrsonima crassifolia</i>		3	3	0.014	3.8	4.2	0.9
<i>Pterodon pubescens</i>		2	2	0.180	2.5	2.8	11.2
<i>Mouriri elliptica</i>		2	2	0.147	2.5	2.8	9.1
<i>Salvertia convallariodora</i>		2	2	0.033	2.5	2.8	2.1
<i>Stryphnodendron coriaceum</i>		2	2	0.011	2.5	2.8	0.7
<i>Connarus suberosus</i>		2	2	0.007	2.5	2.8	0.4
<i>Qualea grandiflora</i>		1	1	0.036	1.3	1.4	2.2
<i>Anacardium occidentale</i>		1	1	0.030	1.3	1.4	1.9
<i>Emmotum nitens</i>		1	1	0.021	1.3	1.4	1.3
<i>Byrsonima sp. folha fina</i>		1	1	0.018	1.3	1.4	1.1
<i>Diospyros hispida</i>		1	1	0.014	1.3	1.4	0.9
<i>Tocoyena formosa</i>		1	1	0.011	1.3	1.4	0.7
<i>Annona coriacea</i>		1	1	0.006	1.3	1.4	0.4
<i>Qualea parviflora</i>		1	1	0.005	1.3	1.4	0.3
<i>Dimorphandra mollis</i>		1	1	0.003	1.3	1.4	0.2
<i>Dalbergia miscolobium</i>		1	1	0.002	1.3	1.4	0.2
<i>Hymenaea stigonocarpa</i>		1	1	0.002	1.3	1.4	0.2

while 50 species were widespread in both isolated and non-isolated savannas.

The number of species unexpectedly increased as the patch of savanna become smaller (Fig. 4.1a), a significant negative linear relationship ($y=-6.204+0.0004x$, $r^2=34$, $P=0.025$) was found between the number of species (y) and the area size (x) for all the isolated savannas, however, little of the variance was explained by the regression.

There was a significant negative non-linear relationship between the number of species present in a study site and its distance (km) from the gravity centre (centroid) of distribution of the central Brazilian savannas ($y=\exp(4.164^{-0.001x})$; $P<0.000$; $r^2=82$) (Fig. 4.1b). A non-linear relationship is due to presence of species of wide Neotropical distribution, which will always be present even at a much greater distance from the centroid (as used in this study) or from any other chosen centre point.

Classification analysis

The dendrogram based on the Sørensen Similarity Indices between the 101 species from all sites (Fig. 4.2) shows a clear first division distinguishing isolated and non-isolated savannas. The second division of the former group separates Humaitá (the richest in species, many of which do not occur in other areas of Brazil) from the other isolated savannas. The second division of the non-isolated savannas distinguishes Chapada dos Parecis (which had 13 species restricted to it) from the others. The analysis distinguishes each of the geographical areas in both the isolated and non-isolated savannas. The values of the Sørensen's index are given in Appendix 4.3.

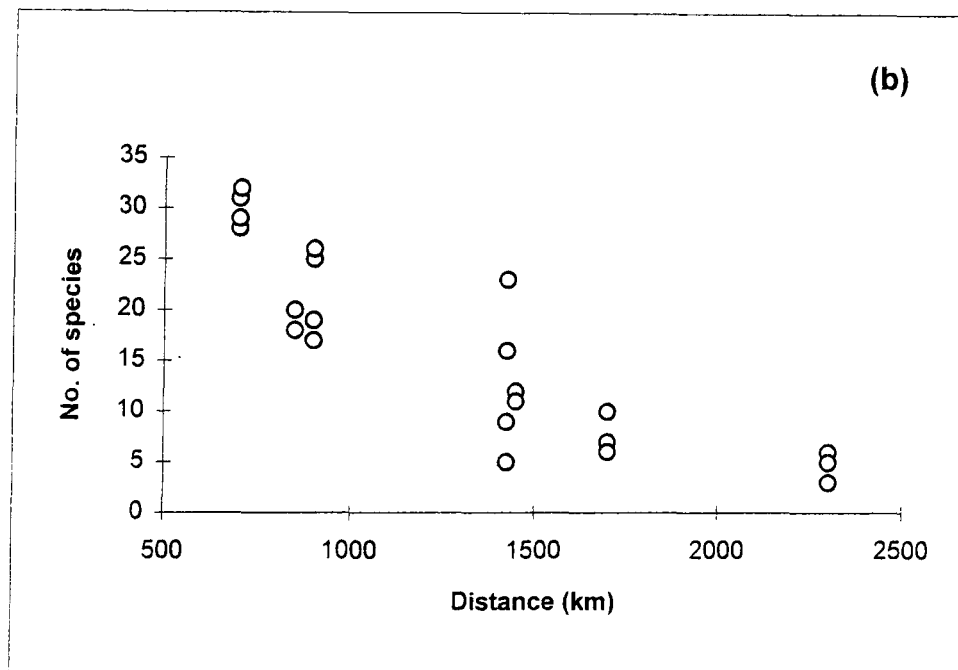
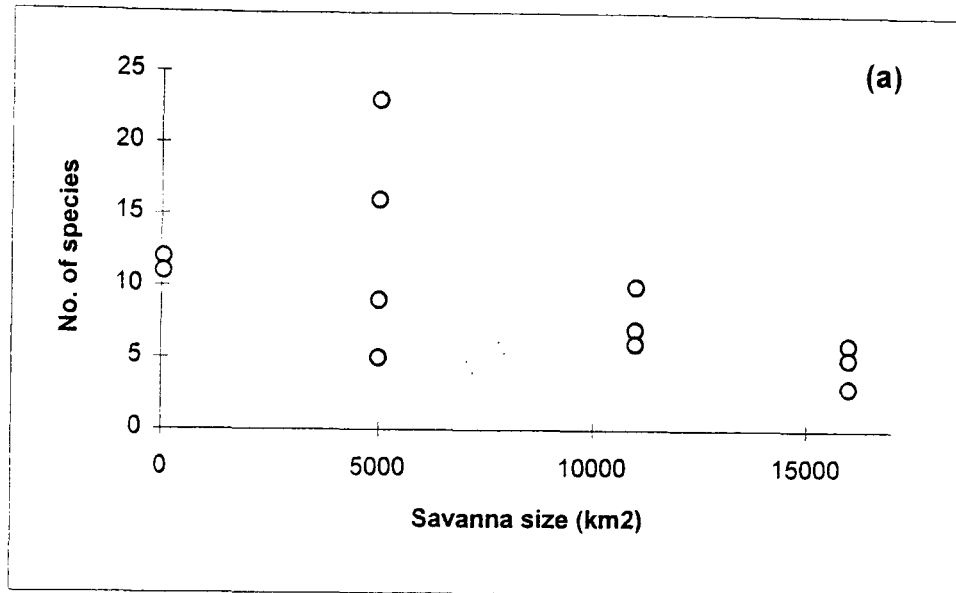


Fig. 4.1. Number of species present per transect (a) in the four isolated savannas in relation to their area size; (b) in the seven savannas studied in relation to their distance from a geographic centroid of the central Brazilian savannas distribution.

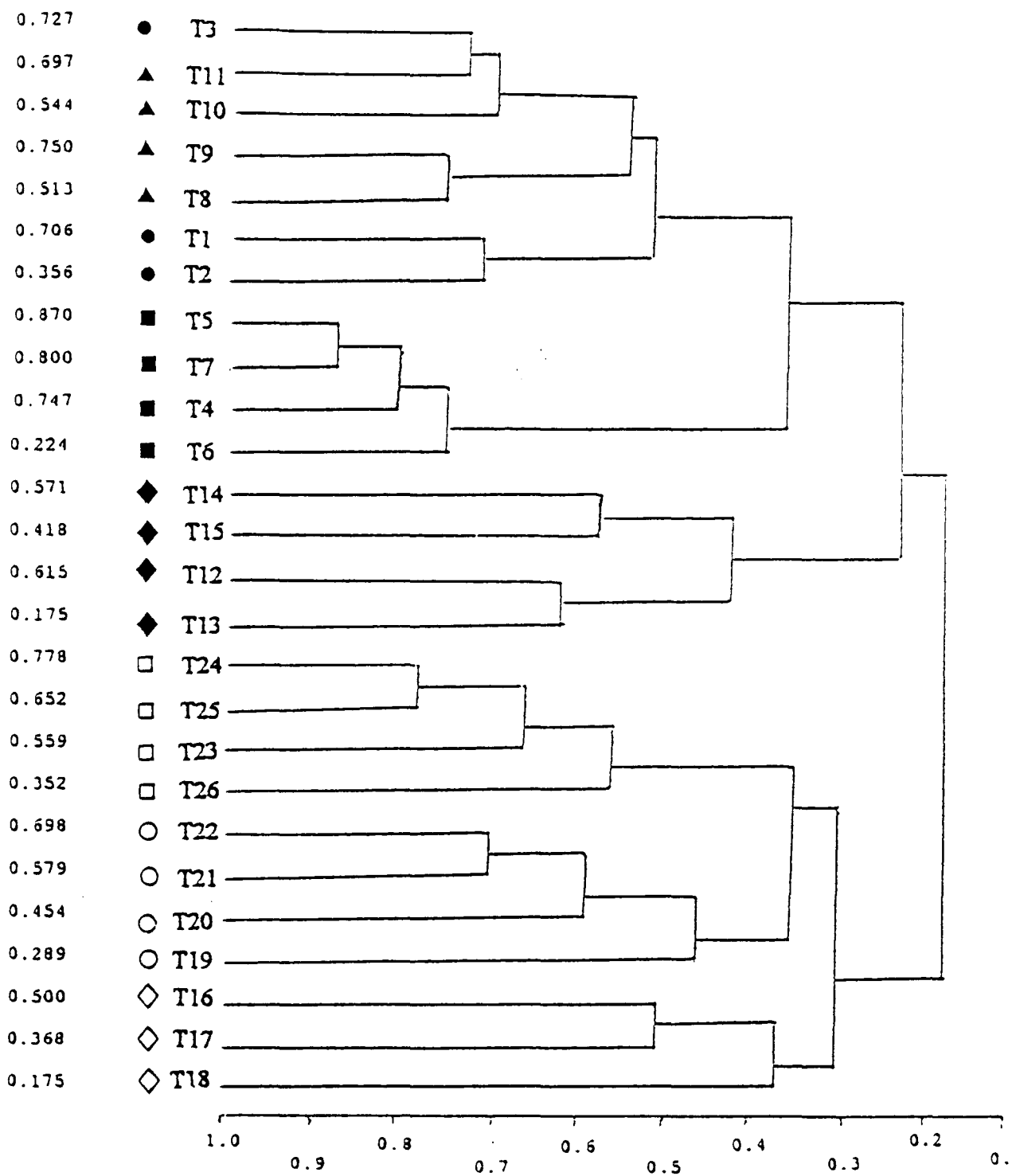


Fig. 4.2. Similarity dendrogram yielded by UPGMA, using Sørensen Similarity Indices based on presence and absence of 101 tree species ≥ 5 cm (recorded by PCQ) from 26 transects from the seven savannas. Open symbols represent non-isolated savannas, closed symbols represent isolated savannas. (●) Amapá, (■) Alter do Chão, (▲) Roraima, (◆) SE Humaitá, (◇) Chapada dos Parecis, (Δ) Redenção and (□) Carolina.

The analysis produced by including the additional 43 species recorded by 'wide patrolling', provides a similar dendrogram (Fig. 4.3) and confirm the previous conclusions.

Ordination analysis

The ordination based on floristic composition and density produced similar results to those yielded by UPGMA using Sørensen Similarity Indices, distinguishing the communities of isolated and non-isolated savannas at an upper level, and each of the geographical communities at a second level (Fig. 4.4; 4.5; 4.6).

The DCA of presence/absence of the 101 species sampled by the PCQ method (Fig. 4.4) shows: (i) the species *Laxoplumeira lesmannii*, *Vochysia grandis*, *Guatteria* aff. *mayapuensis*, *Ochthocosmus barrae* and *Anacardium giganteum* at the extreme of the diagram corresponding to the SE Humaitá transects, (ii) *Roupala montana*, *Himatanthus* aff. *fallax*, *Byrsonima* aff. *intermedia* and *Curatella americana* corresponding to the Roraima and Amapá transects, (iii) *Vatairea macrocarpa*, *Myrcia* cf. *obtusata*, *Sclerolobium paniculatum*, *Tocoyena formosa* corresponding to all the Alter do Chão transects, (iv) *Aspidosperma macrocarpon*, *Eugenia puniceifolia*, *Licania humilis*, *Ouratea spectabilis*, *Piptocarpha rotundifolia*, *Styrax ferrugineus*, *Buchenavia tomentosa*, *Vochysia cinnamomea* corresponding to Chapada dos Parecis on the other extreme of the diagram, while (v) Redenção and Carolina share a large number of species and therefore are grouped together in the centre of the diagram.

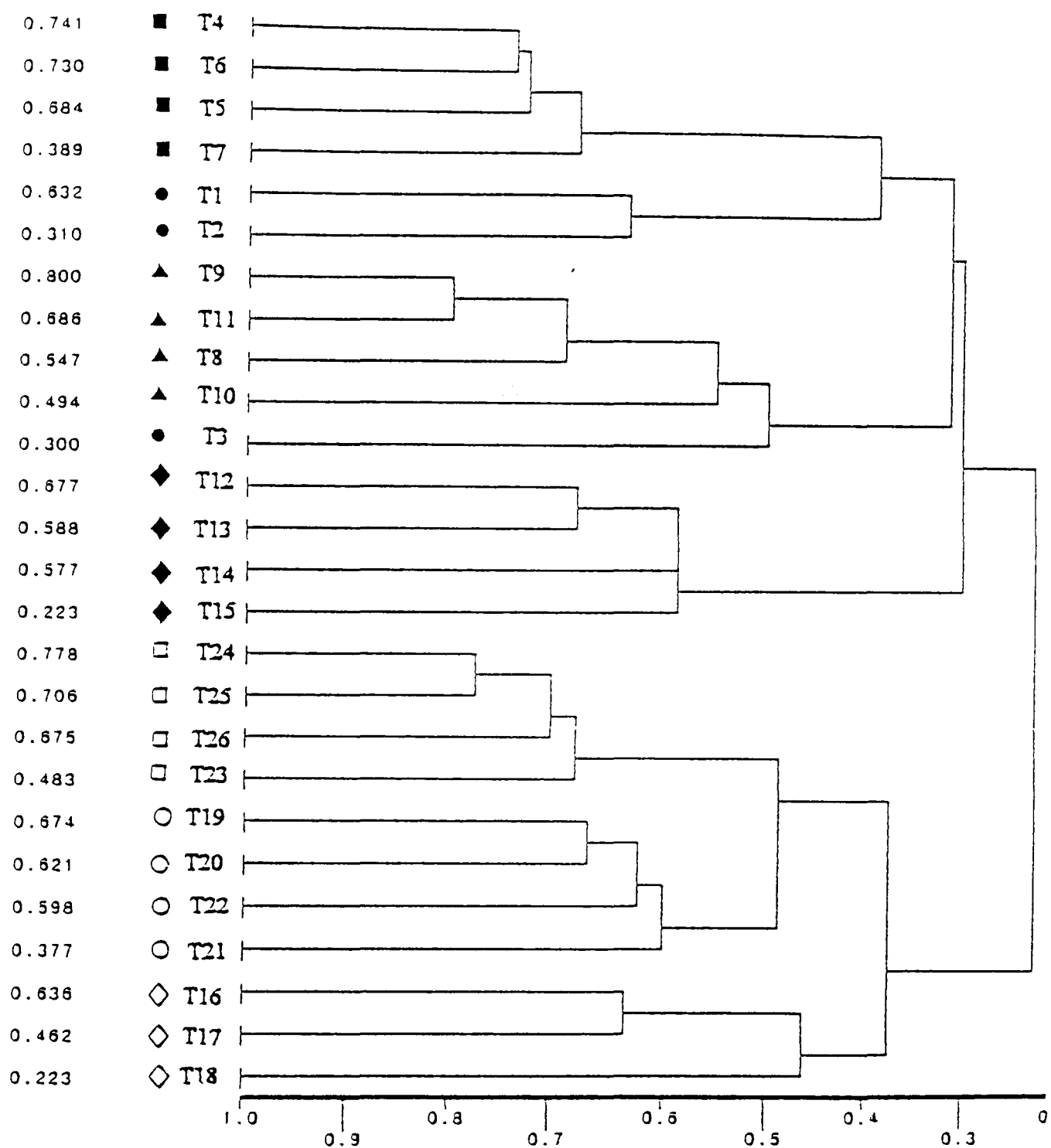


Fig. 4.3. Similarity dendrogram yielded by UPGMA, using Sørensen Similarity Indices based on presence and absence of 144 tree species ≥ 5 cm (recorded by PCQ plus wide patrolling) from 26 transects from the seven savannas. Open symbols represent non-isolated savannas, closed symbols represent isolated savannas. (●) Amapá, (■) Alter do Chão, (▲) Roraima, (◆) SE Humaitá, (◇) Chapada dos Parecis, (Δ) Redenção and (□) Carolina.

- LIST
 0005=Anacgiga, Didydist, Simaamar
 0006=Antoovat, Carasava
 0007=Aspmacr, Eugepuni
 0008=Buchtome, Myrc sp, Vochcinn
 0009=Callfasc, Quaimult
 0010=Carycune, Diotalat, Jacaoras, Stryobov
 0011=Oldy sp, Diotaura, Styferr
 0012=Erytsube, Physscab
 0013=Ferdoval, MYRTTMS166
 0014=Hirtglan, Laxolesm
 0015=Licahumi, Ouraspec, Piotrotu
 0016=Myrc cf, Protunif, Rourindu, Scleaure
 0017=Parkolat, Vochtuca
 0018=Tocalorm, Vatamacr

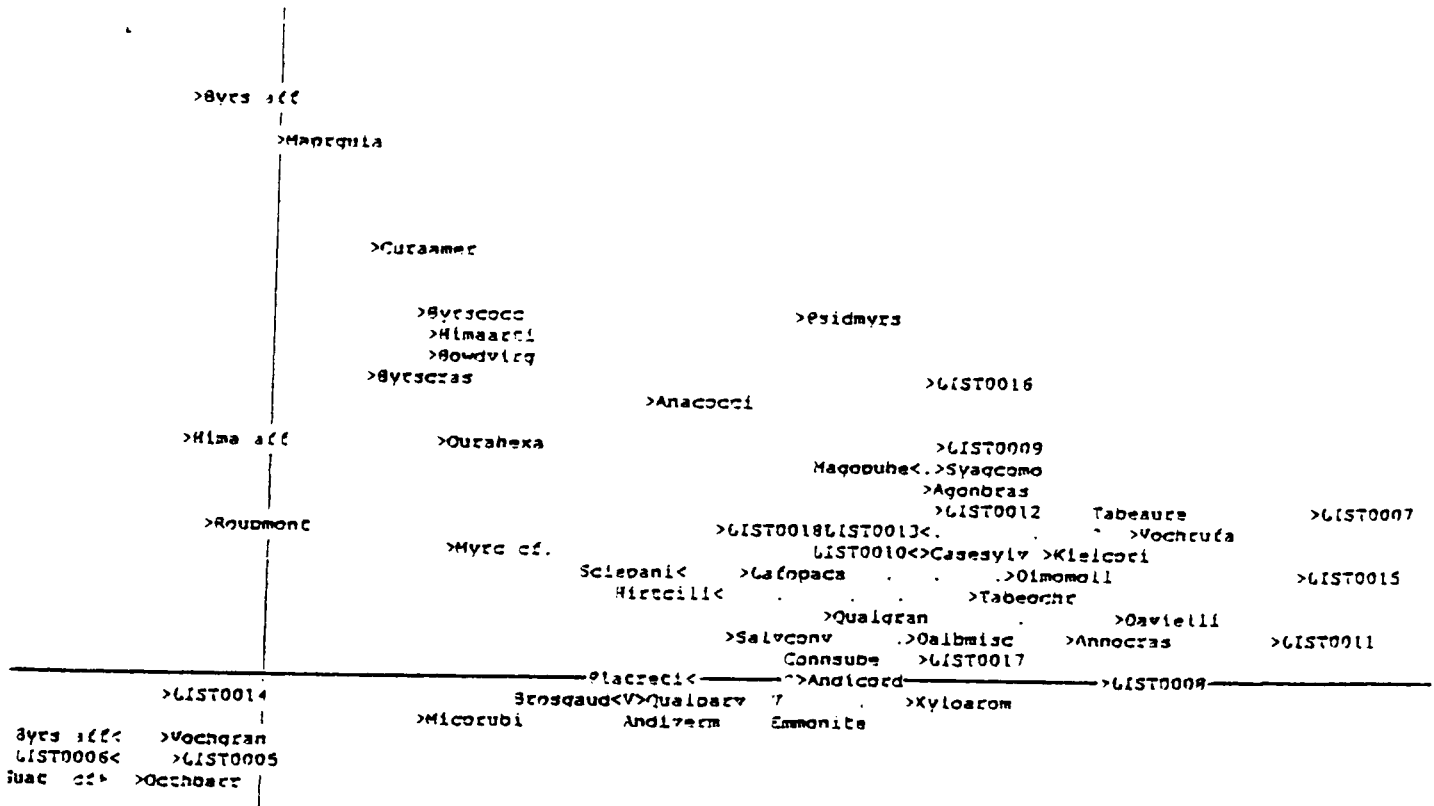
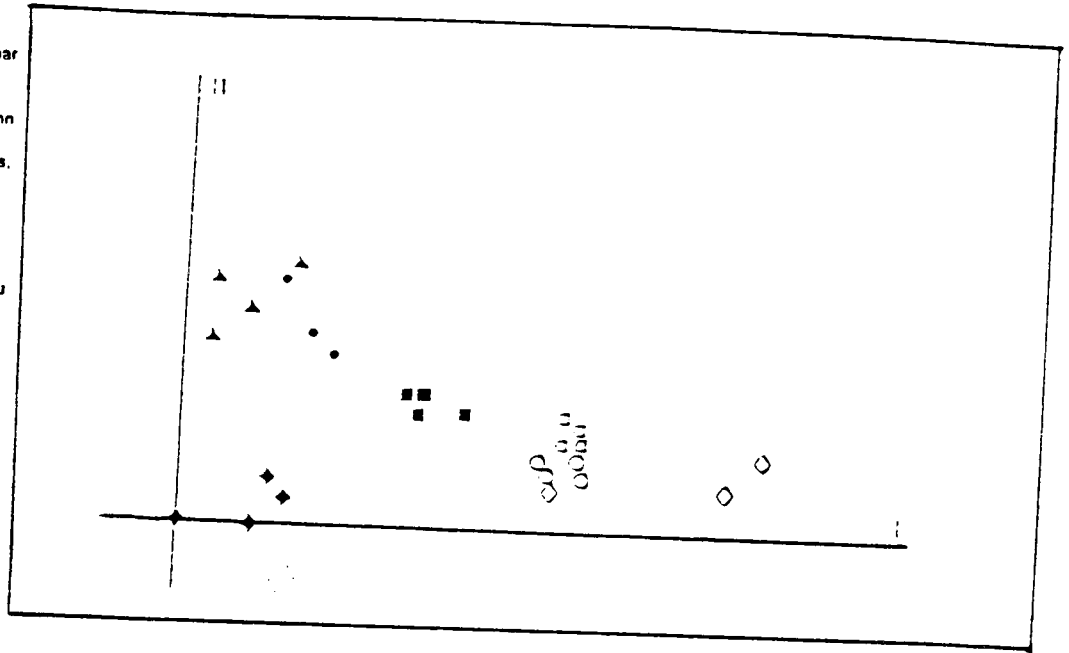


Fig. 4.4. DCA ordination of the 101 species (recorded by the PCQ) present on the 26 transects of the seven savannas based on presence/absence of species. Open symbols represent non-isolated savannas, closed symbols represent isolated savannas. (●) Amapá, (■) Alter do Chão, (▲) Roraima, (◆) SE Humaitá, (◇) Chapada dos Parecis, (Δ) Redenção and (□) Carolina. (The first four components of the analysis have eigenvalues of 0.5567, 0.3446, 0.2714 and 0.1454).

