OBSERVATIONS ON THE VEGETATION OF NORTHEASTERN MATO GROSSO, BRAZIL. IV.* AN ANALYSIS OF THE CERRADO-AMAZONIAN FOREST ECOTONE

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A study was made of the transition between the cerrado and Amazonian forest biomes on the Serra do Roncador in the northeast of Mato Grosso State. Brazil. The transition was sampled by recording the species and circumference at breast height (cbh) of all woody species ≥ 15 cm cbh on five 20 \times 10 m plots in each of the following four communities: ecotonal vegetation (Cerradão areas 1 and 2), and forest (