There was no relevant difference between the pattern from the previous analysis from that of the DCA based on species density for the same 101 species (Fig. 4.5). The latter analysis distinguished the non-isolated savanna groups better, with *Dalbergia miscolobium*, *Vochysia* aff. *lesmanii*, *Parkia platycephala*, *Hancornia speciosa*, *Kielmeyera coriacea* separating Redenção from the Carolina transects.

The DCA analyses of 144 species recorded by 'wide patrolling' based on presence/absence confirmed the pattern found by the previous two analyses (Fig. 4.6). The non-isolated and isolated savannas are in very distinct groups. This time, additional species (*Godmania esculifolia*, *Vitex schomburgkiana*, *Machaerium* sp.) contributed to distinguishing better the Roraima transects from those of Amapá (characterized by *Trattinnickia rhoifolia*, *Rauvolfia pentaphylla*, *Licania longistyla*, *Connarus perottetii*, *Annona paludosa*, *Myrcia cuprea*, *Symplocos guianensis*, *Himatanthus drastricus*).

DISCUSSION

The frequency of the dominant species varied between visually homogeneous transects (2 km - 80 km apart) within the same site. Such variation seems to be common in central Brazilian savannas (Felfili *et al.* 1993). The spatial distribution of tree species in these savannas is a mosaic, with each part of the mosaic showing a different combination of less than 100 species (Felfili & Silva Júnior 1993). Several studies account for this variation on the grounds of a number of environmental variables, including soil depth and water table regime (Oliveira-Filho *et al.* 1989), and latitude and longitude (Ratter & Dargie

LIST

- 0001=Anacgig, Dikydlat, Simaamar
- 0002=Asomacr, Eugepuni
- 0003=Byrs sp., Pteremar
- 0004=Didy sp., Diptaura, Styrferr
- 0005=Diptalat, Jacabras
- 0006=Entegumm, Eriograc
- 0007=Eugedyse, Guap sp., Mabe sp., Myrcrost, Ouracast
- 0008=Hancspec, Klekori
- 0009=Hirtglan, Laxolesm
- 0010=Myrc cf, Protunf, Rourindu, Scleaure
- 0011=Ouraspec, Plotrotu

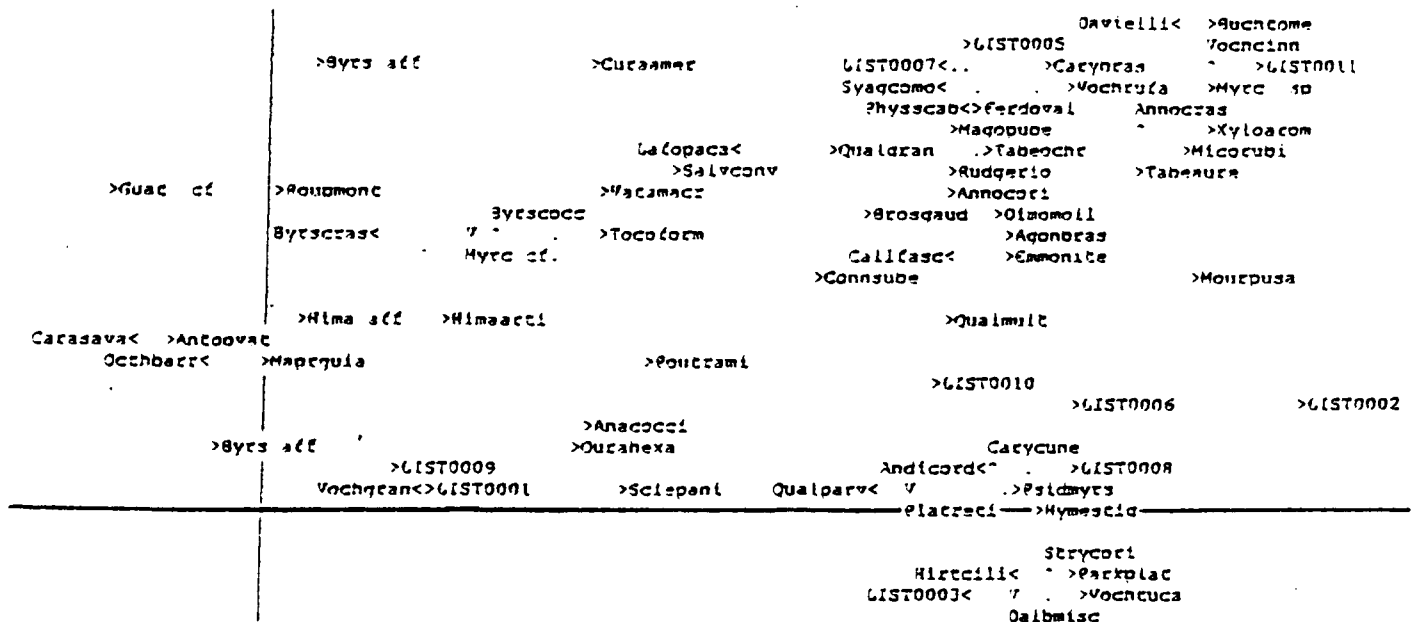
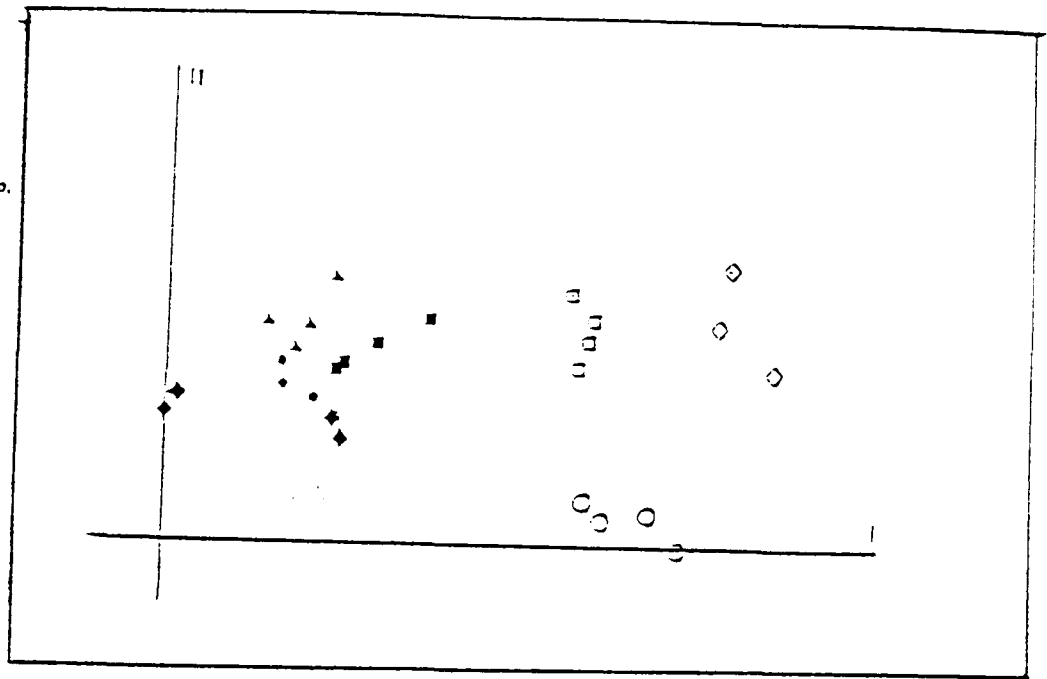


Fig. 4.5. DCA ordination of the 101 species (recorded by the PCQ) present on the 26 transects of the seven savannas based on density of species. Open symbols represent non-isolated savannas, closed symbols represent isolated savannas. (●) Amapá, (■) Alter do Chão, (▲) Roraima, (◆) SE Humaitá, (◇) Chapada dos Parecis, (△) Redenção and (□) Carolina. (The first four components of the analysis have eigenvalues of 0.6623, 0.3530, 0.2352 and 0.1233).

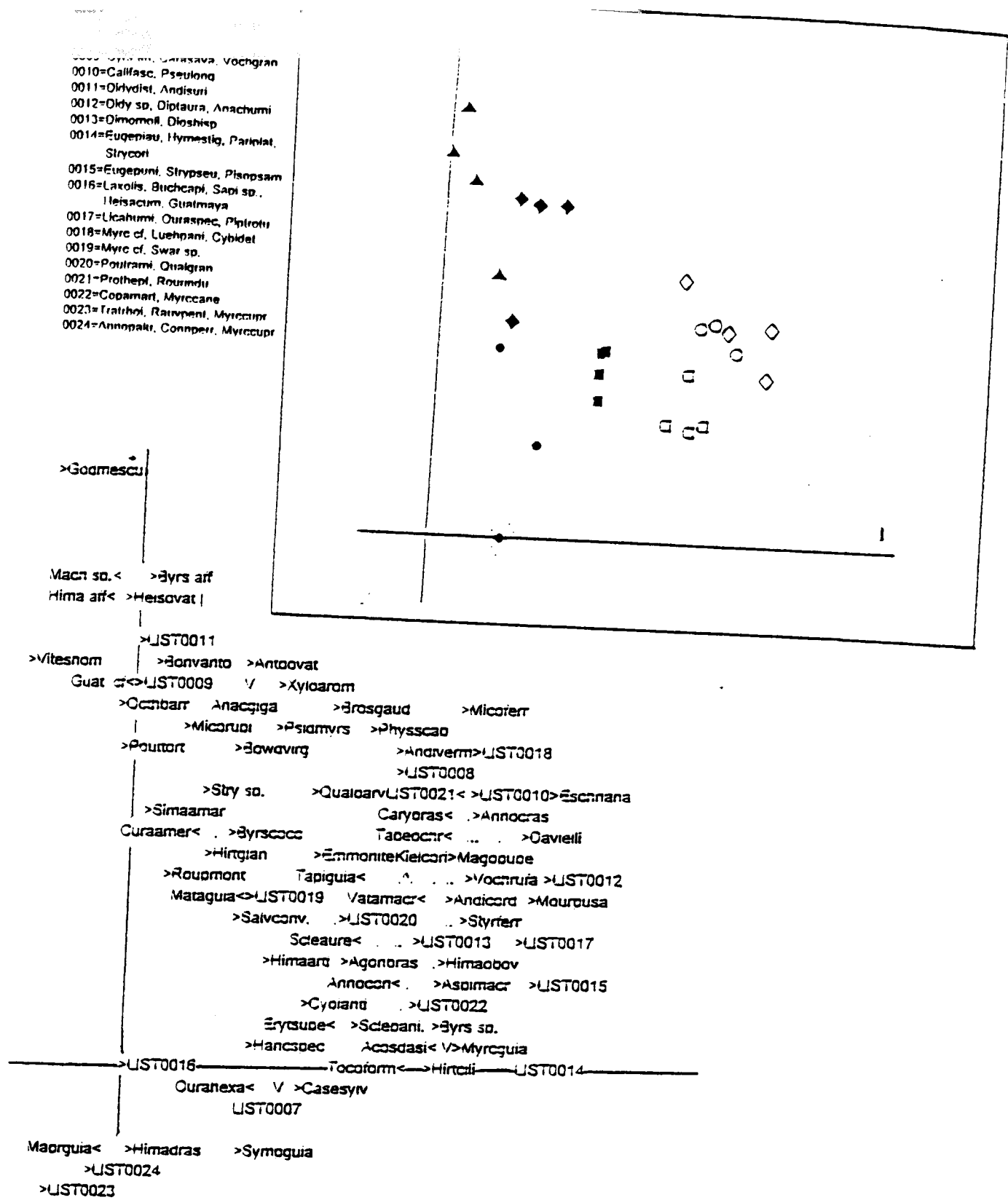


Fig. 4.6. DCA ordination of the 144 species (recorded by 'wide patrolling') present on the 26 transects of the seven savannas based on density of species. Open symbols represent non-isolated savannas, closed symbols represent isolated savannas. (●) Amapá, (■) Alter do Chão, (▲) Roraima, (◆) SE Humaitá, (◇) Chapada dos Parecis, (Δ) Redenção and (□) Carolina. (The first four components of the analysis have eigenvalues of 0.4998, 0.3090, 0.1697 and 0.1053).

1992). In this study soil texture and nutrients also distinguished most of the sites (Chapter 3, Fig. 3.2), although significant differences were found among transects from the same study site.

The classification using cluster analysis (UPGMA) and ordination (DCA) led to similar conclusions. There is a strong separation of the southern Amazonian savannas (part of the northern extension of the core area) and the disjunct savannas isolated in the rain forest. Four main subgroups were distinguished, (a) Southeastern Amazonia (T19-T26), (b) Southwestern Amazonia (T16-T18), both in the same division, and in the second division (c) isolated savannas from south of the Amazon river, and (d) isolated savannas from north of the river.

A similar tendency covering the core area of central Brazil was observed on a much larger scale (Ratter *et al.* 1996). The authors were able to distinguish five large groups. The Southwestern Amazonia group of my study (Chapada dos Parecis) corresponds to their Central western sites, and my Southeastern Amazonia group (Carolina and Redenção) would be included in their Northern sites. My smaller-scale study however, produces a further subdivision and a clear pattern for the Amazonian sites. Studies of species distribution of a family such as Chrysobalanaceae (Prance 1992) indicated a degree of phytogeographic difference between species of central Brazil and Amazonian savannas.

The large number of northeastern Amazonian species present in Humaitá suggest establishment of this savanna from more than one centre of dispersion. It has probably been colonized by species from the llanos, e.g. from localities dominated by *Caraipa* as found by Sarmiento (1984) and by central Brazilian species as mentioned by Kubitzki

(1979). The Amapá savannas have Guyanan species, indicating their establishment involved a northern influence rather than one from central Brazil, while the Roraima savannas are related to the nearby Rupununi and Venezuelan complex, rather than to the vegetation of distant central Brazil.

Implications for evaluation and planning

The government of the state of Amapá showed interest in protecting savanna areas. Therefore a report was provided giving the location of well preserved areas in the north-south strip of savannas running through the state. A paper including these suggestions has been submitted and accepted for publication (Appendix 4.4).

Chapter 5.

Soil organic matter isotopes ($^{13}\text{C}:^{12}\text{C}$) and carbon dating (^{14}C)

INTRODUCTION

Stable carbon isotope analysis uses differences in the natural abundance of the stable carbon isotopes ^{13}C and ^{12}C as tags or tracers and the variation in $^{13}\text{C}/^{12}\text{C}$ ratios is generally measured by ratio mass spectrometry (Rounick & Winterbourn 1986). The δ values are measures of heavy (^{13}C) and light (^{12}C) isotope components. Organic matter is invariably depleted in ^{13}C compared with the standard generally used, PDB (Belemnite from the Peedee formation), therefore $\delta^{13}\text{C}$ values of organic materials are negative, an increase in these values (a less negative figure) means the material is richer in ^{13}C , and it is accompanied by a reciprocal decrease in the light isotope content (O'Leary 1981, Peterson & Fry 1987).

A prerequisite for stable isotope carbon research is to understand the range of carbon isotope abundances found in natural materials and the way it is altered by chemical, physical and biological fractionation processes (Rounick & Winterbourn 1986).

Natural variation of $\delta^{13}\text{C}$ values in plants is due to the fact that during CO_2 assimilation plants discriminate the stable isotope ^{13}C to different extents, according to their C_3 , C_4 or CAM photosynthetic pathways (Bender 1971, Smith & Epstein 1971). The average value for C_3 plants is $\sim -28\text{‰}$ and $\text{C}_4 \sim -13\text{‰}$ (Bender 1971, Smith &

Epstein 1971) and this can reflect vegetation types, where forests are dominated by C₃-pathway plants and savanna grasslands are dominated by C₄ plants. However, the value ranges of C₄ and C₃ plants can differ according to the variation in the isotopic ratio of the local atmospheric CO₂ (-10 to -19‰ and -21 to -36‰ respectively, Troughton *et al.* 1974), light intensity (Park & Epstein 1960, Troughton 1972), and altitude (Körner *et al.* 1988), nevertheless the ranges are still distinct. Some groups such as grasses contain both C₃ and C₄ species (Cowling 1983) and a study in south Brazil (Klink 1989) showed that C₃ grasses tend to occupy cooler shaded habitats and C₄ sunny open habitats. Similar tendencies were discovered in Namibia, southern Africa, (Ellis *et al.* 1980) where the C₃ grasses were found to occupy relatively high moisture regimes with reduced solar radiation and low leaf temperatures and C₄ species hotter temperatures and a wide tolerance of moisture conditions.

Soil organic matter globally contains several-fold more carbon than either the atmosphere or living plant biomass and in general is similar or slightly enriched in ¹³C in comparison with the dominant vegetation (Peterson & Fry 1987). Vegetation changes have numerous consequences for the physical, chemical and biological properties of soil, especially soil organic matter (Mariotti & Peterschmitt 1994). Since the main control of the soil organic matter δ¹³C values is plant litter inputs, it is possible to detect the occurrence of shifts in tropical zones of forest (C₃ dominant plants) to grassland (C₄ dominant grasses) or vice-versa, and to record part of a vegetation history from deeper layers.

The radiocarbon dating (^{14}C) of soil organic matter generally shows an increase of age with depth. The superficial layers usually are modern or up to 100 years, at 1 m deep ages around of 3,000 to 5,000 years are typical, while deeper soil layers up to 6 m can reach 60,000 years (e.g. Absy *et al.* 1991), revealing the age of a specific type of vegetation cover. Thus, the isotopic carbon composition of soil organic matter allows the establishment of an approximate chronology of palaeovegetational changes.

Large scale vegetation changes have been suggested for the Amazon (Ab'saber 1977) and recent palaeoenvironmental studies in a number of regions in Amazonia, using ^{14}C dating and analysis of soil organic matter (Desjardin *et al.* 1991), lake sediments (Turcq *et al.* 1993) in association with pollen records (Van der Hammen 1972, Absy & Van der Hammen 1976, Absy *et al.* 1991), fluvial systems (Latrubesse & Franzinelli 1993, Kromberg & Benchimol 1993) and palaeofauna (Rancy 1993) show several periods of alternation of forest and open vegetation formations during the Quaternary.

The isolated Amazonian savannas surrounded by the rain forest have been suggested as remnants of a formerly more widespread vegetation type possibly connected to the present central Brazilian savannas (Ducke & Black 1953, Egler 1960, Andrade-Lima 1966); however, other workers questioned this (Kubitzki 1983, Eiten 1972). Other floristic studies (Rizzini 1979) have suggested that the central Brazilian savannas have succeeded semideciduous forest and a recent paleopalynological study (Ledru 1993) reveals that an area of savanna in south Brazil was covered in such forest for most of the Pleistocene.

The combination of isotopic composition of the soil organic matter and ^{14}C dating is applied in this study to investigate the age of the isolated savanna patches.

MATERIALS AND METHODS

Soil sampling

The sites of the forest and savanna cores were chosen on flat ground in undisturbed vegetation well away from the present ecotone. In each study site, four soil cores were taken, two in the savanna and two in the surrounding or nearest forest. The distance from the boundary to the area of the forest sampled varied from 200 m to 23 km. In the case of the isolated sites, I tried to place the sample area in a central position. The distance from the boundary to the area of savanna sampled varied from 200 m to 40 km. Due to funding limitations only one core from savanna and one from forest were analyzed for each site. The location of the 13 analysed cores is shown in Fig. 5.1, 5.1a, 5.1b and Appendix 5.1. Only the Chapada dos Parecis had no forest nearby, and therefore the core used for comparison came from the SE Humaitá site (200 km north).

Soil cores were made using a 4 m auger, 0.5 kg of soil were taken at 11 depths (0-0.05, 0.1-0.2, 0.5-0.6, 1.0-1.2, 1.4-1.6, 1.8-2.0, 2.2-2.4, 2.6-2.8, 3.0-3.2, 3.4-3.6, 3.8-4.0 m and in addition at 4.4-4.6 m at the Roraima site). The samples were air dried, sieved (< 2 mm) to remove live roots, ground and again sieved (< 220 μm). Further processing and $^{13}\text{C}:^{12}\text{C}$ analysis were carried out in collaboration with the Center for

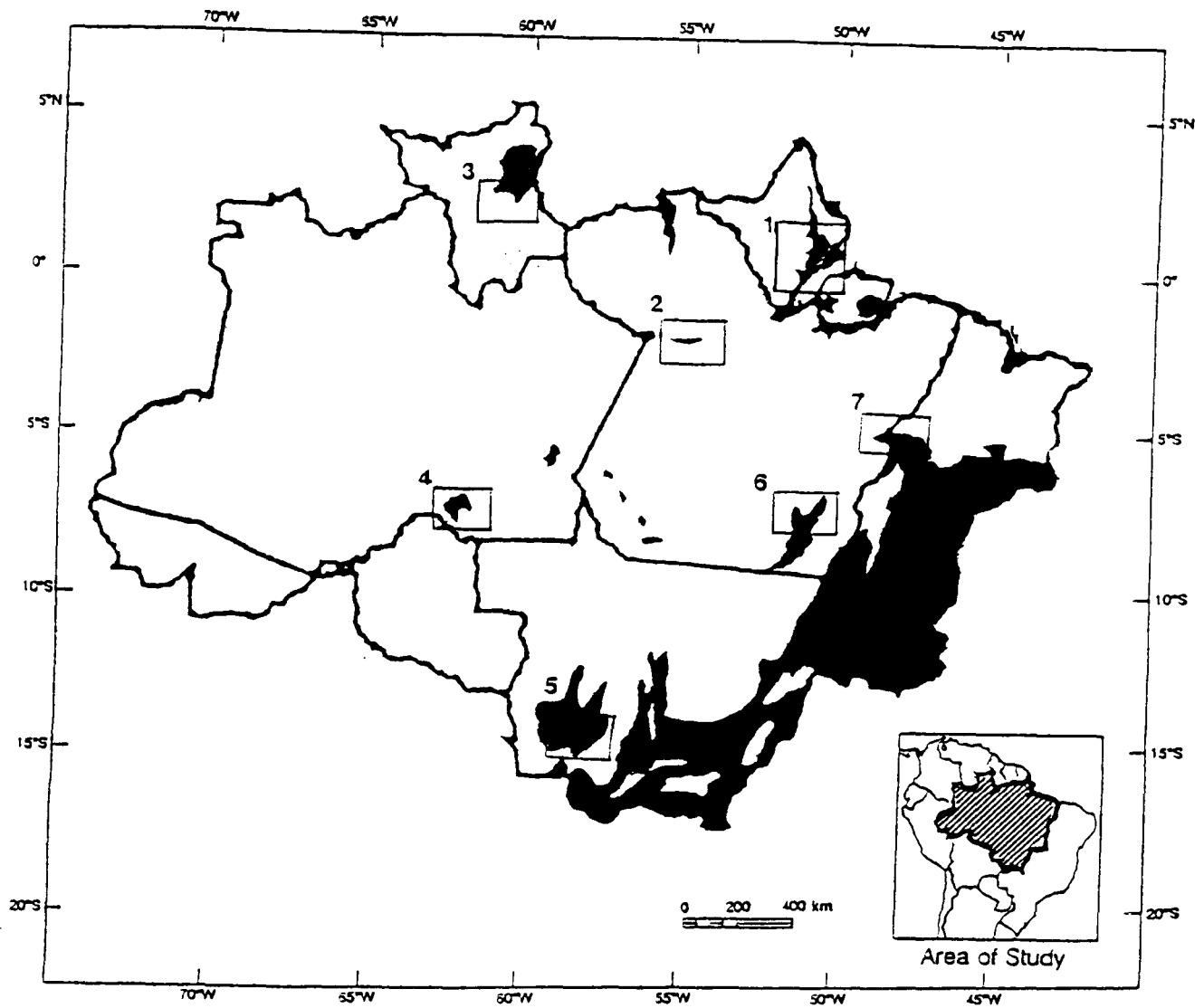


Fig. 5.1. Brazilian Amazon Basin showing the satellite image location of all study sites. (1) Amapá, (2) Alter do Chão, (3) Roraima, (4) SE Humaitá, (5) Chapada dos Parecis, (6) Redenção, (7) Carolina. Areas in black represent the savanna vegetation of the study area.

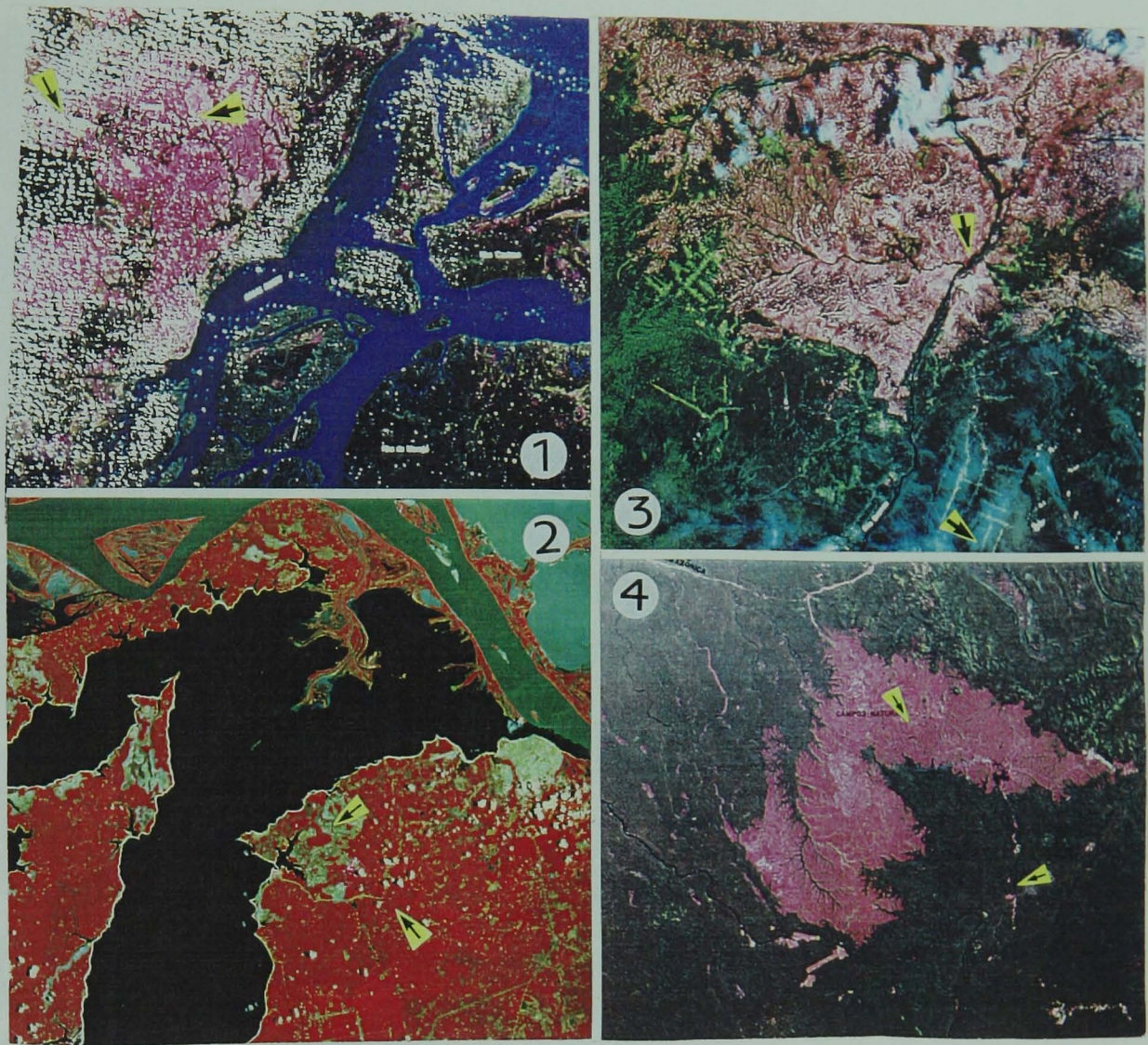


Fig. 5.1a. (1) Amapá, (2) Alter do Chão, (3) Roraima, (4) SE Humaitá. Arrows indicate the location of the soil cores.

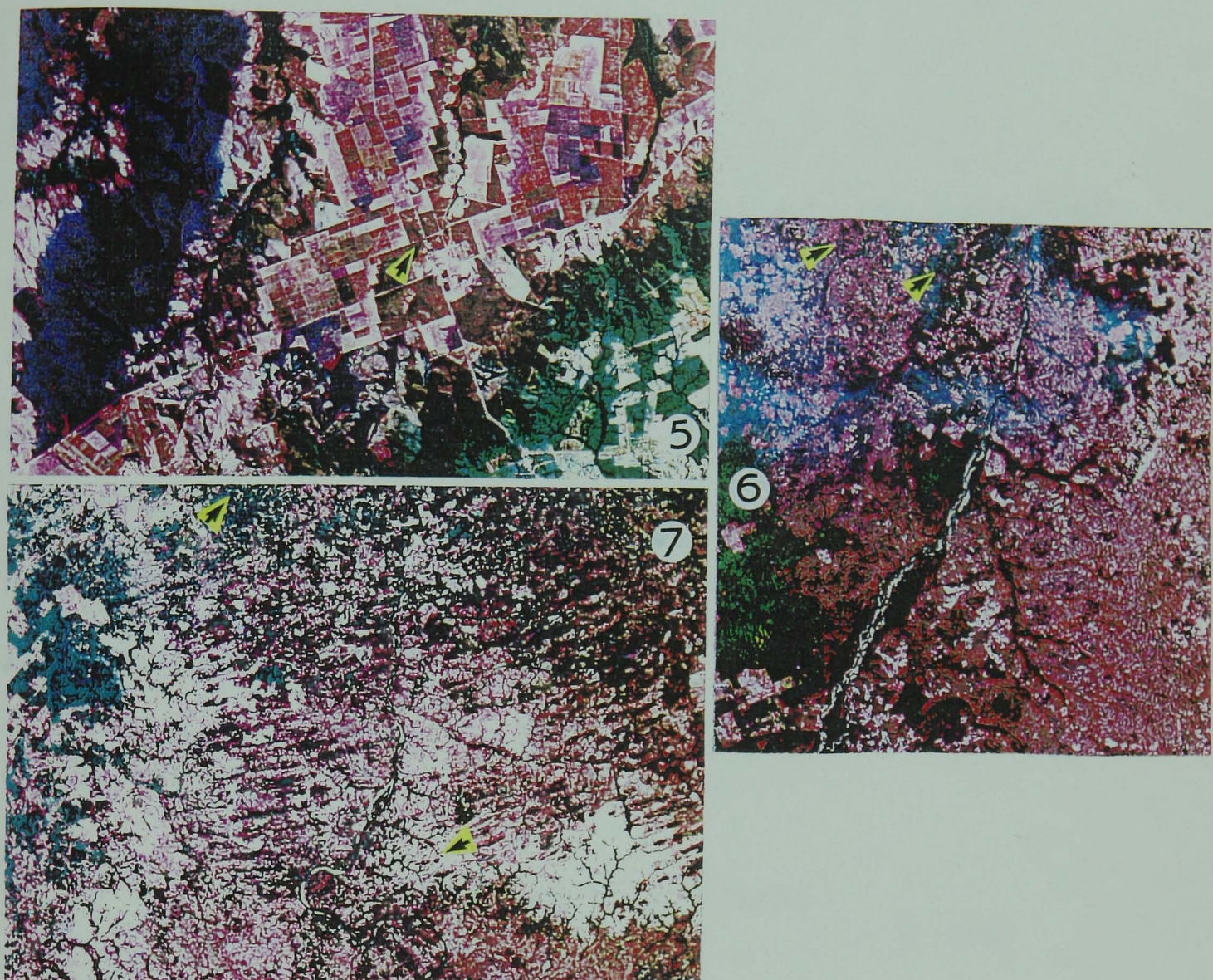


Fig. 5.1b. (5) Chapada dos Parecis, (6) Redenção, (7) Carolina. Arrows indicate the location of the soil cores.

Nuclear Energy in Agriculture (CENA) in Piracicaba, São Paulo, and the ^{14}C dating in the Department of Earth System Science, University of California, Irvine, USA.

Laboratory $\delta^{13}\text{C}$ isotope measurement

The isotopic carbon ratios of soil organic matter analysis were determined by spectrometry on CO_2 , from a 10 g subsample of the sieved soil burned in sealed evacuated pyrex tubes for 12 h at 900°C . Soil organic matter isotope measurements were made with a micromass 602 E mass spectrometer (Finnegan Mat, Bremen, Germany) fitted with double inlet and double collector systems. Standards consisted of the Peedee Belemnite (PDB) formation, from South Carolina, USA, initially employed as a standard by Craig (1957).

The results are expressed in $\delta^{13}\text{C}$ relative to the PDB standard in the conventional δ (‰) notations as:

$$\delta^{13}\text{C}\text{‰} = \left(\frac{[(^{13}\text{C}/^{12}\text{C}_{\text{sample}}) - (^{13}\text{C}/^{12}\text{C}_{\text{standard}})]}{(^{13}\text{C}/^{12}\text{C}_{\text{standard}})} - 1 \right) \times 1,000$$

The negative signal of the results indicate that the quotient $^{13}\text{C}/^{12}\text{C}$ of the sample is smaller than the quotient $^{13}\text{C}/^{12}\text{C}$ of the standard. All results represent the mean of at least two replicate analyses that differed by less than 0.3‰.

Radiocarbon ^{14}C dating

The radiocarbon content of the soil organic matter was determined for the same samples in which $\delta^{13}\text{C}$ was analysed. The carbon dating was made by a liquid scintillation method. The soil organic matter was converted into benzene, and the later analyzed in a low level Packard 1550 liquid scintillation spectrometer. Samples were counted for at least 48 h.

The radiocarbon ages are expressed in years BP (Before Present) and percentage modern carbon (pmc) relative to 95% of the activity of oxalic acid standard in 1950 and normalized to a $\delta^{13}\text{C}$ of 25‰ PDB. The analytical precision was ± 1.0 pmc.

RESULTS

$\delta^{13}\text{C}$ values

The soil profiles of all the savannas studied with the exception of the non-isolated Chapada dos Parecis site, showed a great variation of $\delta^{13}\text{C}$ values in the upper layers, but converging at depth with the values of the nearest forests (Fig. 5.2 and Appendix 5.2). The superficial soil (0-0.05 m) ranged from -16.05 to -24.89‰ ($x=-20.64$, $N=7$), with an average 8‰ higher than that found for C_4 plants (Table 5.1). There was a clear increase of $\delta^{13}\text{C}$ value at first (up to 0.6 m) with values reaching from -21.71 to -13.91 ‰ ($x=-17.77$, $N=7$) followed by a decrease in successive soil layers. The isolated SE Humaitá and the non-isolated Carolina site, showed a stabilization of the value -23.5‰ at 1.8-2.0 m. With the exception of the Chapada dos Parecis, a range

from -27.2 to -22.83 ‰ ($\bar{x}=-24.29$, $N=6$) of $\delta^{13}\text{C}$ was reached in all sites at 3.8-4.0 m, a value indicative of C_3 plant communities. Roraima was the only site sampled at 4.4-4.6 m depth and showed also the value of C_3 plants (26.8‰).

The savanna of Chapada dos Parecis was the only site that had the deepest layers (3.8-4.0 m) with $\delta^{13}\text{C}$ values (-19.04‰) similar to the surface (range from -17.63 to -21.3‰), although between 2.0-2.4 m it had a higher value (-21.3‰) which might indicate a change of the type of vegetation cover during an intermediate period.

All forest soil profiles, whether near isolated or non-isolated savanna sites, had a similar range and shape in the distribution of $\delta^{13}\text{C}$ values, from an average -28.31‰ (-29.56 to -28.35, $N=6$) in the surface to -25.4‰ (-27.07 to -24.48, $N=5$) at 3.8-4.0 m of depth, i.e. values characteristic of C_3 plants in all layers (Fig. 5.2).

^{14}C ages

The ^{14}C age results for soil organic matter are available for present savanna sites in Roraima and in part for SE Humaitá and Carolina. The Roraima core shows transition from forest to savanna vegetation between 4,370 and 2,610 years BP while SE Humaitá shows a similar change between 2,380 and 780 years BP, and Carolina between 2,270 and 100 years BP (Fig. 5.2).

The results from the forest sites close to the isolated forest areas show values indicative of continuous forest cover going back to 6,100 BP in Alter do Chão, 4,900 BP in SE Humaitá and 2,900 BP in Roraima. The core from the forest site at Carolina indicates the presence of forest there 2,250 years BP (Fig. 5.2).

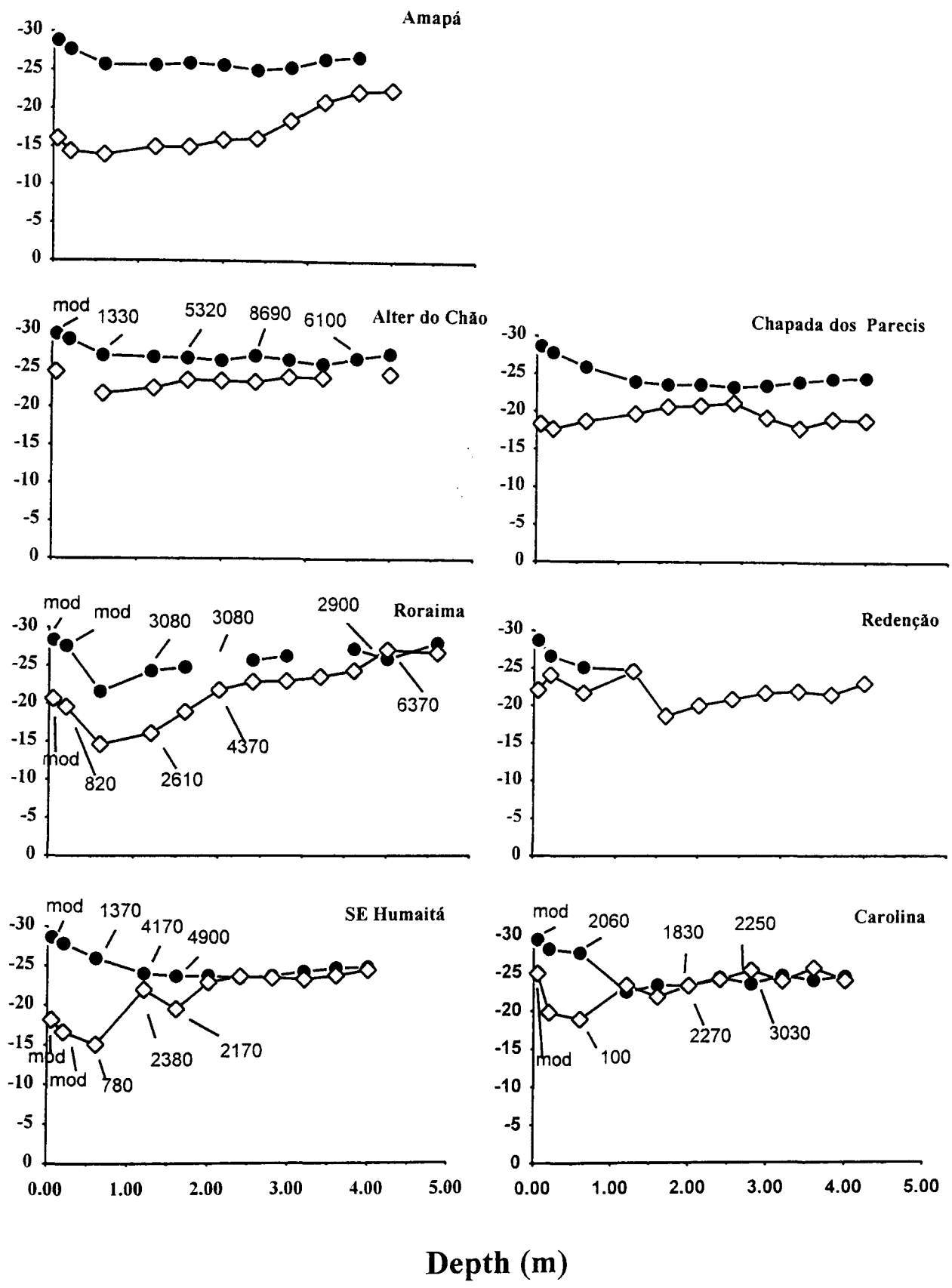


Fig. 5.2. $\delta^{13}\text{C}$ values of soil organic matter from savanna ($-\diamond-$) and forest ($-●-$) cores and the respective ^{14}C ages.

DISCUSSION

The $\delta^{13}\text{C}$ values for Amazonian plants and plant material published in previous studies are summarized in Table 5.1.

The $\delta^{13}\text{C}$ values of superficial soils in all the savannas studied showed lower values than those recorded for C_4 plants but higher than those for C_3 plants (Table 5.1). They were similar to soil organic matter values found in central and southern Brazil under savanna (Desjardin *et al.* 1991) and to a savanna in the Pantanal (Victoria *et al.* 1995). Bird *et al.* (1992), studying particulate organic matter from Amazonian rivers draining woody savannas (cerrado), found higher values than mine, but similar to those found by Martin *et al.* (1990) for savannas protected from fire for 25 years in Lamto, Ivory Coast. It is possible (depending on the density of trees and shrubs) that material derived from the decomposition of wood litter reduces the grass ^{13}C values at the soil surface by dilution. Mariotti & Peterschmitt (1994) recorded the value of -26.8‰ for litter of savanna trees in India, in contrast to their values for grasses of -11.4‰, reinforcing the above conclusions.

Superficial soil organic matter from all forest sites (Appendix 5.2) showed values characteristic of C_3 Amazonian plants (Table 5.1), and in deeper layers this value was increased by 4‰, Desjardin *et al.* (1991), studying five profiles distributed in central and southwestern Amazonia, found the same pattern of curves but increasing only by 2‰. However, another profile from southern Amazonia (NA3, Desjardin *et al.*

TABLE 1. $\delta^{13}\text{C}$ values for Amazonian plants and plant material. SD= standard deviation. n= number of species.

Plant	$\delta^{13}\text{C}$ (‰)	SD or Range	Locality	References
Tree wood (n=16)	-27.6	1.0	Terra firme (unflooded) and inundated forest (várzea and igapó) in the central Amazon	Hedges <i>et al.</i> 1986
Tree leaves (n=15)	-30.1	0.9		
Grasses (n=6)	-12.4	1.0		
Phytoplankton	-33.3		Along Amazonas, Solimões and Japura rivers	Araujo-Lima <i>et al.</i> 1986
Tree leaves (n=26)	-30.0			
Tree seeds	-28.3			
Tree wood	-27.6			
C ₃ macrophytes	-27.6			
Periphyton	-26.8			
C ₄ macrophytes	-12.9	(-18 to -11.9)		
Trees	-31.4	(-24 to -34)	Forest near Manaus	Ducatti <i>et al.</i> 1991
Grasses (n=24)	-13.4	1.2	Amazonian floodplain (várzea)	Victoria <i>et al.</i> 1992
Grass <i>Elionurus muticus</i>	-12.4		Grassy savanna at Pantanal	Victoria <i>et al.</i> 1995
Trees <i>Andira paniculata</i>	-29.1		Transition savanna at Pantanal	
<i>Byrsonima coccolobifolia</i>	-29.7			
<i>Caryocar brasiliense</i>	-28.6			
<i>Cordia glabrata</i>	-27.9			
<i>Curatella americana</i>	-29.4			
<i>Fagara hassleriana</i>	-28.8			
<i>Luehea paniculata</i>	-29.2			
<i>Sapium haematospermum</i>	-29.7			
<i>Simarouba versicolor</i>	-28.8			
<i>Tabebuia caraiba</i>	-26.5			
<i>Alibertia sessilis</i>	-31.1			
<i>Astronium fraxinifolium</i>	-30.1		Arboreal savanna at Pantanal	
<i>Attalea phalerata</i>	-30.1			
<i>Copaifera martii</i>	-31.1			
<i>Diospyros hispida</i>	-29.2			
<i>Magonia pubescens</i>	-29.9			
<i>Ocotea suaveolens</i>	-29.8			
<i>Pouteria ramiflora</i>	-31.7			
<i>Protium heptaphyllum</i>	-32.7			
<i>Rhamnidium elaeocarpum</i>	-30.4			
<i>Sapium haematospermum</i>	-30.6			
<i>Smilax</i> sp.	-30.6			
<i>Sterculia striata</i>	-28.9			
<i>Tabebuia roseo-alba</i>	-29.4			
<i>Trichilia elegans</i>	-30.2			
<i>Vitex cymosa</i>	-33.8			
Grass <i>Paspalum carinatum</i>	-13.7		Amazonian savanna at Alter do Chão	This study
<i>Trachypogon plumosus</i>	-13.3			
Shrubs <i>Casearia javitensis</i>	-30.2			
/Herbs <i>Chamaecrista ramosa</i>	-30.6			
<i>Chomelia parviflora</i>	-32.1			
<i>Declieuxia fruticosa</i>	-31.2			
<i>Eugenia biflora</i>	-31.8			
<i>Erythroxylum suberosum</i>	-29.5			
<i>Galactia jussiana</i>	-28.8			
<i>Hirtella racemosa</i>	-32.2			
<i>Miconia albicans</i>	-30.1			
<i>Miconia fallax</i>	-31.0			
<i>Myrcia sylvatica</i>	-30.1			
<i>Neea ovalifolia</i>	-31.5			
<i>Psychotria barbiflora</i>	-31.4			
Trees <i>Bowdichia virgilioides</i>	-29.2			
<i>Byrsonima crassifolia</i>	-28.5			
<i>Byrsonima coccolobifolia</i>	-27.9			
<i>Myrcia</i> cf. <i>obtusata</i>	-31.4			
<i>Lafoensia pacari</i>	-28.6			
<i>Pouteria ramiflora</i>	-31.8			
<i>Qualea grandiflora</i>	-28.7			
<i>Salvertia convallariodora</i>	-29.2			
<i>Sclerolobium paniculatum</i>	-31.3			
<i>Tocoyena formosa</i>	-28.9			
<i>Xylopia aromatica</i>	-30.9			

1991) showed a different pattern, with values below 1 m as low as -20‰, suggesting a change of vegetation.

The curves of $\delta^{13}\text{C}$ for savannas show an initial increase with depth at first (with the exception of Carolina) and the same trend was observed for forest soils. Similar patterns were found for Central Brazilian savannas (Volkoff & Cerri 1987, Desjardin *et al.* 1991, Victoria *et al.* 1995), African savannas, Congo and Ivory Coast (Schwartz *et al.* 1992, Martin *et al.* 1990) and also for Central America forests, Puerto Rico and Costa Rica (Von Fischer & Tieszen 1995, Veldkamp 1994), German and New Zealand forests (Schleser & Jayasekera 1985, Goh *et al.* 1976). Several explanations have been put forward to account for the enrichment ($\delta^{13}\text{C}$ becoming more positive) between litter and soil layers: (a) recent variation in the ^{13}C content of atmospheric CO_2 (Friedli *et al.* 1986 and Marino & McElroy 1991); (b) illuviation of ^{13}C -enriched dissolved organic matter into lower soil horizons (Nadelhoffer & Fry 1988); or (c) a natural phenomenon reflecting that -25‰ is the $\delta^{13}\text{C}$ value typical for the passive soil organic carbon fraction (Veldkamp 1994).

Despite the limitations on the conclusions due the lack of some carbon dating results, some comments may be made. All the isolated savanna sites studied, i.e. Amapá, Roraima and SE Humaitá, had $\delta^{13}\text{C}$ values which converge at depth with those of the surrounding forest, indicating that forest vegetation covered these sites in the past. The isolated savanna of SE Humaitá seems to be comparatively recent, showing the change to the ^{13}C values of C_3 plants at about 2,380 BP, suggesting that its origin was at about that date (which partially matches with the Holocene dry period around

2,100 BP, suggested by Absy *et al.* 1993). Nevertheless palynological studies from a lake in Carajás, Pará (Absy *et al.* 1991) showed a vegetation dominated by grasses between 5,000 and 7,000 BP. It seems that these isolated savannas were involved in the expansion and contraction of the forest as found for several other regions such Acre (Kromberg & Benchimol 1993), Carajás (Absy *et al.* 1991, Turcq *et al.* 1993), Rondônia (Van der Hammen 1972), Boa Vista, Roraima (Absy *et al.* 1993). However, these isolated savannas apparently were not open vegetation during the strongly arid climate around 8,000 BP (Servant *et al.* 1989). At this period the areas might have been forest or perhaps seasonal woodlands as was found in south Brazil (Ledru 1993). Victoria *et al.* (1995) also conclude that the Pantanal, an area now covered in grassy savanna, was occupied by arboreal vegetation 5,000 - 11,000 years ago.

The non-isolated savanna sites showed two kinds of $\delta^{13}\text{C}$ curves. The southeastern one, Carolina, with $\delta^{13}\text{C}$ values convergent at depth with the nearest forest indicates probable expansion of the central Brazilian savannas into the forest. The most southwestern site studied, Chapada dos Parecis, maintained values characteristic of open vegetation up to 4.0 m. A 1.5 m deep profile (MMT4) made by Desjardin *et al.* (1991) shows the same $\delta^{13}\text{C}$ values for a savanna 400 km east from Chapada dos Parecis. This site of the present study was probably part of an older arid vegetation that dominated large areas of the Amazon (Ab'saber 1977, Van der Hammen 1972).

Chapter 6.

General conclusions

The Neotropical savannas as defined by Sarmiento (1984) have their largest present area of distribution in Central Brazil, and the second largest to the northwest of the Amazon in the llanos of Orinoco, with smaller areas spread over the Amazon region as disjunct patches in the rain forest. However, there have been great changes in area during the Quaternary and the dynamics of expansion and contraction of savanna versus forest has been considered a result of the climatic fluctuations during the period (Flenley 1979, Prance 1982, Sarmiento & Monasterio 1985). The range of the Neotropical savannas can be classified along two main axes of variation: structural and ecological (Sarmiento 1983, Sarmiento & Monasterio 1985). The second of these has been considered in studies of the central Brazilian savannas (cerrados) and a large scale patterns have been discovered. Ratter & Dargie (1992) showed the existence of a remarkable floristic heterogeneity in the cerrados and that there are no species that occur everywhere. They correlated trends in distribution pattern with latitude, longitude and, most strongly, with type of soil. The studies of Castro (1994) and Ratter *et al.* (1996), consisting of large scale analyses of many sites throughout the cerrado region, demonstrated centres of floristic diversity and showed strong biogeographical patterns.

The present study is restricted to seasonal savannas, and provides insight into the variability of soils and vegetation of seven areas: four disjunct Amazonian savannas and

three non-isolated peripheral localities. Isotope techniques were also used as a tool to seek evidence of the past history of the areas. The most prominent findings and conclusions from this study are described below:

- (a) Disjunct Amazonian savannas have been assumed to be on poor sandy soils (Solbrig 1993) and those of the central Brazilian savannas are rather similar, occurring most commonly on well-drained acid latosols and sandy soils, although they are also found on a range of other soils, richer in calcium and magnesium (Haridasan 1992). This investigation confirmed the above, as all sites studied had fairly acid soils with moderate concentrations of aluminium. Two of the three non-isolated sites (Redenção and Chapada dos Parecis) were the richest in nutrients but the third (Carolina) was on a poor sandy soil. However, soil properties varied significantly along most transects under the same type of vegetation, showing the occurrence of relatively small-scale mosaics in savanna soils.
- (b) The floristic composition of disjunct Amazonian savannas varies from site to site and even varies significantly along transects at the same site. The disjunct sites were more depauperate in number of species compared to those studied in the periphery of the core area. *Byrsonima crassifolia* was the only species present in all seven sites, but even then was not present in all transects. A floristic influence from central Brazil is found at Alter do Chão and SE Humaitá, while Amapá and Roraima seem to have a northern floristic influence. SE Humaitá had the highest number of tree species that were not recorded from the other sites studied, several of them with a western Amazonian distribution, indicating more than one source of floristic influence this site. The classification analyses based on both species similarity and on density clearly separated the flora from disjunct and peripheral sites into distinct groups, suggesting the former may not have a central Brazilian

origin - Prance (1992) reached a similar conclusion from systematic studies in the family Chrysobalanaceae.

(c) The disjunct islands of savanna in Amazonia have been considered as possible outliers of a formerly continuous savanna extending out from the central Brazilian 'core area' under a more arid climate in the Pleistocene (Brown & Ab'saber 1979, Cole 1986, Bigarella & Ferreira 1985). This idea was contradicted by others (e.g. Irion 1982), who, from studies of lake sediments, concluded that such a continuous central Amazonian savanna never existed. The isotope studies of the present research provided $\delta^{13}\text{C}$ values indicating a vegetation change from C_4 to C_3 plants for most of the present island savanna areas at sometime from 2,000 to 6,000 BP, showing that forest cover existed during a part of the Holocene. These results confirm the findings from a recent study analyzing organic matter from 21 forest soils in Brazil (Martinelli *et al.* 1996 in press). This work indicates that, with the exception of Terra Nova, the other six sites in the Amazon area had forest cover, although dates were provided only for Altamira (4,390 BP) and Paragominas (22,470 BP), and not for Capitão Poço, Manaus, Oriente Novo and S. Domingos,

In support of the above conclusion, recent human ecology studies made in caves inside a forest patch at Monte Alegre, near Santarém (PA) (Roosevelt 1993) found that humans lived there between 11,500-10,000 and 8,000-6,000 B.P. using resources of a semi-deciduous tropical forest similar to the one found outside the cave today, suggesting a persistent forest in lowland Amazonia at those dates. Interdisciplinary studies should be used as a major strategy to give a more accurate understanding of the dynamics of late Pleistocene - Holocene landscape history of the Amazon basin.

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Appendix 3.1. Data for all surface soil samples.

SITES	pH _{H2O}	OM (%)	P μg g ⁻¹	K	Ca	Mg	Al	Clay	Coarse sand	Fine sand	Silt									
												Meq.100g ⁻¹			Meq.100g ⁻¹			Meq.100g ⁻¹		
												Meq.100g ⁻¹			Meq.100g ⁻¹			Meq.100g ⁻¹		
Amapá	T1	4.9	0.65	2.8	0	0.06	0.02	0.32	12	7	79	2								
		4.9	0.70	2.9	0	0.10	0.05	0.32	14	13	71	2								
		5.0	0.55	2.8	0	0.13	0.07	0.34	16	6	78	0								
		4.9	0.80	2.6	5	0.08	0.04	0.52	11	9	80	0								
		5.0	0.65	2.8	1	0.14	0.08	0.36	15	7	78	0								
	T2	4.9	0.80	2.9	1	0.10	0.04	0.40	17	41	42	0								
		4.9	1.00	3.0	2	0.28	0.15	0.36	17	35	48	0								
		5.0	0.95	2.9	2	0.07	0.03	0.43	17	39	44	0								
		4.0	1.16	3.2	5	0.10	0.03	0.58	22	35	42	1								
		4.9	1.11	2.7	1	0.10	0.05	0.48	22	36	41	1								
		5.2	0.92	3.2	24	0.06	0.07	0.45	21	36	42	1								
	T3	5.1	1.50	3.2	12	0.07	0.12	0.95	47	22	28	3								
		5.0	1.26	2.8	5	0.03	0.05	1.09	44	25	27	4								
		6	1.36	2	3	0.08	0.17	0.93	41	31	23	5								
	Alter do Chão	T5	5.0	1.76	9.4	11	0.08	0.03	0.36	9	47	44	0							
		5.1	0.08	4.4	0	0.50	0.02	0.41	3	80	17	0								
		5.1	0.95	4.4	0	0.07	0.03	0.67	4	81	15	0								
		5.2	0.50	5.4	0	0.08	0.04	0.47	2	86	12	0								
		5.2	0.95	6.8	3	0.09	0.03	0.78	4	41	55	0								
T4		4.8	1.56	11.0	4	0.20	0.08	1.21	4	77	19	0								
		5.0	1.16	6.1	0	0.07	0.03	0.86	7	59	34	0								
		5.0	0.75	4.9	0	0.06	0.03	0.51	4	67	29	0								
		5.1	0.85	4.2	0	0.08	0.02	0.60	5	66	29	0								
		5.2	0.45	4.6	0	0.08	0.02	0.42	4	77	19	0								
T6		4.8	2.06	15.3	7	0.10	0.05	1.26	8	67	25	0								
		4.9	0.85	8.6	2	0.08	0.02	0.63	5	77	18	1								
		4.9	1.36	7.7	5	0.07	0.03	0.73	4	41	55	0								
		4.8	2.01	7.3	1	0.06	0.02	1.49	9	47	44	0								
		4.8	1.51	4.1	3	0.06	0.04	1.47	8	67	25	0								
T7		4.3	0.67	2.0	0	0.09	0.02	0.63	5	60	35	0								
		4.4	1.54	2.8	1	0.07	0.03	0.98	5	43	52	0								
		4.5	0.87	3.4	2	0.10	0.05	0.80	7	40	53	0								
		4.5	1.18	3.6	4	0.12	0.05	0.91	5	43	52	0								
		4.5	0.87	3.5	4	0.12	0.05	0.77	5	41	54	0								
Roraima	T8	4.8	0.51	2.1	12	0.41	0.24	0.15	23	32	44	1								
		4.7	0.46	1.6	27	0.41	0.42	0.12	23	29	47	1								
		4.7	0.67	1.0	6	0.44	1.23	0.10	35	16	47	2								
		4.6	0.67	2.0	12	0.18	0.26	0.51	31	19	48	2								
		5.1	2.20	2.2	34	4.11	0.53	0.13	21	16	48	15								
	T9	4.7	0.87	0.8	21	1.06	0.15	0.02	48	16	30	6								
		4.9	0.87	1.5	16	0.81	1.80	0.10	23	41	34	2								
		4.6	0.31	0.8	4	0.35	0.77	0.08	41	20	35	4								
		4.8	0.51	1.0	8	4.55	0.73	0.20	23	41	35	1								
		4.7		1.0	6			0.33	26	36	37	1								

Appendix 3.1.continued.

SITES	pH _{H2O}	OM (%)	P μg g ⁻¹	K	Ca	Mg Meq.100g ⁻¹	Al	Clay	Coarse sand	Fine sand	Silt						
												μg g ⁻¹		Meq.100g ⁻¹		(%)	
T10	5.4	3.38	2.8	92	5.11	3.88	0.01	18	31	33	18						
	5.3	0.87	1.6	52	1.61	0.33	0.03	24	31	33	12						
	5.2	2.25	2.2	79	1.72	0.14	0.03	23	17	33	27						
	4.9	1.79	1.6	67	1.64	1.50	0.11	35	16	31	18						
	5.1	1.84	2.3	45	1.18	0.77	0.04	37	22	30	11						
T11	4.6	0.36	2.2	4	0.17	0.09	0.32	9	64	27	0						
	4.6	0.31	1.7	0	0.08	0.04	0.33	7	74	19	0						
	4.3	0.36	2.0	3	0.10	0.07	0.28	7	65	28	0						
	4.4	0.36	2.1	10	0.10	0.06	0.36	9	64	27	0						
	4.7	0.36	1.8	1	0.08	0.05	0.35	10	58	32	0						
Humaitá	4.4	0.77	1.8	6	0.05	0.03	0.79	4	36	60	0						
T12	4.4	2.02	2.0	15	0.04	0.05	0.98	6	44	50	0						
	4.5	1.59	1.2	14	0.05	0.05	0.98	7	40	53	0						
	4.3	1.29	1.6	13	0.05	0.06	1.20	5	43	52	0						
	4.5	1.38	2.0	25	0.04	0.06	1.10	6	48	46	0						
	T13	4.6	0.46	0.9	12	0.13	0.04	0.64	10	24	65	1					
4.4		1.18	1.4	23	0.07	0.03	1.16	18	30	36	16						
4.4		1.18	1.0	16	0.05	0.09	1.36	13	35	49	3						
4.4		1.49	1.2	9	0.06	0.08	0.61	31	19	47	3						
4.3		1.54	1.2	17	0.06	0.05	0.95	22	30	45	3						
T15	4.5	1.02	1.2	19	0.07	0.08	1.02	34	16	45	5						
	4.4	1.02	1.0	12	0.05	0.05	0.91	13	38	46	3						
	4.4	0.31	1.3	26	0.06	0.12	0.97	8	37	54	1						
	4.5	1.28	1.2	23	0.05	0.09	1.62	25	34	38	3						
	4.6	1.49	1.0	18	0.07	0.06	1.09	23	35	40	2						
	4.8	1.38	1.3	28	0.05	0.06	1.01	20	10	55	15						
	4.6	1.13	0.6	11	0.06	0.08	0.88	24	40	34	2						
Chapada dos Parecis	5.2	1.36	5.5	4	0.03	0.01	0.64	25	42	32	1						
T16	5.1	1.17	1.3	26	0.05	0.03	0.76	20	54	25	1						
	4.9	1.51	0.5	73	0.03	0.04	0.80	26	49	24	1						
	5.0	1.46	0.3	66	0.04	0.04	0.73	24	49	26	1						
	5.1	1.41	0.3	33	0.04	0.03	0.64	26	37	36	1						
	T17	4.9	1.07	4.5	25	0.02	0.02	0.84	10	54	36	0					
4.8		0.83	7.6	44	0.02	0.02	0.92	7	50	43	0						
4.8		0.73	2.6	52	0.03	0.01	0.62	7	48	45	0						
4.9		1.07	1.4	50	0.04	0.02	1.00	9	49	42	0						
4.9		0.97	1.4	51	0.02	0.01	0.84	8	48	44	0						
T18	4.9	0.63	5.5	84	0.03	0.02	0.50	7	52	41	0						
	5.0	0.73	0.7	17	0.03	0.02	0.60	7	57	36	0						
	4.9	0.44	0.8	10	0.02	0.01	0.36	6	60	34	0						
	4.9	0.49	0.7	46	0.02	0.01	0.35	8	53	39	0						
	4.9	0.63	1.0	12	0.01	0.01	0.47	10	57	33	0						

Appendix 3.1.continued.

SITES	pH _{H2O}	OM (%)	P µg g ⁻¹	K µg g ⁻¹	Ca Meq.100g ⁻¹	Mg Meq.100g ⁻¹	Al Meq.100g ⁻¹	Clay (%)	Coarse sand (%)	Fine sand (%)	Silt (%)
Redenção T19	4.8	2.2	1.9	32	0.88	0.44	0.17	17	48	33	2
	4.8	1.9	1.6	21	0.17	0.06	0.48	19	49	30	2
	4.7	1.5	1.9	19	1.09	0.27	1.12	13	54	32	1
	4.8	2.7	1.3	63	0.20	0.07	1.15	21	40	37	2
	4.8	1.0	1.7	21	0.19	0.08	1.50	12	52	35	1
T21	4.8	2.2	3.6	37	0.14	0.06	0.78	27	30	38	5
	4.8	3.4	3.6	26	0.10	0.04	0.86	23	43	30	4
	4.8	1.7	4.0	26	0.15	0.05	0.82	25	37	34	4
	5.0	2.5	3.8	33	0.36	0.20	0.64	27	35	34	4
	4.8	1.5	4.0	24	0.07	0.03	0.74	26	49	21	4
	4.8	1.4	3.8	19	0.16	0.09	0.56	18	48	32	2
	4.9	2.5	4.6	19	0.30	0.09	0.54	11	46	42	1
T20	4.8	1.3	5.3	36	0.68	0.17	0.82	14	40	39	7
	4.8	1.3	5.0	48	0.63	0.18	0.78	14	48	31	7
	4.8	1.7	5.5	48	0.70	0.23	0.68	12	44	38	6
	4.8	1.4	5.4	37	0.40	0.30	0.73	11	53	31	5
	4.8	1.3	5.7	36	0.45	0.25	0.59	9	54	31	6
	5.0	1.5	3.5	43	0.20	0.10	0.55	23	47	27	3
T22	5.0	2.4	2.6	43	0.14	0.09	0.97	41	29	21	9
	5.1	2.2	2.7	39	0.23	0.17	0.85	37	23	33	7
	4.9	3.2	2.9	63	0.40	0.22	1.09	36	30	26	8
	5.2	3.5	3.0	62	0.80	0.35	0.70	39	29	22	10
	4.9	3.1	3.3	56	0.29	0.11	1.19	42	29	18	11
Carolina	5.2	0.5	1.8	1	0.07	0.02	0.37	3	50	47	0
	4.6	0.7	1.7	3	0.20	0.03	0.37	3	52	45	0
T23	4.4	1.1	1.7	5	0.32	0.06	0.65	3	56	41	0
	4.7	0.9	1.8	5	0.60	0.08	0.41	3	67	30	0
	5.0	0.9	1.6	4	0.18	0.04	0.57	3	50	47	0
T24	4.0	0.6	2.6	2	0.19	0.03	0.49	3	72	25	0
	5.1	0.5	1.9	3	0.15	0.04	0.38	3	63	34	0
	4.7	0.4	1.4	2	0.08	0.02	0.30	3	61	36	0
	4.4	0.7	1.8	2	0.07	0.02	0.57	3	75	22	0
T25	4.9	0.8	1.5	2	0.08	0.02	0.64	3	68	29	0
	4.8	1.1	1.4	1	0.06	0.03	0.72	4	54	42	0
	4.9	0.7	1.3	1	0.12	0.04	0.51	3	63	34	0
	4.8	0.6	1.6	3	0.12	0.05	0.60	3	76	21	0
	5.1	0.5	1.2	2	0.10	0.03	0.30	3	61	36	0
T26	4.6	0.6	1.5	6	0.07	0.03	0.54	7	50	43	0
	4.9	0.8	1.3	6	0.07	0.03	0.56	9	34	57	0
	5.0	0.6	1.1	3	0.10	0.03	0.39	6	56	38	0
	4.8	0.3	1.0	5	0.11	0.03	0.51	10	35	55	0
	4.7	1.2	1.7	12	0.19	0.09	0.59	11	27	62	0

Appendix 4.1. List of the 101 species recorded by PCQ at the 26 transects, with additional 43 (**in bold**) from wide patrolling around the transects.

SPECIES	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	T16	T17	T18	T19	T20	T21	T22	T23	T24	T25	T26
<i>Acosmium dasycarpum</i> (Vogel) Yakovlev	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Aegiphila lhotskyana</i> Cham.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Agonandra brasiliensis</i> Miers	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0
<i>Anacardium cf. giganteum</i> Hanc. ex. Engl.	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0
<i>Anacardium cf. humile</i> St.Hil.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Anacardium occidentale</i> L.	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1
<i>Andira cordata</i> Arroyo ex R. T. Pennington	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	1
<i>Andira surinamensis</i> (Bondt.) SPLITZ. ex Pulle	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Andira vermifuga</i> (Mart.) Benth	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	1	0
<i>Annona coriacea</i> Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1
<i>Annona crassiflora</i> Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0
<i>Annona paludosa</i> Aubl.	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Antonia ovata</i> Pohl	0	0	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0
<i>Aspidosperma macrocarpon</i> Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0
<i>Bonyunia antoniifolia</i> Progel	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bowdichia virgilioides</i> Kunth	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	0	1	1	1	1
<i>Brosimum gaudichaudii</i> Trécul	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>Buchenavia capitata</i> (Vahl) Eichler	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Buchenavia tomentosa</i> Eichler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Byrsonima aff. cydoniifolia</i> Adr. Juss.	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Byrsonima aff. intermedia</i> Adr. Juss.	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Byrsonima coccolobifolia</i> Kunth	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	1	1	0	0	0	0
<i>Byrsonima crassifolia</i> (L.) Kunth	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1	1	1	1
<i>Byrsonima</i> sp. 'folha fina'	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1
<i>Callisthene fasciculata</i> (Spreng.) Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
<i>Caraipa savannarum</i> Kubitzki	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Caryocar brasiliense</i> Cambess.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	0
<i>Caunochiton kappleri</i> (Sagot ex Engl.) Ducke	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Connarus peirotetii</i> (DC.) Planchon	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix 4.1. (cont.)

	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	T16	T17	T18	T19	T20	T21	T22	T23	T24	T25	T26
<i>Connarus suberosus</i> Planch.	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	1	1	1	1	1	1	1	1
<i>Copaifera martii</i> Hayne	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Couepia paraensis</i> (Mart. & Zucc.) Benth. subsp. <i>cerradoana</i> Prance	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Curatella americana</i> L.	1	1	1	0	0	0	1	1	1	1	1	1	0	1	1	0	0	0	1	1	1	1	0	0	0	1
<i>Cybianthus detergens</i> Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Cybistax antisiphylitica</i> Mart.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
<i>Dalbergia miscolobium</i> Benth.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1
<i>Davilla elliptica</i> A. St.-Hil.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0
<i>Didymopanax distractiflorum</i> Harms	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Didymopanax</i> sp. TMS 405	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Dimorphandra gardneriana</i> Tul.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Dimorphandra mollis</i> Benth.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1
<i>Diospyros hispida</i> DC.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	0	1
<i>Dipteryx alata</i> Vogel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Diptychandra aurantiaca</i> Tul. subsp. <i>aurantiaca</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Emmotum nitens</i> (Benth.) Miers	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	1	0	1	0	1	1	1
<i>Enterolobium gummiferum</i> (Mart.) J. Macbr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
<i>Eriotheca gracilipes</i> (Schum.) Robyns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1
<i>Erythroxylum suberosum</i> A. St.-Hil.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0
<i>Eschweilera nana</i> (Berg) Miers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Eugenia dysenterica</i> DC.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Eugenia piauhensis</i> Berg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
<i>Eugenia puniceifolia</i> (Kunth) DC.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Ferdinandusa ovalis</i> Pohl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	0	0	0
<i>Godmania esculifolia</i> (Humboldt, Bonpland & Kunth) Standley	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Guapira</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

Appendix 4.1. (cont.)

	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	T16	T17	T18	T19	T20	T21	T22	T23	T24	T25	T26
<i>Guatteria cf. pohliana</i> Schtdl.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Guatteria cf. mayapensis</i> Kunth	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hancornia speciosa</i> Gomez	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	0	1	0	1	1	1	1
<i>Heisteria acuminata</i> (Humboldt & Bonpland) Engler	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heisteria ovata</i> Benth.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Himatanthus articulatus</i> (Vahl) Woodson	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Himatanthus drasticus</i> (Mart.) Plumel	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Himatanthus obovatus</i> (Müll. Arg.) Woodson	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1
<i>Himatanthus aff. fallax</i> (Müll. Arg.) Plumel comb. nov.	0	0	0	0	0	0	0	1	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Hirtella ciliata</i> Mart. & Zucc.	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
<i>Hirtella glandulosa</i> Spreng.	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0
<i>Hymenaea stigonocarpa</i> Mart. & Zucc.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
<i>Jacaranda brasiliensis</i> Pers.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Kielmeyera coriacea</i> (Spreng.) Mart.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	0	1	1	1
<i>Kielmeyera lathrophyton</i> Saddi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Lafoensia pacari</i> A. St.-Hil.	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	1	1	0	1	1	1	0	1	0	0	1
<i>Laxoplumeria tesmannii</i> Markgraf	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Licania humilis</i> Cham. & Schlecht.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
<i>Licania longistila</i> (Hook. f.) Fritsch	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Luehea paniculata</i> Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Mabea fistulifera</i> Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Machaerium</i> sp. TMS 278	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Magonia pubescens</i> A. St.-Hil.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0
<i>Maprounea guianensis</i> Aubl.	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Matayba guianensis</i> Aubl.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Miconia ferruginata</i> DC.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Miconia rubiginosa</i> (Bonpl.) DC.	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Mouriri elliptica</i> Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
<i>Mouriri pusa</i> Gardner	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	0

Appendix 4.1. (cont.)

	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	T16	T17	T18	T19	T20	T21	T22	T23	T24	T25	T26	
<i>Myrcia canescens</i> Berg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Myrcia cuprea</i> Kiaersk.	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Myrcia guianensis</i> (Aubl.) DC.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Myrcia</i> cf. <i>obtusata</i> (Schaer) Berg	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Myrcia rostrata</i> DC.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Myrcia</i> cf. <i>splendens</i> (Sw.) DC.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Myrcia</i> sp. TMS 414	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
MYRTACEAE TMS166	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
<i>Occhthocosmus barrae</i> Hall. f.	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ouratea castaneaefolia</i> Engl.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Ouratea hexasperma</i> (St. Hil.) Benth.	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1
<i>Ouratea</i> aff. <i>spectabilis</i> (Mart.) Engler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
<i>Parkia platycephala</i> Benth.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
<i>Physocalymma scaberrimum</i> Pohl	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0
<i>Piptocarpha rotundifolia</i> (Less.) Baker	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
<i>Pisonia</i> cf. <i>psammophila</i> Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Plathymenia reticulata</i> Benth.	1	0	0	1	1	0	1	0	0	0	0	1	1	1	0	1	1	0	0	1	1	1	1	1	1	1	1
<i>Platonia insignis</i> Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	
<i>Pouteria ramiflora</i> (Mart.) Radlk.	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	1	1	1	1	1
<i>Pouteria torta</i> (Mart.) Radlk.	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Protium heptaphyllum</i> (Aubl.) E. K. Marchal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0
<i>Pseudobombax longiflorum</i> (Mart. & Zucc) Robyns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
<i>Psidium myrsinoides</i> Berg	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0
<i>Pterodon emarginatus</i> Benth.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1
<i>Qualea grandiflora</i> Mart.	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	1	1	0	1	1	1	1	1	1	0	0	1
<i>Qualea multiflora</i> Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0
<i>Qualea parviflora</i> Mart.	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
<i>Rauvolfia pentaphylla</i> Ducke	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Roupala montana</i> Aubl	1	1	0	0	1	1	1	0	1	1	0	1	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0
<i>Rourea induta</i> Planch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0

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Appendix 4.1. (cont.)

	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	T11	T12	T13	T14	T15	T16	T17	T18	T19	T20	T21	T22	T23	T24	T25	T26
<i>Rudgea erioloba</i> Benth.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
<i>Salacia crassifolia</i> (Mart.) Peyr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0
<i>Salvertia convallariodora</i> A. St.-Hil.	1	0	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1
<i>Sapium</i> sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sclerolobium aureum</i> (Tul.) Benth.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
<i>Sclerolobium paniculatum</i> Vogel	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Simarouba amara</i> Aubl.	0	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0
<i>Simarouba versicolor</i> A. St.-Hil.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
<i>Strychnos pseudoquina</i> A. St.-Hil.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Stryphnodendron coriaceum</i> Benth.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
<i>Stryphnodendron obovatum</i> Benth.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	1
<i>Stryphnodendron</i> sp.	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Styrax ferrugineus</i> Nees & Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0
<i>Swartzia</i> sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Syagrus comosa</i> (Mart.) Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0
<i>Symplocos guianensis</i> Gürke	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Tabebuia aurea</i> Benth. & Hook.	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1
<i>Tabebuia ochracea</i> (Cham.) Standl.	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	1	1	1	0	1	0	1	1	0	0	1
<i>Tapirira guianensis</i> Aubl.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Tocoyena formosa</i> (Cham. & Schlttdl.) Schum.	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1
<i>Trattinickia rhoifolia</i> Willd.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vatairea macrocarpa</i> (Benth.) Ducke	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0
<i>Vitex</i> cf. <i>schomburgkiana</i> Schau.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vochysia cinnamomea</i> Pohl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Vochysia grandis</i> Mart. var. <i>uaupensis</i> (Spruce) Warm.	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Vochysia</i> aff. <i>lehmannii</i> Hier.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Vochysia rufa</i> (Spreng.) Mart.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0
<i>Xyloptia aromatica</i> Lam.	0	0	0	0	1	0	1	1	0	0	0	1	1	1	1	0	1	0	1	1	1	0	1	0	0	0

Appendix 4.2. List of specimens collected during this study, TMS = T. M. Sanaiotti and R = J. A. Ratter. Herbarium symbols follow the international code. Site and (Transect) numbers follow Table 2.1.

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
AMARANTHACEAE				
<i>Gomphrena</i> sp.	R 6688	UB, E, K	7(23)	
ANACARDIACEAE				
<i>Anacardium</i> cf. <i>giganteum</i> Hanc. ex. Engl.	TMS185	INPA, E	4	150 km Transamazonica, 54 km to Bodocó
<i>Anacardium</i> cf. <i>humile</i> St. Hil.	TMS417	INPA, MPEG, E	5(16)	
<i>Anacardium</i> sp.	TMS314	INPA, E	4	150 km Transamazonica, 15 km to Bodocó
<i>Astronium</i> sp.	TMS219	INPA, E	3	10 km N Surumu River
ANNONACEAE				
<i>Annona coriacea</i> Mart.	R 6697	UB, E	7(23)	
<i>Annona crassiflora</i> Mart.	TMS445	INPA	5(18)	
<i>Annona jahnii</i> Saff.	TMS248	INPA, UB, E	3	18.5 km N of bridge Cauamé River
<i>Duguetia</i> sp.	R 6710	UB, E, K	7	2 km S Pedra Caída to Carolina
<i>Duguetia</i> cf. <i>lepidota</i> (Miq.) Pulle	R 6768, R6769	UB, E, K	7	Close to Rio Lajes, at the new club
<i>Guatteria</i> cf. <i>maypurensis</i> Kunth	TMS202	INPA, E	4(12)	
<i>Guatteria</i> cf. <i>pohlana</i> Schtdl.	TMS281	INPA, MPEG, E	4(14)	
APOCYNACEAE				
<i>Aspidosperma macrocarpon</i> Mart.	R 6708	UB, E, K	7	2 km S Pedra Caída to Carolina
	TMS439	INPA, E	5(18)	
<i>Aspidosperma</i> cf. <i>multiflorum</i> A. DC.	TMS225	INPA, UB, E	3	BR174, side road S Surumu River
<i>Caraipa savannarum</i> Kubitzki	TMS178,184	INPA, E	4	18 km S Humaitá
<i>Hancornia speciosa</i> Gomez	R 6720	UB, E, K	7(24)	
<i>Himatanthus fallax</i> (Müll. Arg.) Plumel comb. nov.	TMS316	INPA, E	4	150 km SE Humaitá, about 30 km to Bodocó
<i>Himatanthus</i> cf. <i>obovatus</i> (Müll. Arg.) Woods.	R 6723	UB, E, K	7(25)	
	TMS161	INPA, UB, E	6(19)	
	TMS164	INPA, UB, E	6(21)	
	TMS165	INPA	6(21)	
	TMS401	INPA	5(16)	
	TMS431	INPA, E	5(18)	
<i>Himatanthus semilunatus</i> Markgraf	TMS195	INPA, MPEG, E	4(12)	
<i>Laxoplumertia tessmannii</i> Markgraf	TMS284	INPA, UB, E	4	19 km L. of Bodocó to Igarapé Preto
<i>Rauvolfia pentaphylla</i> Ducke	TMS483	INPA, UB, MPEG, E	1	APA Curiaú, 21km N Macapá

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
ARALIACEAE				
<i>Didymopanax cf. distractiflorum</i> Harms	TMS307	INPA, E	4	150 km SE Humaitá, 80 km to Bodocó
? <i>Didymopanax utiarityensis</i> Hoehne	TMS469	INPA	5(17)	
<i>Didymopanax</i> sp.	TMS287c	E	4	22 km L of Bodocó to Igarapé Preto
<i>Didymopanax</i> sp.	TMS405	E	5(16)	
ASCLEPIADACEAE				
<i>Blepharodon bicuspidatum</i> Fourn.	TMS540	INPA	2	Peninsula in front of Alter do Chão
BIGNONIACEAE				
<i>Godmania aesculifolia</i> (Kunth) Standl.	TMS238	E	3(8)	
<i>Jacaranda brasiliana</i> Pers.	R 6683	UB, E, K	7	10 km N of Pedra Caida (MA)
	TMS261	INPA, E	3	40 km NE Boa Vista to Passarão
<i>Tabebuia ochacea</i> (Cham.) Standl.	R 6743	UB	7	Top of Serra da Madeira
	TMS204	INPA, E	4	150 km Trasmazonica, 90 km to Bodocó
<i>Tabebuia aurea</i> Benth. & Hook.	TMS205	INPA, E	4	150 km Trasmazonica, 90 km to Bodocó
	TMS441	INPA, E	5(18)	
	TMS447	INPA, E	5(16)	
	TMS468	E	5(17)	
BOMBACACEAE				
<i>Eriotheca gracilipes</i> (K.Schum.) A. Robyns	TMS413	INPA, E	5(16)	
BORAGINACEAE				
<i>Cordia trichotoma</i> (Vell.) Arraub. ex Steud.	R 6767	UB, E, K	7	Close to Rio Lajes, at the new club
BURSERACEAE				
<i>Trattinickia rhoifolia</i> Willd.	TMS252	INPA, MPEG, E	3	18 km East of bridge Branco River
	TMS267	INPA, E	3	45 km S Boa Vista to Mucajaí
CACTACEAE				
<i>Cereus hexagonus</i> (L.) Miller	TMS223	INPA, E	3	2 km N Parimé River
	TMS256	INPA, E	3	40 km NE Boa Vista to Passarão
CARYOCARACEAE				
<i>Caryocar brasiliense</i> Cambess.	TMS419	INPA, E	5(16)	
	TMS472	E	5	BR364 to Porto Velho, 8km crossing MT170

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
CELASTRACEAE				
? <i>Salacia crassifolia</i> (Mart.) Peyr	R 6751v	UB	7	Top of Serra da Madeira
CHRYSOBALANACEAE				
<i>Couepia paraensis</i> (Mart. & Zucc.) Benth. ssp. <i>cerradoana</i> Prance	R 6686	UB, E, K	7(23)	
<i>Hirtella ciliata</i> Mart. ex Zucc.	R 6776	UB, E, K	7	Fazenda Braganca
<i>Hirtella glandulosa</i> Spreng.	TMS200	INPA, E	4(12)	
<i>Licania humilis</i> Cham. & Schlecht.	TMS403	E	5(16)	
	TMS442a	E, K	5(18)	
COCHLOSPERMACEAE				
<i>Cochlospermum orinocense</i>	R 6791	UB, E, K	7	20 km N of Carolina
COMBRETACEAE				
<i>Buchenavia capitata</i> (Vahl) Eichl.	TMS312		4(12)	
<i>Buchenavia tomentosa</i> Eichl.	R 6761v	UB, E	7	Between Carolina and Estreito
	R 6763	UB, E, K	7	Close to Rio Lajes at Pousada Lajes
	TMS407	E	5(16)	
	TMS420	INPA, UB, E	5(17)	
	TMS427	INPA, UB, MPEG, E	5(17)	
<i>Combretum duarteianum</i> Camb.	R 6760	UB, E, K	7	Between Carolina and Estreito
<i>Combretum leprosum</i> Mart.	R 6770	UB, E, K	7	Close to Rio Lajes, at the new club
<i>Terminalia fagifolia</i> Mart. & Zucc.	R 6704v	UB, E	7	2 km S Pedra Caida to Carolina
COMPOSITAE				
<i>Eremanthus</i> cf. <i>rondoniensis</i> MacLeish & Schumacher	TMS470	INPA, E	5(17)	
<i>Piptocarpha rotundifolia</i> (Less.) Baker	TMS416	INPA, UB, E	5(16)	
CONNARACEAE				
? <i>Conarus favosus</i>	TMS265	INPA, UB, E	3	47 km NE Boa Vista to Passarão
<i>Conarus suberosus</i> Planchon	R 6699	UB, E	7(23)	
	TMS305	E	4(12)	
	TMS415	INPA, UB, E	5(16)	
<i>Rourea grosourdyana</i> Baill. var. <i>grosourdyana</i>	TMS247	INPA, E	3	18.5 km N of bridge Cauamé River

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
CYPERACEAE				
<i>Bulbostylis paradoxa</i> (Spreng.) Lindm.	TMS170	INPA, E	6(22)	
<i>Bulbostylis lanata</i> C.B. Clarke	TMS292	INPA, E	4(14)	
<i>Lagenocarpus</i> sp.	TMS456	INPA, E	5(16)	
DILLENIACEAE				
<i>Doliocarpus</i> aff. <i>ellipticus</i> Sprague & Williams	R 6707	UB, E, K	7	2 km S Pedra Caida to Carolina
<i>Davilla elliptica</i> St.Hil.	TMS406	INPA, MPEG, E	5(16)	
EBENACEAE				
<i>Diospyros hispida</i> A. DC.	R 6714	UB, E, K	7	2 km S Pedra Caida to Carolina
	TMS411	INPA, E	5(16)	
	TMS435	INPA, UB, E	5(18)	
<i>Diospyros sericea</i> DC.	R 6706	UB, E	7	
ERIOCAULACEAE				
<i>Paepalanthus</i> sp.	R 6755	UB, E, K	7	Top of Serra da Madeira
<i>Paepalanthus</i> sp.	R 6772	UB, E	7(23)	
<i>Paepalanthus</i> sp.	TMS295	INPA	4(14)	
ERYTHROXYLACEAE				
<i>Erythroxylum citrifolium</i> St. Hil.	TMS538	INPA, E	2	Peninsula in front of Alter do Chão
<i>Erythroxylum</i> cf. <i>deciduum</i> St. Hil.	TMS296	INPA, E	4	150 km SE Humaitá, 61.5 km to Bodocó
	TMS479	E	5	BR364 to Porto Velho, 8 km crossing MT 170
<i>Erythroxylum suberosum</i> St. Hil.	R 6748v	UB, E, K	7(26)	
<i>Erythroxylum</i> cf. <i>vernicosum</i> O. E. Schult.	TMS228	INPA, E	3	BR174, side road S Surumu River
EUPHORBIACEAE				
<i>Hancornia speciosa</i> Gomez	TMS194	INPA, UB, MPEG, E	4(12)	
<i>Jatropha elliptica</i> (Pohl) M Arg.	R 6693	UB, E, K	7(23)	
<i>Mabea</i> sp.	R 6735	UB, E, K	7(26)	
	TMS288	INPA, MPEG, E	4(14)	
<i>Manihot</i> sp.	R 6724		7(25)	
<i>Pera</i> cf. <i>bicolor</i> (Klotzsch) Müll. Arg.	TMS213	INPA, UB, E	3	10 km N Surumu River
<i>Sapum</i> sp.	TMS301	INPA, E	4(12)	

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
FLACOURTIACEAE				
<i>Casearia sylvestris</i> Swartz	R 6718	UB, E, K	7(24)	
	TMS208	INPA, UB, E	4	150 km Transamazonica, 90 km to Bodocó
<i>Casearia</i> cf. <i>unifolia</i> Vahl ex Vent.	TMS245	INPA, E	3	18.5 km N of bridge Cauamé River
<i>Ryania speciosa</i> Vahl	TMS539	INPA, E	2	Peninsula in front of Alter do Chão
GENTIANACEAE				
<i>Symphyllophyton caprifolioides</i> Gilg	R 6742	UB, E, K	7	Top of Serra da Madeira
<i>Schultesia angustifolia</i> Griseb.	TMS231	INPA, UB, E	3	11km S Surumu River
GUTTIFERAE				
<i>Kielmeyera coriacea</i> Mart.	TMS303	INPA, E	4(12)	
	TMS429	INPA, E	5(17)	
	TMS432	INPA, E	5(18)	
<i>Kielmeyera lathrophyton</i> Saddi	TMS163	INPA, UB, E	6(19)	
<i>Kielmeyera rubriflora</i> Cambess.	TMS430	INPA, UB, E	5(17)	
<i>Platonia insignis</i> Mart.	R 6685v	UB, E, K	7(23)	
	R 6696a	UB, E	7(23)	
	R 6747v	UB, E	7(26)	
	R 6745v	UB, E	7(26)	
<i>Vismia</i> sp.				
HIPPOCRATEACEAE				
<i>Salacia</i> sp.	TMS451	UB	5(16)	
HUMIRIACEAE				
<i>Sacoglottis matogrossensis</i> Malme	R 6700	UB, E, K	7	2 km S Pedra Caida to Carolina
ICACINACEAE				
<i>Emmotum nitens</i> (Benth.) Miers	R 6725		7(3)	
	TMS192	INPA, UB, MPEG, E	4(12)	
	TMS426	INPA, UB, MPEG, E	5(17)	
IXONANTHACEAE				
<i>Ochthocosmus barrae</i> Hall. f.	TMS275	INPA, E	4(14)	

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
LABIATAE				
<i>Hyptis rubicunda</i> Pohl ex Benth.	R 6737	UB, E, K	7	Top of Serra da Madeira
<i>Hyptis suaveolens</i> (L.) Poit.	R 6759	UB, E, K	7	Between Carolina and Estreito
LECYTHIDACEAE				
<i>Cariniana domestica</i> (Mart.) Miers	R 6787	UB, E, K	7	20 km N of Carolina, back roads
<i>Eschweilera nana</i> (Berg) Miers	TMS427a, 464 TMS464	INPA, UB, E INPA, UB, MPEG	5(17) 5(17)	
LEGUMINOSAE				
<i>Acosmium steyermarkii</i> Stirton	TMS224	INPA, UB, E	3	BR174, side road S Surumu river
<i>Acosmium</i> cf. <i>nitens</i> (Vog.) Yakovl.	TMS263	INPA, E	3	47 km NE Boa Vista to Passarão
<i>Anadenanthera peregrina</i> (L.) Speg. var. <i>peregrina</i>	TMS255	INPA, UB, E	3	40 km NE Boa Vista to Passarão
<i>Andira cordata</i> Arroyo ex R. T. Pennington & H. C. Lima	R 6716	UB, E, K	7(24)	
<i>Andira surinamensis</i> (Bondt.) Splitz. ex Pulle	TMS209	INPA, E		150 km Transamazonica, 90 km to Bodocó
	TMS222	INPA, E	3	13 km N Cauaruaua River
<i>Andira vermifuga</i> (Mart.) Benth	R 6729v	UB, E, K	7(25)	
	TMS449	E	5(16)	
	TMS460	INPA	5(17)	
<i>Andira</i> cf. <i>vermifuga</i> (Mart.) Benth	TMS287	INPA, E	4	22 km L of Bodocó to Igarapé Preto
	TMS461	E	5(17)	
<i>Bauhinia</i> aff. <i>nitida</i> Benth	TMS197	INPA	4(12)	
<i>Bauhinia holophylla</i> (Bongard) Steudel	TMS466	INPA	5(17)	
<i>Bauhinia dubia</i> G. Don	R 6727v	UB, E	7(25)	
	R 6783	UB, E, K	7	Fazenda Braganca
<i>Bauhinia unguolata</i> L. agg.	R 6757	UB, E, K	7	Between Carolina and Estreito
<i>Bowdichia virgilioides</i> Kunth	TMS182	INPA, E	4	150 km Transamazonica, 54 km to Bodocó
	TMS310	INPA, UB, MPEG, UEC, E	4	150 km Transamazonica, 80 km to Bodocó
	TMS465	E	5(17)	
<i>Camptosema coriaceum</i> Benth.	R 6717	UB, E, K	7(24)	
<i>Cassia moschata</i> Kunth	TMS260	INPA, UB, E	3	40 km NE Boa Vista to Passarão

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
<i>Copaifera martii</i> Hayne	R 6703	UB, E, K	7	2 km S PEdra Caida to Carolina
	R 6733	UB, E, K	7(25)	
	R 6726v	UB, E	7(25)	
	R 6775	UB, E, K	7	Fazenda Braganca
<i>Copaifera pubiflora</i> Benth.	TMS258	INPA, UB, E	3	40 km NE Boa Vista to Passarão
<i>Dimorphandra gardneriana</i> Tul.	R 6692	UB, E, K	7(23)	
<i>Dimorphandra</i> sp.	R 6687	UB, E	7(23)	
<i>Dimorphandra mollis</i> Benth.	TMS408	INPA, UB, MEG, E	5(16)	
<i>Dioclea</i> sp.	R 6721	UB, E	7(24)	
<i>Dioclea latifolia</i> Benth.	R 6750	UB, E, K	7	Top of Serra da Madeira
<i>Dipythandra aurantiaca</i> Tul. subsp. <i>aurantiaca</i>	TMS409	INPA, UB, MPEG, UEC, E, K	5(16)	
<i>Hymenaea stignocarpa</i> Mart. var. <i>pubescens</i> Benth.	R 6779	UB, E, K	7	Fazenda Braganca
<i>Indigofera lespedezioides</i> Kunth	TMS233	INPA, E	3	11 km S Surumu River
<i>Inga ingoides</i> (Rich.) Willd.	R 6789	UB, E, K	7	20 km N of Carolina, back roads
<i>Machaerium</i> sp.	TMS237	INPA, E	3(8)	
<i>Macroptilium gracile</i> (Poepp. ex Benth.) Urban	TMS229	INPA, E	3	11 km S Surumu River
<i>Martiodendron mediterraneum</i> (Mart. ex Benth.) Koeppen	R 6765, R6766	UB, E, K	7	Close to Rio Lajes, at the new club
<i>Mimosa calliandroides</i> Hoehne	TMS220	INPA, UB	3	10 km N Surumu River
<i>Parkia platycephala</i> Benth.	R 6682	UB, E, K	7	15 km N of Colina (GO)
<i>Parkia ulei</i> (Harms) Kuhlmann var. <i>ulei</i>	TMS286	INPA, UB, MPEG, E	4	24 km L of Bodocó to Igarapé Preto
<i>Peltogyne paniculata</i> Benth. subsp. <i>pubescens</i> (Benth.) M. F. da Silva	TMS210	INPA, E	3	10 km N Surumu River
<i>Plathymenia reticulata</i> Benth.	TMS308	INPA, UB, E	4	150 km SE Humaitá, 80 km to Bodocó
	R 6732	UB, E, K	7(26)	
	TMS188	INPA, E	4(12)	
	TMS203	INPA, E	4	150 km Trasmazonica, 90 km to Bodocó
	TMS423	INPA	5(17)	
	TMS448	INPA	5(16)	
<i>Pterodon emarginatus</i> Vog.	R 6773	UB, E, K	7	Close to Transect I
	TMS478	INPA, UB, E	5	BR364 to Porto Velho, 8 km crossing M1170

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
<i>Stryphnodendron coriaceum</i> Benth.	R 6713v	UB, E, K	7(23)	
<i>Stryphnodendron obovatum</i> Benth.	R 6732	UB, E, K	7(26)	
<i>Stryphnodendron</i> sp.	TMS187	INPA, UB, MPEG, E	4(12)	
<i>Stryphnodendron</i> sp.	TMS450	E	5(16)	
<i>Swartzia flaemingii</i> Raddi	R 6786	UB, E, K	7	15 km N of CArolina, back roads
<i>Swartzia</i> sp.	TMS217	INPA, E	3	10 km N Surumu River
<i>Swartzia</i> sp.	TMS243	INPA, K	3	18.5 km N of bridge Caumé River
<i>Swartzia</i> sp.	TMS257	INPA, UB, E	3	40 km NE Boa Vista to Passarão
<i>Vigna fimula</i> (Benth.) Marechal, Mascherpa Sterinier	R 6741	UB, E, K	7	Top of Serra da Madeira
LOGANIACEAE				
<i>Antonia ovata</i> Pohl	R 6709	UB, E, K	7	2 km S Pedra Caida to Carolina
	TMS246	INPA, UB, E	3	18.5km N of bridge Cauamé River
<i>Bonyunia antoniifolia</i> Progel	TMS207	INPA, E	4	150km Transamazonica, 90km to Bodocó
	TMS480,481	INPA, E	4	150 km SE Humaitá, 30 km to Bodocó
	TMS482	INPA, E	4(14)	
<i>Strychnos pseudoquina</i> A. St.-Hil.	R 6753v	UB, E	7	Top of Serra da Madeira
	TMS437	INPA, UB, E	5(18)	
LYTHRACEAE				
<i>Lafoensia vandelliana</i> Cham. & Schldl.	R 6736	UB, E, K	7(26)	
<i>Lafoensia pacari</i> A. St.-Hil.	TMS196	INPA, UB, E	4(12)	
	TMS453	E	5(16)	
<i>Physocalymma scaberrimum</i> Pohl	TMS206	INPA, E	4	150 km Transamazonica, 90 km to Bodocó
MALPIGHIACEAE				
<i>Banisteriopsis</i> sp.	TMS 227	INPA, UB, E		BR174, side road S Surumu River
<i>Byrsonima</i> sp.	R 6702	UB, E, K	7	2 km S Pedra Caida to Carolina
<i>Byrsonima</i> sp.	R 6740	UB, E, K	7	Top of Serra da Madeira

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
<i>Byrsonima cydoniifolia</i> DC.	TMS236	INPA, E	3(8)	
	TMS254	INPA, UB, E	3	30 km NE Boa Vista to Passarão
	TMS302	E	4(12)	
	TMS319,320	INPA, E	4	150 km SE Humaitá, 80 km to Bodocó
<i>Byrsonima coccolobifolia</i> Kunth	TMS421	INPA, E	5(17)	
	TMS458	INPA, E	5(17)	
<i>Byrsonima</i> cf. <i>crassifolia</i> (L.) Kunth.	TMS199	INPA, MPEG, E	4(12)	
	TMS273	INPA, MPEG, E	4	5km S Bodocó
	TMS304	INPA, UB, MPEG, E	4(12)	
	TMS425,428	INPA, UB, E	5(17)	
<i>Byrsonima</i> cf. <i>eriopoda</i> DC.	TMS176	INPA, E	4	18 km S Humaitá
	TMS318	INPA, UB, E	4	150 km SE Humaitá, about 50 km to Bodocó
<i>Byrsonima</i> aff. <i>intermedia</i> Adr. Juss.	R 6778v	UB, E, K		Fazenda Braganca
	TMS234	INPA, UB, E	3(8)	
	TMS262	E	3	47 km NE Boa Vista to Passarão
? <i>Byrsonima sericea</i> DC.	TMS177	INPA, UB, MPEG, E	4	18 km S Humaitá
<i>Byrsonima verbascifolia</i> (L.) Rich.	TMS235	INPA, UB, E	3(8)	
	TMS438	INPA, UB, E	5(18)	
	TMS452	INPA, E	5(16)	
<i>Byrsonima spicata</i> (Cav.) DC.	TMS268	E	3	45 km S Boa Vista to Mucajai
<i>Heteropterys byrsonimifolia</i> Adr. Juss.	R 6752v	UB, E	7	Top of Serra da Madeira
<i>Tetrapterys discolor</i> (G. F. W. Meyer) DC.	R 6771	UB, E, K	7	Close to Rio Lajes, at the new club
MALVACEAE				
<i>Hibiscus fuscicollatus</i> Desr.	TMS287a	INPA	4	22 km L of Bodocó to Igarapé Preto
MARCGRAVIACEAE				
<i>Norantea</i> cf. <i>guianensis</i> Aubl.	TMS201	INPA, UB, MPEG, E	4(12)	
MELASTOMATACEAE				
<i>Bellucia acutata</i> Pilger	TMS174	INPA, UB, GOE, E	4	18 km South Humaitá
<i>Macarrea thyrsoiflora</i> DC. sensu Renner	TMS280	INPA, E	4(14)	

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
<i>Miconia ciliata</i> (Rich.) DC.	TMS272	INPA, E	4	5km S Bodocó
<i>Miconia ferruginata</i> DC.	R 6754v	UB, E	7	Top of Serra da Madeira
	TMS467	INPA, E	5(17)	
<i>Miconia rubiginosa</i> (Bonpl.) DC.	TMS266	INPA, UB, E	3	45 km S Boa Vista to Mucajaí
	TMS 289	INPA, UB, E	4(14)	
	TMS424	INPA, E	5(17)	
	TMS462	INPA, E	5(17)	
<i>Mouriri elliptica</i> Mart.	R 6698	UB, E, K	7(23)	
	TMS412	INPA, E	5(16)	
<i>Mouriri pusa</i> Gardner	R 6694	UB, E, K	7(23)	
<i>Tibouchina</i> sp.	TMS274	INPA, MPEG, E	4	5km S Bodocó
<i>Tococa nitens</i> (Benth.) Triana	TMS270	INPA, MPEG, E	4	5km S Bodocó
	R 6715		7(24)	
MORACEAE				
<i>Brosimum gaudichaudii</i> Trec.	TMS311	INPA, E	4	150 km Se Humaitá, 80 km to Bodocó
MYRISTICACEAE				
<i>Virola subsessilis</i> (Benth.) Warb.	TMS443	INPA, E	5(18)	
MYRTACEAE				
<i>Eugenia piauhiensis</i> Berg	R 6730v	UB, E	7(25)	
<i>Eugenia puniceifolia</i> Kunth DC.	TMS436	UB	5(18)	
<i>Myrcia</i> cf. <i>canescens</i> Berg	R 6712	UB, E	7	2 km S Pedra Caida to Carolina
	R 6728v	UB, E	7(25)	
<i>Myrcia</i> cf. <i>splendens</i> (SW.) DC.	TMS169	INPA, E	6(22)	
<i>Myrcia guianensis</i> (Aubl.) DC.	TMS160	INPA, UB, E	7(24)	
<i>Myrcia</i> cf. <i>obtusata</i> (Schauer) Berg	TMS516,517	INPA, UB, E	2	Peninsula in front of Alter do Chão
<i>Myrcia</i> cf. <i>sylvatica</i> (Mey.) DC.	TMS171	INPA, UB, E, GOE	4	14 km SW Humaitá
<i>Myrcia</i> sp.	TMS166	INPA, UB, E	6(22)	
	TMS414	UB, E	5(16)	
	TMS471	E	5(17)	
	TMS474	E	5	BR364 to Porto Velho, 8 km crossing M1170

R 6781v UB, E, K 7 Fazenda Braganca

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
<i>Psidium multiflorum</i> Camb.	TMS444	INPA,UB,E	5(18)	
<i>Psidium myrsinoides</i> Berg	R 6777	UB, E, K	7	Fazenda Braganca
	TMS239	UB,E	3(98)	
NYCTAGINACEAE				
<i>Pisonia cf. psammophila</i> Mart.	TMS442	E	5(18)	
OCTINACEAE				
<i>Ouratea aff. fieldingiana</i> (Gardner) Engler	TMS226	INPA, E	3	BR174, side road S Surumu River
<i>Ouratea aff. hexasperma</i> (St. Hil.) Benth.	TMS298	INPA, E	4	150 km SE Humaitá, 63.5km to Bodocó
<i>Ouratea aff. inundata</i> Spruce	TMS282	INPA, MPEG, E	4(14)	
<i>Ouratea spectabilis</i> (Mart.) Engler	TMS418	INPA, E	5(16)	
<i>Ouratea aff. superba</i> Engl.	TMS297	INPA, UB, E	4	150 km SE Humaitá, 61.5km to Bodocó
<i>Ouratea</i> sp.	TMS459	INPA	5(17)	
OLACACEAE				
<i>Cathedra acuminata</i> (Benth.) Miers	TMS277	INPA, E	4(14)	
<i>Cathedra paraensis</i> H. Sleumer	R 6782, R 6784	UB, E, K		Fazenda Braganca
<i>Chaunochiton kappleri</i> (Sagot ex Engl.) Ducke.	R 6695, R 6696	UB, E, K	7(23)	
<i>Heisteria cf. acuminata</i> (Humboldt & Bonpland) Engler	TMS193	INPA, E	4(12)	
<i>Heisteria ovata</i> Benth.	TMS299	INPA, UB, E	4	150 km SE Humaitá, 63.5km to Bodocó
OPILIACEAE				
<i>Agonandra brasiliensis</i> Miers	TMS264	INPA, E	3	47km NE Boa Vista to Passarão
	TMS300	INPA, E	4(12)	
PALMAE				
<i>Astrocaryum campestre</i> Mart.	R 6722	UB, E, K	7(25)	
<i>Syagrus comosa</i> Mart.	R 6738	UB, E, K	7	Top of Serra da Madeira
<i>Syagrus petraea</i> (Mart.) Becc.	TMS454	INPA, E, K	5(16)	
POACEAE				
<i>Actinocladum verticillatum</i> (Nees) McClure ex Sodars.	TMS315	INPA, E	4	150 km SE Humaitá, 15 km to Bodocó
<i>Andropogon fasciatus</i> Sw.	TMS241	INPA, E	3(8)	

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
<i>Leptocoryphium lanatum</i> (Kunth) Nees	TMS291	INPA	4(14)	
<i>Paspalum lanciflorum</i> Trin.	TMS221	INPA, E	3	10 km N Surumu River
<i>Paspalum setiglume</i> Chase	TMS293	INPA, E	4(14)	
<i>Streptostachys ramosa</i> Zuloaga & Soderstrom	TMS455	INPA, UB, E	5(16)	
<i>Trachypogon spicatus</i> (L. f.) Kuntze	TMS240	INPA, E	3(98)	
	TMS242	INPA	3	18.5 km N of bridge Caumé River
<i>Thrasya petrosa</i> (Trin.) Chase	TMS230	INPA, UB, E	3	11 km S Surumu River
PROTEACEAE				
<i>Roupala montana</i> Aubl.	TMS276	INPA, E	3(14)	
RUBIACEAE				
<i>Alibertia edulis</i> (L.C. Rich.) A. Rich. ex DC.	R 6762	UB, E, K	7	Between Carolina and Estreito
	TMS172	INPA, UB, E	4	14 km SW Humaitá
<i>Chomelia brasiliana</i> A. Rich.	R 6749v	UB, E, K	7	Top of Serra da Madeira
<i>Chomelia parviflora</i> (Müll. Arg.) Müll. Arg.	R 6756v	UB, E, K	7	Top of Serra da Madeira
	R 6758	UB, E, K	7	Between Carolina and Estreito
<i>Ferdinandusa ovalis</i> Pohl	R 6705	UB, E, K	7	2 km S Pedra Caida to Carolina
	TMS463	INPA, E	5(17)	
<i>Isertia parviflora</i> Vahl	TMS211	INPA, E	3	10 km N Surumu River
<i>Morinda tenuiflora</i> (Benth.) Steyerem.	TMS215,216	INPA, E	3	10 km N Surumu River
<i>Palicourea rigida</i> Kunth	TMS214	INPA, E	3	10 km N Surumu River
	TMS244	INPA, E	3	18.5 km N of bridge Caumé River
<i>Palicourea nitidella</i> (Müll. Arg.) Standley	TMS271	INPA, E	4	5 km S Bodocó
<i>Rudgea erioloba</i> Benth.	TMS167	INPA, E	6(22)	
<i>Tocoyena brasiliensis</i> Mart.	TMS175	INPA, UB, MPEG, E	4	18 km S Humaitá
<i>Tocoyena neglecta</i> N.E. Brown	TMS212	INPA, E	3	10 km N Surumu River
RUTACEAE				
<i>Zanthoxylum carabaeum</i> Lamarck	TMS259	INPA, E	3	40 km NE Boa Vista to Passarão
SAPOTACEAE				
<i>Chrysophyllum</i> sp.	R 6711	UB, E	7	2 km S Pedra Caida to Carolina

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
<i>Manilkara amazonica</i> (Huber) Standley	R 6701	UB, E, K	7	2 km S Pedra Caída to Carolina
<i>Pouteria ramiflora</i> (Mart.) Radlk.	R 6684	UB, E	7(23)	
	R 6689	UB, E, K	7(23)	
	TMS180	INPA, UB, E	4	150 km Transamazonica, 54 km to Bodocó
	TMS283	INPA, UB, MPEG, E	4(14)	
<i>Pouteria torta</i> (Mart.) Radlk.	TMS309	INPA, E	4	150 km Transamazonica, 80 km to Bodocó
SCHIZAEACEAE				
<i>Lygodium volubile</i> Sw.	R 6790	UB, E, K	7	20 km N of Carolina
SCROPIULARIACEAE				
<i>Buchnera palustris</i> (Aubl.) Spreng.	TMS232	INPA, E	3	11 km S Surumu River
SIMAROUBACEAE				
<i>Simaba glabra</i> Engl.	R 6719	UB, E, K	7(24)	
<i>Simarouba amara</i> Aubl.	TMS306	INPA, E	4	150 km SE Humaitá, 80 km to Bodocó
SMILACACEAE				
<i>Smilax irrorata</i> Mart. ex Grisebach	TMS173	INPA, E	4	18 km S Humaitá
STERCULIACEAE				
<i>Helicteres macropetala</i> Adr. Juss.	R 6746	UB, E, K	7	Top of Serra da Madeira
STYRACACEAE				
<i>Styrax ferrugineus</i> Nees & Mart.	TMS404	E	5(16)	
TILIACEAE				
<i>Luehea speciosa</i> Willd.	TMS249	INPA, UB, E	3	81 km N of bridge Cauamé River
VERBENACEAE				
<i>Aegiphila integrifolia</i> (Jacq.) Jacks.	TMS251	INPA, UB, MPEG, E	3	18 km E of bridge Branco River
<i>Aegiphila</i> aff. <i>thotzkyana</i> Cham.	TMS484	INPA, E	1	APA Curiaú, 21 km N Macapá
<i>Vitex schomburgkiana</i> Schau.	TMS269	INPA, MPEG, E	3(11)	

Appendix 4.2. (cont.)

	Collecting number	Herbarium lodged	Site (Transect) numbers	Location outside Transects
VOCHYSIACEAE				
<i>Callisthene fasciculata</i> (Spreng.) Mart.	R 6764	UB, E, K	7	Close to Rio Lajes, at the new club
	TMS168	INPA, E	6(22)	
<i>Qualea grandiflora</i> Mart.	TMS475,476	INPA, UB, MPEG, E	5	BR 364 to Porto Velho, 8 km crossing MT170
<i>Qualea multiflora</i> Mart.	TMS477	INPA, UB, E	5	BR 364 to Porto Velho, 8 km crossing MT170
<i>Qualea parviflora</i> Mart.	R 6690	UB, E, K	7(23)	
	TMS181	INPA, E	4	150 km Transamazonica, 54 km to Bodocó
	TMS189,191	INPA, MPEG, E	4(12)	
	TMS317	INPA	4	150 km Transamazonica, 80 km to Bodocó
	TMS402	INPA, UB, E	5(16)	
	TMS422	INPA, E	5(17)	
<i>Salvertia convallariodora</i> A. St.-Hil.	TMS179	INPA, E	4	14 km Southwest Humaitá
	TMS198	INPA, E	4(12)	
<i>Vochysia cinnamomea</i> Pohl	TMS400	INPA, UB, MPEG, E	5(16)	
<i>Vochysia ferruginea</i> Mart.	TMS285	INPA, UB, MPEG, E	4	8 km L of Bodocó to Igarapé Preto
<i>Vochysia grandis</i> Mart. var. <i>uaupensis</i> (Spruce) Warm.	TMS190	INPA, UB, MPEG, E	4(12)	
<i>Vochysia haenkeana</i> Mart.	R 6785	UB, E, K	7	15 km N of Carolina, back roads
<i>Vochysia rufa</i> Mart.	R 6774	UB, E, K	7	Close to Transect 23
	TMS162	INPA, E	6(19)	
	TMS440	INPA, E	5(18)	
<i>Vochysia sessilifolia</i> Warm.	TMS279	INPA, MPEG, E	4(14)	
? <i>Vochysia tucanorum</i> (Spreng.) Mart.	R 6691	UB, E, K	7(23)	

A floristic study of the savanna vegetation of the state of Amapá, Brazil, and suggestions for its conservation

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ABSTRACT - A total of 61 tree and large shrub and 69 smaller species were recorded in 11 surveys of savanna areas from the south to the north of the state of Amapá. Quantitative phytosociological data were collected for four areas. Almost all the important woody species with high IVI values are of widespread distribution and occur in the Central Brazilian cerrado vegetation. Two families of great importance in the tree flora of the cerrados, the Leguminosae and the Vochysiaceae, are very poorly represented in the Amapá savannas, the former by two and the latter by only one species. In common with other Amazonian savannas, those of Amapá are floristically depauperate when compared to the core area of Brazilian cerrado vegetation. Soil samples collected in most of the sites surveyed had low pH and mineral availability.

KEY WORDS: Cerrado, phytosociology, savanna, Amapá, Brazil.

RESUMO - Um total de 61 espécies de árvores e arbustos grandes e 69 espécies de menor porte foram registradas em 11 levantamentos conduzidos do sul ao norte das savanas do estado do Amapá. Quatro levantamentos incluíram coleta de dados fitossociológicos quantitativos. A grande maioria das espécies lenhosas com valores de IVI mais elevados apresentam ampla distribuição e ocorrem nos cerrados do Brasil Central. Leguminosae e Vochysiaceae, duas famílias de grande importância na flora arbórea dos cerrados do Brasil Central, são pouco representadas nas savanas do Amapá. A primeira por duas e a segunda por apenas uma espécie na área. As savanas do Amapá, como outras savanas amazônicas, são floristicamente pobres em comparação com a área core dos cerrados brasileiros. Amostras de solos coletadas para a maioria dos locais visitados apresentaram pH e nível de nutrientes baixos.

PALAVRAS-CHAVE: Cerrado, fitossociologia, savana, Amapá, Brasil.

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INTRODUCTION

In addition to the 2 million km² of cerrado (tree savanna) that dominate the natural vegetation of Central Brazil, there are large disjunct patches of savanna across Amazonia. The Amazonian savannas are structurally similar to the cerrados, although they are often classified separately owing to the absence of certain characteristic cerrado species and their different soils and climate (Eiten 1978). Despite the growing number of published studies on these areas, much remains unclear as to their structure, species composition, and floristic links with other savanna areas, both within Brazil and in the adjoining countries of Venezuela, Colombia, Surinam and Guyana.

Amapá has 11,000 km² of isolated savanna limited to a long strip stretching in a NE direction along most of the state and a number of important studies on this vegetation have been undertaken (Magnanini 1952; Azevedo 1967; Ledoux 1968, 1969; RADAM 1974; Ab'Sáber 1982). Azevedo (1967), for example, found a gradient of savanna formations in the state, from cerrado-type savannas to treeless campos and seasonal swamps dominated by tall grasses and sedges, with similar formations occurring on Marajó Island (Bastos 1984).

The present work is devoted to a floristic study of the savannas of the state of Amapá and seeks to describe their structure and composition and to investigate their links with other savanna areas.

DESCRIPTION OF THE STUDY AREA

Amapá is the most north-easterly state of Brazil and covers an area of 136,450 km². It is bounded to the NE by the Atlantic Ocean and SE by the Rio Amazonas, and shares its northernmost frontier with French Guiana. To the SW, the Rio Jari delimits its border with the state of Pará.

The climate is tropical and maritime with high temperatures all year round and is classified as Köppen's Amw' of the tropical rain climate (Eidt 1968). The mean annual temperature is 26°C, with the mean annual rainfall ranging between 2321 mm and 3250 mm. There is a short dry season of two to three months duration between August and October which is most pronounced in the southern half of the state (IRDA/IBGE 1966).

RADAM (1974) recognises three distinct ecological regions in Amapá. These are defined as closed forest (105,000 km²), savanna (11,000 km²) and coastal formations, consisting principally of mangrove, várzea (seasonally inundated forest) and flooded grasslands (20,000 km²). The vegetation pattern reflects the geology of the state which is underlain in its entirety by the ancient Guyanan shield, with Tertiary and Quaternary deposits present on its eastern coastal border (Formação Barreiras). The savanna soils, as defined by RADAM, are principally dystrophic yellow latosols (orthox, Sanches 1976).

Until 15 years ago the savannas were relatively well-preserved, despite the long history of colonization of the state. However, in recent years urbanisation, agricultural expansion and especially the establishment of forestry plantations, mainly of *Pinus caribaea* (McDonald & Fernandes 1984), have rapidly reduced the area of unmodified savanna. We estimate from existing maps that at least 30% of the savanna area has been altered to date.

Between July 1993 and March 1994, we visited 11 areas of savanna in the localities listed below which cover a wide range of the latitudinal distribution of this vegetation within the state (Figure 1):

- (1) APA do Curiaú (Environmentally Protected Unit), 9 km N de Macapá (00°02'N, 51°03'W)
- (2) 27 km N of Macapá (00°14'N, 51°06'W)
- (3) EMBRAPA-CPAF station (The National Agricultural Research Agency, Centre for Agroforestry Research of Amapá), 45 km N of Macapá (00°25'N, 51°17'W)
- (4) Opposite the entrance to EMBRAPA-CPAF station, 45 km N of Macapá (00°25'N, 51°17'W)
- (5) Ministry of Defence area, 53 km N of Macapá (00°27'N, 51°05'W)
- (6) Gleba Pedreira - AMCEL (Amapá Celulose S.A.), 78 km N of Macapá (00°40'N, 51°45'W)
- (7) 113-114 km N of Macapá (00°46'N, 51°18'W)
- (8) 4 km N of Ferreira Gomes bridge (00°54'N, 51°11'W)
- (9) 50 km S of Tartarugalzinho (01°09'N, 51°02'W)
- (10) 5 km S of Tartarugalzinho (01°40'N, 50°50'W)
- (11) 5 km S of Calçoene (02°28'N, 50°59'W).

RADAM (1974) classified sites 1 to 10 as tree savannas (cerrado parque) and site 11 as isolated grassland (campo cerrado/cerrado parque).

MATERIALS AND METHODS

Floristic surveys were made at all sites by general observation and collecting, special attention being given to the woody species. Voucher specimens are lodged in the herbaria of the Centro Zoobotânico of Macapá (HAMAB), the Instituto Nacional de Pesquisas da Amazônia (INPA), the University of Brasília, DF (UB), and the Royal Botanic Garden Edinburgh, Scotland (E). General observations were made at the sites of quantitative surveys, at random stops along the roads and occasionally near forest/savanna boundaries.

Quantitative data for the woody plant component were collected at four sites: 4, 6, 8 and 9. The Point-Centred Quarter method (PCQ), as described by Mueller-Dombois & Ellenberg (1974), was used where the average height of the woody vegetation was in excess of 2 m. Twenty points were used for each transect (sites 4 and 8). Quadrats of 20 m x 50 m were used when the vegetation was lower than 2 m or when its open nature made the PCQ method inappropriate (two quadrats for site 6 and three quadrats for site 9). Both methods were applied in areas at least 200 m away from the nearest forest, to avoid inclusion of any forest species, and following the topography to avoid vegetation gradients.

In all surveys, species, height, and diameter at 1.3 m (breast height) above ground level were recorded for all individuals with a diameter ≥ 5 cm and ≥ 10 cm. Where trunks divided below 1.3 m the diameter of all branches at this height were recorded. The diameter of inclined trees was measured at 1.3 m from the base along the line of the trunk. The number of individuals, relative density, relative frequency, basal area (calculated either from single trunk or multiple branches), relative dominance and importance value index (IVI = Rel. dens. + Rel. dom. + Rel. freq.) were calculated for each species using the

FITOPAC program, package version 2.0 (G. Shepherd, unpublished, University of Campinas, SP, Brazil).

In each of the study areas where quantitative data of vegetation were collected, between two and five randomly selected samples of soil were collected from 0-10 cm depth. A single soil sample was taken where only floristic surveys were undertaken. Chemical and granulometric analyses of these samples were carried out at EMBRAPA-CPAC (The National Agricultural Research Agency, Centre for Agricultural Research of the Cerrado).

Two multivariate analyses were used in order to seek latitudinal patterns in the structure and distribution of the vegetation, and the soil types. However, the conclusions from these analyses are of limited value since there was no replication of samples at each latitude.

The soil information of seven sites was analysed by Principal Component Analysis (PCA), using the correlation option in the CANOCO Program Version 3.1 (ter Braak 1988), with all data log-transformed to reduce the variance.

The floristic information (presence and absence of species) of all 11 study sites was analysed by TWINSpan (a divisive hierarchical classification by Two-Way Indicator Species Analysis) using the package VESpan II (Malloch, 1988). Species occurring only on the forest border were excluded from the analyses.

RESULTS

A list of all tree and large shrubs species recorded at the 11 survey localities is given in Table 1. The complete species list (including herbs and other low species) for all areas visited is presented in the Appendix. As anyone who has worked in savanna vegetation knows, it is often difficult to decide the correct growth-form category of a species, and therefore it is important to explain the criteria we have used. Our 'trees and large shrubs' include those shrubs which exceed 1 m in height and have long-lived woody aerial stems. Plants with short-lived woody shoots usually produced in a single flush of growth from a xylopodium (hemixyles, or renewable shrubs), e.g. many species of *Cassia* (*sens. lat.*), *Mimosa*, Malpighiaceae etc.) are not included in this category. 'Smaller shrubs (including hemixyles) and herbs' are lumped together as a single category in the Appendix, while lianas and climbers, and parasites, are given distinct categories. Detailed phytosociological data are given in Tables 2-3 and synthesized in Table 4. The results of the soil analyses are shown in Table 5.

A total of 130 species were observed of which 61 were trees or large shrubs. However, during the quantitative surveys, only 12 species were recorded with a diameter at breast height (dbh) of ≥ 5 cm and no single area surveyed had more than 10 woody species. It was rare for the larger woody plants to achieve heights in excess of 4 m, or for the occasional emergents (usually *Byrsonima crassifolia*, *Himatanthus articulatus* and, occasionally, *Roupala montana*) to exceed 6m. All areas were characterised by their dwarfed stature, which was of a lower and more open structure compared to the cerrado *sensu stricto* of Central Brazil.

The commonest species observed were *Byrsonima crassifolia* and *Himatanthus articulatus* which occurred at every study site. All areas showed a few species with similar high IVI ranks, principally *Byrsonima crassifolia*, *Himatanthus articulatus*, *Ouratea hexasperma* and *Byrsonima coccolobifolia*. *Curatella americana*, *Tocoyena formosa*, *Salvertia convallariodora*, *Roupala montana*, *Byrsonima crassa*, *Aegiphila* cf. *parviflora*. *Anacardium occidentale* and *Rauvolfia pentaphylla* were present in lower numbers. The analysis of the measurements of trees with dbh \geq 10 cm showed no change in the order of IVI values, except for an added record of *Trattinickia rhoifolia* at site 8, therefore these results are not presented. None of the sites had species exceptional for savannas, except for the two northernmost areas where *Humiria balsamifera*, *Chrysobalanus icaco* and a *Bactris* sp. were recorded.

The majority of areas had under 100 individuals per hectare, but an exception (site 4) had more than 200 individuals (Table 4). A latitudinal gradient in physiognomy was observed, with the northernmost sites tending to have a more strongly developed herbaceous layer and fewer trees and shrubs.

A visual estimate of the ground cover of the savanna areas visited ranged from 40% to 100% and tended to be dominated by the grass *Trachypogon plumosus* and the sedge *Bulbostylis spadicea*, with *Scleria cyperina*, *Rhynchospora barbata* and *Paspalum carinatum* also common.

The TWINSPLAN classification of the floristic information indicates a latitudinal pattern existing within the savanna, with all the northern sites (sites 7 to 11) separated from the southern sites on the basis of their component species (Fig. 2). Site 11 is classified distinctly from all other sites at the first division due to a high percentage of its flora (*Bactris* sp. *Chrysobalanus icaco*, *Clusia* sp. *Duroia duckei* and *Ouratea castanaefolia*)

only noted at this site. Species identified by TWINSPAN as being strongly preferential to the southern areas of savanna include *Bowdichia virgilioides*, *Aegiphila* cf. *parviflora* and *Salvertia convallariodora*. The authors also noted apparent distribution gradients of some other principal species such as *Byrsonima verbascifolia* which dramatically increased in abundance in the north of the state. Some species, *Byrsonima crassifolia*, *B. coccolobifolia*, *Himatanthus articulatus*, *Ouratea hexasperma*, *Annona paludosa* and *Curatella americana* were widely distributed.

The soils of all areas ranged from sandy to clayey, and were strongly to medium acid ($\text{pH} \leq 5.5$). They were poor in nutrients, and low in organic matter, with the soil surface frequently indurated by iron concretions (Table 5).

The ordination of the areas based on soil information shows a pattern which is highly correlated to vegetation physiognomy (Fig. 2). The eigenvalues for the four PCA axes were 0.43, 0.167, 0.137 and 0.086. The cumulative percentage variance for the axes were, respectively, 43.4%, 60.1%, 73.9% and 82.5%. The first axis was positively correlated with fine sand (FS), and negatively correlated with coarse sand (CS), silt and clay, whilst axis II was positively correlated to pH and magnesium (Mg) and negatively correlated to phosphorus (P) and calcium (Ca). The study sites with average vegetation height (sites 6 and 9) were negatively correlated with axis I, and contained high levels of clay (>30%). Sites with higher height averages (sites 3, 4, 7 and 8) were positively correlated with axis I, and had lower clay levels (between 15-20% for site 4 and 8, and 30% for sites 3 and 7). However, site 2, also of higher vegetation height showed a negative correlation with Axis I and had high clay values ($\geq 40\%$). Only one site, with a high vegetation height (site 11), showed an extremely high negative correlation with axis I. The soils of this site contained only fine sand (74%) with a clay composition up to 25%, and contained species characteristic of a waterlogged habitat

(Bactris sp., the acaulescent form of Byrsonima verbascifolia and several species of Utricularia).

DISCUSSION

The savanna vegetation of Amapá is poor in species compared to the cerrados of Central Brazil. It is not uncommon for cerrado areas to harbour more than 100 tree and large shrub species (Ratter 1980; Gibbs et al. 1983; Pott et al. 1986; Oliveira-Filho & Martins 1991; Felfili et al. 1993), while the present study recorded only 61, despite surveying 11 savanna areas covering two degrees of latitude. Previous floristic studies conducted in the state of Amapá (Azevedo 1967; RADAM 1974) recorded a total of 14 species of trees. Only two species from these studies, an unidentified member of Burseraceae (breu branco, probably *Protium* sp. or *Tetragastris unifoliolata* (Engl.) Quatr.) (Azevedo 1967) and a species of *Qualea* (RADAM 1974) were not found in this study.

The relative species poorness of the Amazonian savannas is well documented. Milliken & Ratter (1989) recorded 31 tree and large shrub species in a *Curatella americana/Byrsonima crassifolia* campo on Maracá island in Roraima, whilst the current authors have recorded 46 such species in the savannas near Alter do Chão, Pará (of which Miranda (1993) found 19 species within a 3.5 ha area). Other accounts of relatively depauperate floras in the savannas of Brazilian Amazonia and also those of Guyana, Surinam, Venezuela and Colombia have been published by a number of authors (Egler 1960; Takeuchi 1960; Blydenstein 1967; Goodland 1966; van Donselaar 1965; Bastos 1984; Gottsberger & Morawetz 1986). Although the majority of these sites are species poor, relatively diverse floras have also been documented for some isolated savanna areas in Amazonia: for instance, Janssen (1986) listed 67 species of trees for the savannas near Humaitá, in the state of Amazonas. The reasons for the paucity of species in most of these areas remains unclear, although the presence of a

perched high water-table has been proposed as a contributing factor (Sarmiento & Monasterio 1975).

All of the species dominating the woody component of the Amapá savannas are common in the Brazilian cerrados. *Curatella americana* and *Byrsonima crassifolia* are widespread in South and Central American savannas and their ability to withstand periodic waterlogging, enabling them to colonise a wide variety of sites, is well-known (see, for instance, Foldats & Rutkis 1975; Ratter 1992). The savannas of Amapá are dominated by only a few species, and this appears to be a common feature of many of the Amazonian savannas. Although *C. americana* and *B. crassifolia* are usually among the dominant species in most Amazonian savannas, there is much variation between sites in the other principal species. In Amapá, *Himatanthus articulatus*, *Ouratea hexasperma* and *Byrsonima coccolobifolia* are the most common, followed by *B. crassifolia* and *C. americana*. However, Gottsberger & Morawetz (1986) noted *Physocalymma scaberrimum* (a species not recorded in Amapá) as being one of the dominants in Humaitá, while Takeuchi (1960) reported that *Cassia flexuosa* (also unrecorded in Amapá) is sometimes found as a monodominant in the savannas of Roraima state. This variation in the principal species probably has as much to do with chance as with ecological preferences. The lack of both floristic and ecological information limits further discussion.

The only unusual woody species recorded were *Chrysobalanus icaco* (also recorded by Azevedo (1967)) and *Humiria balsamifera*, both recorded north of the city of Amapá. The occurrence of these species was associated with the presence of well-drained sandy soils, and our samples collected from the two white sand sites (10 and 11) were very different in texture from all the others (due to the absence of coarse sand) and showed the lowest levels of calcium, magnesium, phosphorus and organic matter. In fact, white sand woodlands are a

typical habitat of *H. balsamifera* across northern South America (Granville 1982; van Donselaar 1965). Milliken & Ratter (1989) recorded it associated with *Curatella americana* and *Byrsonima crassifolia* on Maracá island, Roraima, and Bastos (1984) on Marajó Island. *Chrysobalanus icaco* is very characteristic of the low savanna scrub which occurs behind the strand line of the Central American (Furley and Ratter 1992) and northern South American coast (Huber 1898, on Marajó Island) and this habitat resembles that of the Amapá savannas.

In contrast to the Central Brazilian cerrados, only one species of the Vochysiaceae (*Salvertia convallariodora*) and two of the Leguminosae (*Anadenanthera peregrina* and *Bowdichia virgilioides*) were found. These are two of the most important woody families of the cerrado in terms of both vegetation cover and number of species. *Qualea grandiflora*, *Q. multiflora* and *Q. parviflora* of the Vochysiaceae are amongst the most widespread cerrado tree species (Ratter & Dargie 1992) but there are no substantiated records from the savannas of Amapá, although RADAM (1974) refer to the presence of a '*Qualea*'. *Q. parviflora* is not found in savannas further north than Humaitá, Amazonas state (Janssen 1986), whilst *Q. grandiflora* is found as far north as Monte Alegre, just north of the Amazon river (Andrade-Lima 1958). There are no records of either of these species from the savannas of Roraima state. *Salvertia convallariodora* shows an interesting pattern of distribution in Amapá where it is abundant in the south and absent in the north. The presence of great numbers of apparently young or dwarf plants was noted in areas where few trees of this species occurred and perhaps a process of northward colonization is occurring. Amapá represents the northernmost Brazilian distribution of *S. convallariodora*, although it has been recorded as far north as Surinam (Kubitzki 1983). Of the two species of Leguminosae, *Anadenanthera peregrina* was only found on the savanna border with gallery forest, while *Bowdichia virgilioides* shows the same distribution pattern as *S. convallariodora*, being present in the south and absent in the

north. This species is abundant from the cerrados of São Paulo in the south to the savannas of Venezuela in the north.

The tree savannas we studied in Amapá were of small stature, with low and sparse trees compared to those of the majority of cerrado vegetation in Central Brazil. This is in common with many Amazonian savannas, but there are exceptions: the savannas of Alter do Chão. Pará, for example, have a dense tall woody component and show a classic cerrado form. Many factors might be involved in the prevalence of dwarf savannas in Amazonia (e.g. soil nutrients and water-table depths) and this would provide an interesting field for further investigation.

Some of the most common ground cover species in Amapá, such as species of *Trachypogon*, *Bulbostylis* and *Paspalum* are also the principal species in other Amazonian savannas (Egler 1960, Takeuchi 1960, Sanaiotti & Magnusson 1995).

The soils at all sites were sandy to clayey and strongly to medium acid, with low levels of silt ($\leq 4\%$). Similar soil properties were found by Souza *et al.* (1992) and RADAM (1974), although in both cases greater levels of silt were recorded ($\geq 10\%$).

Currently the only conservation unit in Amapá that includes the savanna ecosystem is the APA do Curiaú in the south of the state. This includes less than 2% of the total savanna area of the state, and to ensure adequate protection of the savanna vegetation of Amapá, more effective conservation units need to be established. These should take into account the latitudinal gradient described in this study. From our studies, we have suggested to the Amapá local Government Environmental Department (CEMA) the following five savanna areas that could provide the focus of any future conservation initiatives within the state:

- 1) Área do Exército (Ministry of Defence area), 53 km N of Macapá
- 2) Gleba Pedreira - AMCEL, 78 km N of Macapá
- 3) Between 40-48 km north of Macapá on the BR 156

4) Between the towns of Amapá and Calçoene

5) 10 km S of Tartarugalzinho

The criteria used in the choice of these sites were degree of naturalness and representation of the range of savanna vegetation types to be found in the state. Our investigations are preliminary, but provide a basis for further floristic studies aimed at the selection of further conservation areas.

As well the floristic aspect, fauna and habitat use must be considered when suggesting conservation areas. Since the Central Brazilian savannas are known to support large numbers of migratory birds (Antas 1983), one of us (T.M.S.) recorded non-resident species of birds for all sites visited as a subsidiary to the main vegetation study. Three migratory species were observed throughout the state from north to south, including the rare *Piranga rubra*. Also observed were *Tyrannus savana* and, in the várzea, *Leistes militaris*.

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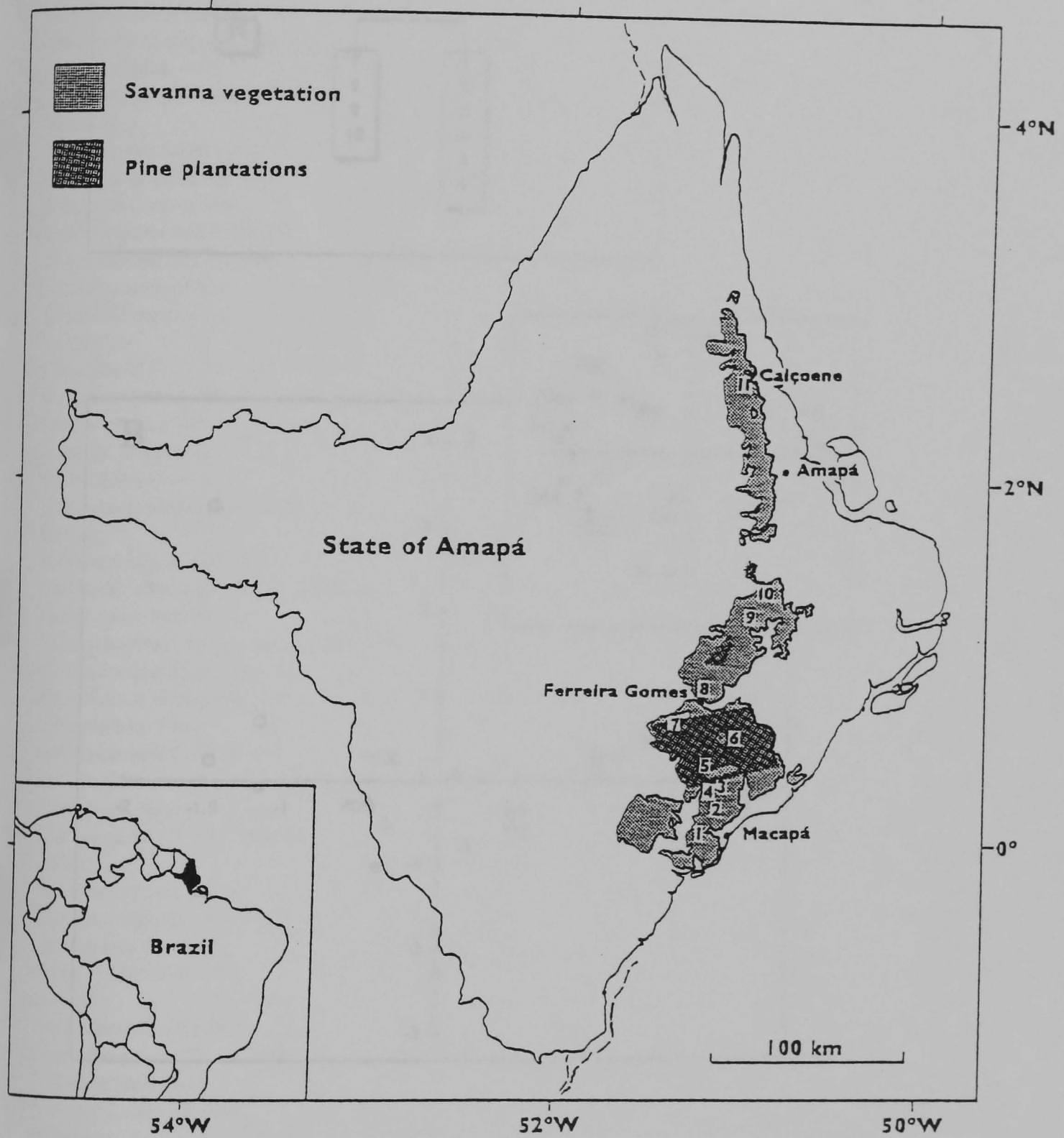


Figure 1. Distribution of the savanna vegetation of Amapá showing the 11 study sites and areas replaced by pine plantations.

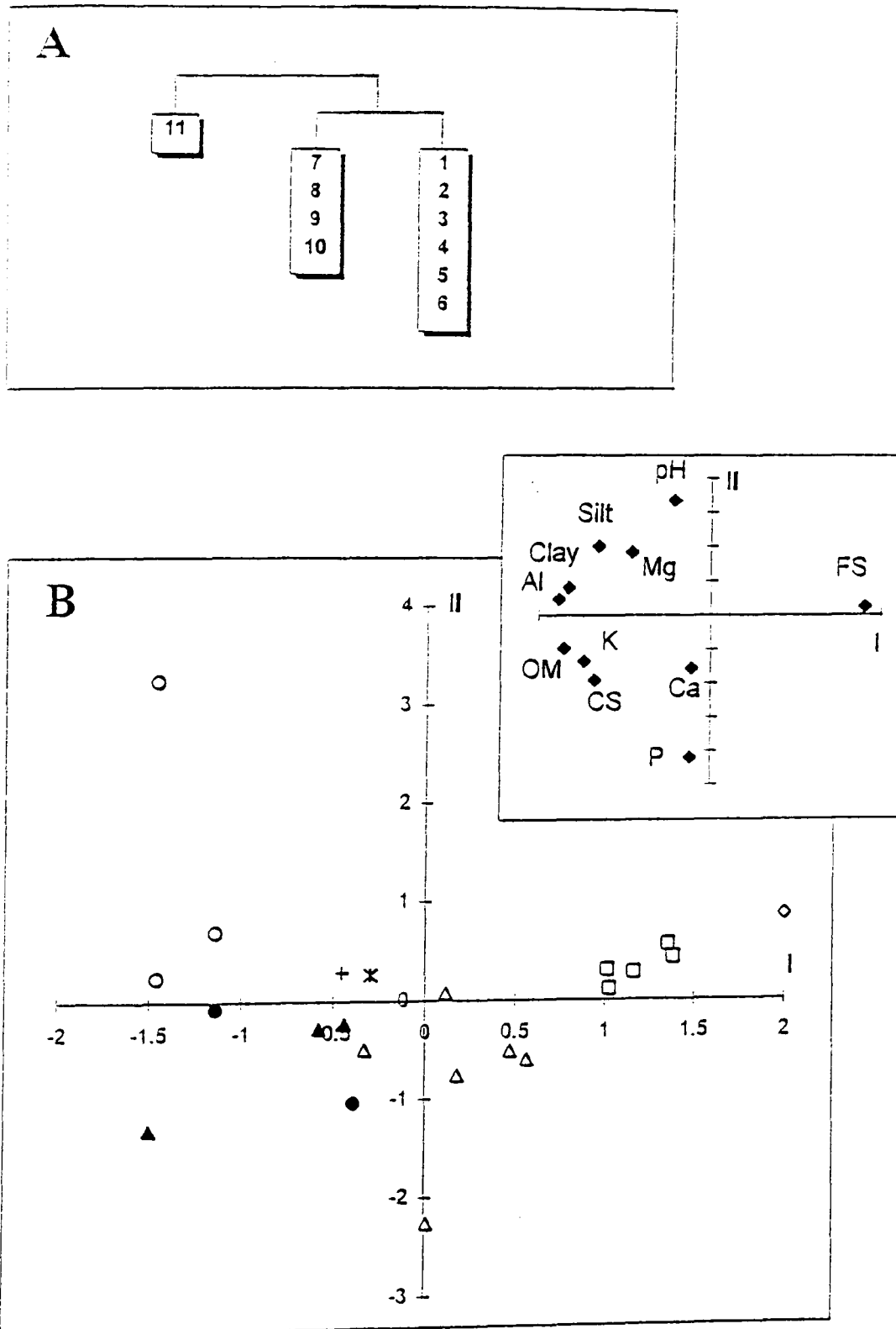


Figure 2. (A) TWINSpan hierarchical classification of the 11 study sites after two levels of division. (B) PCA of 22 (0-10 cm) soil samples from eight study sites: (○) site 2, (□) site 4, (△) site 8, (◇) site 11, (+) site 3, (×) site 7, (●) site 6, (▲) site 9. Open symbols = vegetation height about 3 m, closed symbols = vegetation height above 4 m, others = vegetation near forest borders.

Table 1. List of all tree and large shrub species occurring in the 11 survey sites (N=59). (s) present only as a small shrub (b) present only on the border with gallery forest.

SPECIES	SITES										
	1	2	3	4	5	6	7	8	9	10	11
<i>Aegiphila</i> cf. <i>cremata</i> Moldenke	x	-	-	-	-	-	-	-	-	-	-
<i>Aegiphila</i> cf. <i>parviflora</i> Moldenke	x	x	x	x	x	-	-	-	-	-	-
<i>Anacardium occidentale</i> L.	-	x	-	x	-	-	-	x	-	x	-
<i>Anadenanthera peregrina</i> Speg.	b	-	-	-	-	-	-	-	-	-	-
<i>Annona paludosa</i> Aubl.	s	x	x	s	s	s	x	x	-	s	-
<i>Astronium fraxinifolium</i> Schott.	-	-	b	-	-	-	-	-	-	-	-
<i>Bactris</i> sp.	-	-	-	-	-	-	-	-	-	-	x
<i>Bowdichia virgilioides</i> Kunth	x	x	b	x	-	-	-	-	-	-	-
<i>Byrsonima coccolobifolia</i> Kunth	x	x	x	x	x	x	x	x	x	-	-
<i>Byrsonima</i> cf. <i>crassa</i> Nied.	-	x	x	x	x	-	-	x	-	-	-
<i>Byrsonima crassifolia</i> (L.) Kunth	x	x	x	x	x	x	x	x	x	x	x
<i>Casearia grandiflora</i> Cambess.	-	-	-	x	x	x	x	x	-	-	-
<i>Casearia sylvestris</i> Sw.	x	x	x	s	-	x	-	x	-	-	-
<i>Chrysobalanus icaco</i> L.	-	-	-	-	-	-	-	-	-	-	x
<i>Clusia</i> sp.	-	-	-	-	-	-	-	-	-	-	x
<i>Coccoloba</i> sp.	-	-	b	-	-	-	-	-	-	-	x
<i>Conarus perottetii</i> (DC.) Planch. var. <i>angustifolium</i> Radlk.	x	-	-	s	-	-	-	-	-	-	-
<i>Cupania diphylla</i> Vahl	-	-	-	-	-	x	-	-	-	-	-
<i>Curatella americana</i> L.	x	x	x	x	x	x	x	x	x	-	-
<i>Duroia duckei</i> Huber	-	-	-	-	-	-	-	-	-	-	x
<i>Erythroxylum suberosum</i> A. St. Hil.	s	s	s	-	-	-	-	-	-	-	-
<i>Guettarda</i> sp.	-	-	b	-	-	-	-	-	-	-	-
<i>Hancornia speciosa</i> Nees & Mart.	x	-	-	-	-	-	-	x	-	-	-
<i>Himatanthus articulatus</i> (Vahl) R. E. Woodson	x	x	x	x	x	x	x	x	x	x	x
<i>Hirtella ciliata</i> Mart. ex Zucc.	x	-	-	x	-	x	-	-	-	x	x
<i>Hirtella racemosa</i> Lam. var. <i>hexandra</i> (Willd. ex R. & S.)	-	-	-	-	-	-	x	x	-	x	x
<i>Humiria balsamifera</i> (Aubl.) St. Hil.	-	-	-	-	-	-	-	-	-	x	x
<i>Hymenolobium</i> cf. <i>petraeum</i> Ducke	b	-	-	-	-	-	-	-	-	-	-
<i>Inga marginata</i> Willd.	-	-	b	-	-	-	-	-	-	-	-
<i>Jacaranda copaia</i> (Aubl.) D. Don	-	-	-	-	-	x	-	-	-	-	-
<i>Lacistema aggregatum</i> (Berg) Rusby	-	-	s	-	-	-	x	-	-	-	-
<i>Lafoensia</i> cf. <i>pacari</i> A. St. Hil.	-	-	-	-	-	-	-	x	-	-	-
<i>Licania longistyla</i> (Hook. f.) Fritsch	-	-	-	-	-	-	x	-	-	x	-
<i>Luehea</i> sp.	-	-	b	-	-	-	-	-	-	-	-
<i>Maprounea guianensis</i> Aubl.	s	-	-	-	-	-	-	x	-	-	-
<i>Mezilaurus lindaviana</i> Schwacke & Mez	b	-	b	-	-	-	-	-	-	-	-
<i>Myrcia cuprea</i> Kiaersk.	x	-	-	x	-	-	x	-	-	-	-
<i>Myrcia</i> cf. <i>fallax</i> (Rich.) DC.	-	-	-	-	-	x	-	-	-	-	-
<i>Myrcia</i> sp.	-	-	-	-	-	-	-	-	-	-	x
<i>Ouratea castaneaefolia</i> Engl.	-	-	-	-	-	-	-	-	-	-	-
<i>Ouratea hexasperma</i> (St. Hil.) Benth.	x	x	x	x	-	x	x	x	x	x	-
<i>Palicourea rigida</i> Kunth	s	s	x	s	-	x	s	x	x	s	-
<i>Plathymenia reticulata</i> Benth.	-	-	b	-	-	-	-	-	-	-	-
<i>Psidium</i> sp.	-	-	x	x	-	-	-	-	-	-	-
<i>Rauvolfia pentaphylla</i> Ducke	x	-	-	-	-	x	x	-	-	-	-
<i>Roupala montana</i> Aubl.	x	-	b	x	-	x	x	-	-	-	-
<i>Salvertia convallariodora</i> St. Hil.	x	x	x	x	x	x	-	-	-	-	-
<i>Sapium longifolium</i> Boj.	x	-	-	-	-	-	-	-	-	-	-
<i>Simarouba amara</i> Aubl.	-	x	b	-	-	x	-	-	-	-	-
<i>Simarouba versicolor</i> St. Hil.	x	-	-	-	-	-	s	-	-	-	-
<i>Siparuna guianensis</i> Aubl.	-	-	-	-	-	-	-	x	-	-	-
<i>Synolocos guianensis</i> Guerke	-	-	-	-	-	-	-	-	-	-	-
<i>Tabebuia aurea</i> Benth. & Hook.	x	-	b	-	-	x	-	-	-	-	-
<i>Tabebuia serratifolia</i> Rolfe A. O. F.	-	-	b	-	-	-	-	-	-	-	-
<i>Tabebuia serratifolia</i> Rolfe A. O. F.	x	-	-	x	-	x	x	x	-	-	-
<i>Tocovena formosa</i> (C. & S.) Schum.	-	-	-	-	-	-	-	x	-	x	-
<i>Trattinnickia rhoifolia</i> Willd.	b	-	-	-	-	-	-	-	-	-	-
<i>Vismia guianensis</i> (Aubl.) Choisy	-	-	x	x	-	x	-	-	-	-	-
<i>Vitex</i> sp.	x	-	b	-	-	-	-	x	-	-	-
<i>Xylopia aromatica</i> Lam.	-	-	-	-	-	x	-	-	-	-	-

Table 2. Phytosociological data for the two savanna areas surveyed with 20 point PCQ transects (>5cm dbh).

SPECIES	Opposite Embrapa station (site 4)						4 km N of Ferreira Gomes (site 8)					
	n	Total ba	Rel. dens.	Rel. dom.	Rel. freq.	IVI	n	Total ba	Rel. dens.	Rel. dom.	Rel. freq.	IVI
<i>Byrsonima crassifolia</i>	28	0.36	35.00	32.64	29.08	96.73	34	0.58	42.50	41.28	31.25	108.05
<i>Himatanthus articulatus</i>	11	0.21	13.75	18.94	14.55	47.23	26	0.78	32.50	30.88	35.42	105.58
<i>Ouratea hexasperma</i>	15	0.23	18.75	20.38	21.80	60.94	1	0.05	1.25	2.67	2.08	6.07
<i>Byrsonima coccolobifolia</i>	12	0.13	15.00	11.91	14.55	41.46	11	0.20	13.75	10.46	16.67	40.62
<i>Roupala montana</i>	3	0.03	3.75	2.67	3.64	10.06	0	0	0	0	0	0
<i>Curatella americana</i>	3	0.04	2.50	3.03	3.64	9.17	2	0.02	2.50	1.39	4.17	8.10
<i>Hirtella ciliata</i>	3	0.06	3.75	5.30	3.64	12.68	0	0	0	0	0	0
<i>Tocoyena formosa</i>	3	0.02	3.75	1.90	3.64	9.29	0	0	0	0	0	0
<i>Bowdichia virgilioides</i>	2	0.02	2.50	1.77	3.64	7.91	0	0	0	0	0	0
<i>Anacardium occidentale</i>	1	0.02	1.25	1.46	1.82	4.53	5	0.25	6.25	13.02	8.33	27.94
<i>Maprounea guianensis</i>	0	0	0	0	0	0	1	0.01	1.25	0.30	2.08	3.64
Totals	81	1.12	100	100	100	300	80	1.89	100	100	100	300

n = number of individuals; ba = basal area (m²/ha); Rel.dens. = relative density; Rel.dom. = relative dominance; Rel.freq. = relative frequency; IVI = importance value index.

Table 3. Phytosociological data for the two savanna areas surveyed with 50 x 20m quadrats (>5cm dbh) (two quadrats for site 6 and three for site 9).

SPECIES	50km S of Tartarugalzinho (site 9)						Gleba Pedreira da AMCEL (site 6)					
	n	Total ba	Rel. dens.	Rel. dom.	Rel. freq.	IVI	n	Total ba	Rel. dens.	Rel. dom.	Rel. freq.	IVI
<i>Ouratea hexasperma</i>	15	0.32	50.00	40.79	27.28	118.05	5	0.17	31.25	27.99	28.57	87.81
<i>Byrsonima crassifolia</i>	8	0.16	26.67	19.97	27.27	73.92	7	0.17	43.75	27.92	28.57	100.24
<i>Byrsonima coccolobifolia</i>	4	0.17	13.33	21.41	18.18	52.93	3	0.18	18.75	29.51	28.57	76.83
<i>Himatanthus articulatus</i>	1	0.01	3.33	6.60	9.09	19.02	1	0.09	6.25	14.58	14.29	35.12
<i>Curatella americana</i>	1	0.08	3.33	10.30	9.09	22.73	0	0	0	0	0	0
<i>Palicourea rigida</i>	1	0.01	3.33	0.93	9.09	13.35	0	0	0	0	0	0
Totals	30	0.75	100	100	100	300	16	0.61	100	100	100	300

n = number of individuals; ba = basal area (m²/ha); Rel.dens. = relative density; Rel.dom. = relative dominance; Rel.freq. = relative frequency; IVI = importance value index.

Table 4. Phytosociological information of the four savannas surveyed (> 5cm dbh). Area = area surveyed; n = number of individuals; ns = number of species; nf = number of families; ba = basal area per hectare; ah = average height.

Site	Site no.	Method	no. of samples	Area (ha)	n	ns	nf	ba (m ² /ha)	ah (m)	Density/ha
Opposite EMBRAPA	4	PCQ	20	0.38	80	10	9	1.12	3.95	213
4 km N of Ferreira Gomes	8	PCQ	20	1.29	80	7	6	1.89	4.50	62
Gleba Pedreira-AMCEL	6	Q	2	0.20	16	4	3	0.61	3.11	80
50 km S of Tartarugalzinho	9	Q	3	0.30	30	6	5	0.75	3.03	100

Table 5. Soil pH, exchangeable aluminium (Al), calcium (Ca), magnesium (Mg), phosphorus (P) and potassium (K), organic matter (OM), coarse sand (CS), fine sand (FS) and particle size composition for 0-10 cm deep soil samples for seven areas. Values are means of the sample numbers (N) indicated.

Site	site no.	pH H ₂ O	OM (%)	P (ug g ⁻¹)	K (ug g ⁻¹)	Ca (meq / 100g ⁻¹)	Mg (meq / 100g ⁻¹)	Al (meq / 100g ⁻¹)	Clay (%)	CS (%)	FS (%)	Silt (%)
27 km N of Macapá (N = 3)	2	5.4	1.37	2.7	6.7	0.06	0.11	0.99	44	26	26	4.0
Inside EMBRAPA (N = 1)	3	4.9	1.56	2.7	3.0	0.18	0.10	0.84	32	15	52	1.0
Opposite EMBRAPA (N = 5)	4	4.9	0.67	2.8	1.2	0.10	0.05	0.37	14	8	77	0.8
Gleba Pedreira-AMCEL (N = 2)	6	4.7	1.69	2.5	3.0	0.10	0.05	0.85	41	32	27	1.0
113-114 km N of Amapá (N = 1)	7	4.9	1.51	2.6	2.0	0.15	0.05	0.78	33	19	47	1.0
4 km N of Ferreira Gomes (N = 6)	8	4.8	0.99	3.0	5.8	0.11	0.06	0.45	19	37	43	0.5
50 km S of Tartarugalzinho (N = 3)	9	4.8	2.19	2.9	7.0	0.17	0.08	0.68	33	26	40	1.3
5 km S of Calçoene (N = 1)	11	4.5	0.35	2.4	0.0	0.07	0.04	0.08	25	1	74	0.0

Species of all species of tree, shrubs and herbs observed in the 11 study areas. *Rhabdodendron amazonicum* and *Virola sebifera* were only recorded outside the study areas. (w) trees and large shrubs; (h) small shrubs and herbs; (p) parasite; (l) liana or herbaceous climber.

<i>Aegiphila</i> cf. <i>cremata</i> Moldenke	w	<i>Lacistema aggregatum</i> (Berg) Rusby	w
<i>Aegiphila</i> cf. <i>parviflora</i> Moldenke	w	<i>Lafoensia</i> cf. <i>pacari</i> A. St. Hil.	w
<i>Alibertia elliptica</i> (Cham.) K. Schum.	h	<i>Licania longistyla</i> (Hook. f.) Fritsch	w
<i>Amasonia campestris</i> (Aubl.) Moldenke	h	<i>Luehea</i> sp.	w
<i>Anacardium occidentale</i> L.	w	<i>Macroptilium lathyroides</i> (L.) Urban	h
<i>Anadenanthera peregrina</i> Speg.	w	<i>Manihot</i> sp.	h
<i>Annona paludosa</i> Aubl.	w	<i>Maprounea guianensis</i> Aubl.	w
<i>Aristida</i> sp.	h	<i>Merremia aturensis</i> Hallier f.	h
<i>Asironium fraxinifolium</i> Schott.	w	<i>Mezilaurus lindaviana</i> Schwacke & Mez	w
<i>Bacris</i> sp.	w	<i>Miconia alata</i> DC.	h
<i>Borreria</i> sp.	h	<i>Miconia albicans</i> (Sw.) Triana	h
<i>Bowdichia virgilioides</i> Kunth	w	<i>Miconia ciliata</i> Benth.	h
<i>Buchnera palustris</i> Spreng.	h	<i>Miconia rufescens</i> (Aubl.) DC.	h
<i>Bulbosylis spadicea</i> Kunth	h	<i>Moutabea</i> sp.	h
<i>Byrsonima coccolobifolia</i> Kunth	w	<i>Myrcia cuprea</i> Kiaersk.	w
<i>Byrsonima</i> cf. <i>crassa</i> Nied.	w	<i>Myrcia fallax</i> (Rich.) DC.	w
<i>Byrsonima crassifolia</i> (L.) Kunth	w	<i>Myrcia sylvatica</i> DC.	h
<i>Byrsonima verbascifolia</i> Rich. ex A. Juss.	h	<i>Myrcia</i> sp.	w
<i>Casearia grandiflora</i> Cambess.	w	<i>Ouratea castaneaeifolia</i> Engl.	w
<i>Casearia sylvestris</i> Sw.	w	<i>Ouratea hexasperma</i> (A. St. Hil.) Benth.	w
<i>Cassytha</i> sp.	p	<i>Pagamea guianensis</i> Aubl.	h
<i>Chamaecrista desvauxii</i> (Collad.) Killip	h	<i>Palicourea rigida</i> Kunth	w
<i>Chamaecrista diphylla</i> Greene	h	<i>Paspalum carinatum</i> Fluegge	h
<i>Chamaecrista ramosa</i> (Vogel) H. S. Irwin & R. C. Barneby	h	<i>Perama hirsuta</i> Aubl.	h
<i>Chrysobalanus icaco</i> L.	w	<i>Plathymentia reticulata</i> Benth.	w
<i>Clidemia sericea</i> D. Don	h	<i>Polygala apressa</i> Benth.	h
<i>Clusia</i> sp.	w	<i>Polygala variabilis</i> Kunth	h
<i>Coccoloba</i> sp.	w	<i>Polygala thimoutou</i> Aubl.	h
<i>Cochlospermum regium</i> (Schrank) Pilg.	h	<i>Psidium</i> sp.	w
<i>Comolia lytrarioides</i> (Steud.) Naud.	h	<i>Psychotria barbiflora</i> DC.	h
<i>Connarus perottetii</i> (DC.) Planch. var. <i>angustifolium</i> Radlk.	w	<i>Psychotria</i> sp.	h
<i>Cordia multispicata</i> Cham.	h	<i>Rauvolfia pentaphylla</i> Ducke	w
<i>Coutoubea</i> sp.	h	<i>Rhabdodendron amazonicum</i> (Spr. ex. Benth.) Hub.	w
<i>Cupania diphylla</i> Vahl	w	<i>Rhynchospora barbata</i> (Vahl) Kunth	h
<i>Curatella americana</i> L.	w	<i>Roupala montana</i> Aubl.	w
<i>Curtia tenuifolia</i> (Aubl.) Knobl.	h	<i>Rourea</i> sp.	h
<i>Davilla rugosa</i> Poir.	l	<i>Salvertia convallariodora</i> A. St. Hil.	w
<i>Declieuxia fruticosa</i> (Willd. ex. R. & S.) O. Ktze.	h	<i>Sapium longifolium</i> Boj.	w
<i>Derris floribunda</i> (Benth.) Ducke	l	<i>Sauvagesia erecta</i> L.	h
<i>Desmodium barbatum</i> Benth. & Oerst.	h	<i>Scleria cyperina</i> Kunth	h
<i>Dioclea</i> sp.	l	<i>Sebastiania</i> sp.	h
<i>Diodia</i> sp.	h	<i>Simarouba amara</i> Aubl.	w
<i>Dolioscarpus</i> cf. <i>brevipedicellatus</i> Garcke	l	<i>Simarouba versicolor</i> A. St. Hil.	w
<i>Duroia duckei</i> Huber	w	<i>Sipanea pratensis</i> Aubl.	h
<i>Eriosema</i> sp.	h	<i>Siparuna guianensis</i> Aubl.	w
<i>Erythroxylum suberosum</i> A. St. Hil.	w	<i>Sisyrinchium incurvatum</i> Gardn.	h
<i>Eugenia biflora</i> DC.	h	<i>Stylosanthes guianensis</i> Sw.	h
<i>Eugenia puniceaifolia</i> DC.	h	<i>Symplocos guianensis</i> Guerke	w
<i>Galactia jussiaena</i> Kunth	h	<i>Tabebuia aurea</i> Benth. & Hook.	w
<i>Guettarda</i> sp.	w	<i>Tabebuia serratifolia</i> Rolfe A. O. F.	w
<i>Habenaria</i> sp.	h	<i>Tabernaemontana flavicans</i> (R.&S.) Miers	h
<i>Hancornia speciosa</i> Nees & Mart.	w	<i>Ternstroemia</i> cf. <i>delicatarula</i> Choisy	h
<i>Heliconia psittacorum</i> L.f.	h	<i>Tibouchina aspera</i> Aubl.	h
<i>Himatanthus articulatus</i> (Vahl) R. E. Woodson	w	<i>Tocovena formosa</i> (C. & S.) Schum.	w
<i>Hirtella ciliata</i> Mart. ex Zucc.	w	<i>Trachypogon plumosus</i> Nees	h
<i>Hirtella racemosa</i> Lam. var. <i>hexandra</i> (Willd. ex R. & S.)	w	<i>Trattinickia rhoifolia</i> Willd.	w
<i>Humiria balsamifera</i> (Aubl.) A. St. Hil.	w	<i>Turnera brasiliensis</i> Willd. ex Schult.	h
<i>Hypolytrum</i> cf. <i>pulchrum</i> (Rudge) Pffef.	h	<i>Turnera ulmifolia</i> L.	h
<i>Hypolytrum</i> sp.	h	<i>Turnera</i> sp.	h
<i>Hymenobium</i> cf. <i>petraeum</i> Ducke	w	<i>Utricularia</i> spp. (2 species)	h
<i>Ichthyothere terminalis</i> (Spreng.) Malme	h	<i>Virola sebifera</i> Vahl	w
<i>Inga marginata</i> Willd.	w	<i>Vismia cayennensis</i> (Aubl.) Choisy	h
<i>Irlbachia caerulea</i> (Aubl.) Griseb.	h	<i>Vismia guianensis</i> (Aubl.) Choisy	w
<i>Jacaranda copaia</i> (Aubl.) D. Don	w	<i>Vitex</i> sp.	w
		<i>Xylopia aromatica</i> Lam.	w
		<i>Xyris</i> sp.	h

Amapá (savanna) - 45 km N of Macapá on the road BR 156, opposite the EMBRAPA-CPAF station (00° 27'N, 51° 39'W). (Forest) - 31 km on the road BR 210, W of Porto Grande towards Serra do Navio, going into a farm 2 km along a secondary road (00° 37'N, 51° 39'W).

Alter do Chão (savanna) - 15 km from Alter do Chão on the road PA 457 towards Santarém, then 10 km along the road to Ponta de Pedra (02° 28'S, 54° 54'W). (Forest) - 12 km E of Alter do Chão, on the road PA 457 towards Santarém, then 2 km south on a road to a farm (02° 33'S, 54° 52'W).

Roraima (savanna) - on the road from Boa Vista to Igarapé Água boa de Cima, 3 km after the bridge, (02° 54'N, 60° 32'W). (Forest) - 5 km E of Boa Vista, after crossing the Branco River, 72 km S on the road BR 170 to the colonization settlement "Confiança 3" (02° 16'S, 60° 43'W).

Humaitá (savanna) - 150 East of Humaitá city, along the Tranzamazônica Highway (BR230), from there 80 km S on the road towards Bodocó (08° 30'S, 61° 38'W). (Forest) - 23 km S of Bodocó (09° 45'S, 61° 25'W).

Chapada dos Parecis (savanna) - on the road MT 170, 3 km N after crossing the road BR 364 (14° 19'S, 58° 02'W). (Forest) - 200 km N of the savanna core (described for Humaitá forest - 09° 45'S, 61° 25'W).

Redenção (savanna) - 18 km E of the city of Redenção, on the road PA 287 towards Conceição do Araguaia (08° 08'S, 49° 54'W). (Forest) - 80 km E of the city of Redenção, on the road PA 287 towards Conceição do Araguaia (08° 16'S, 49° 22'W).

Carolina (savanna) - T23, 18 km N of the city of Carolina on the road BR 230 (or 010) towards Estreito (7° 11'S, 47° 25'W). (Forest) - 10 km on the road BR 226 from Darcinópolis (state of Tocantins) towards Estreito, then 30 km on a road towards the Mumbuca river (47° 44'W, 6° 31'S).

Appendix 5.2. Soil organic matter $\delta^{13}\text{C}$ values (‰) for all sites.

Depth (m)	Amapá		Alter do Chão		Roraima		SE Humaitá	
	Forest	Savanna	Forest	Savanna	Forest	Savanna	Forest	Savanna
0.0 - 0.05	-28.82	-16.05	-29.56	-24.58	-28.35	-20.60	-28.58	-18.10
0.1 - 0.2	-27.67	-14.34	-26.7	-21.7	-27.57	-19.73	-27.77	-16.58
0.5 - 0.6	-25.69	-13.91	-26.69	-21.71	-21.56	-14.44	-25.91	-15.00
1.0 - 1.2	-25.75	-14.99	-26.52	-22.17	-24.29	-16.10	-23.98	-21.95
1.4 - 1.6	-25.97	-15.00	-26.39	-23.3	-24.8	-18.90	-23.64	-19.45
1.8 - 2.0	-25.64	-16.59	-26.19	-23.26		-20.04	-23.72	-22.88
2.2 - 2.4	-25.13	-16.20	-26.74	-23.28	-25.73	-20.89	-23.43	-23.58
2.6 - 2.8	-25.55	-18.64	-26.37	-23.96	-26.33	-21.42	-23.67	-23.42
3.0 - 3.2	-26.75	-21.16	-25.62	-23.17		-21.49	-24.23	-23.24
3.4 - 3.6	-27.06	-22.56	-27.1	-24.2	-27.31	-23.37	-24.64	-23.72
3.8 - 4.0		-22.83	-27.07	-24.37	-26.2	-23.65	-24.74	-24.41
4.4 - 4.6						-26.65		

Depth (m)	Chapada dos Parecís		Redenção		Carolina	
	Forest	Savanna	Forest	Savanna	Forest	Savanna
0.0 - 0.05	-28.58	-18.20	-28.83	-22.01	-29.37	-24.89
0.1 - 0.2	-27.77	-17.63	-26.58	-24.02	-28.07	-19.74
0.5 - 0.6	-25.91	-18.69	-25.05	-21.63	-27.60	-18.86
1.0 - 1.2	-23.98	-19.73	-24.71	-24.53	-22.47	-20.72
1.4 - 1.6	-23.64	-16.87		-18.59	-23.35	-21.83
1.8 - 2.0	-23.72	-20.90		-19.99	-23.27	-23.27
2.2 - 2.4	-23.43	-21.14		-20.84	-24.35	-24.09
2.6 - 2.8	-23.67	-19.35		-21.65	-23.50	-25.30
3.0 - 3.2	-24.23	-17.98		-21.9	-24.58	-23.90
3.4 - 3.6	-24.64	-19.02		-21.48	-23.91	-24.90
3.8 - 4.0	-24.74	-19.04		22.99	-24.48	-23.97
4.4 - 4.6						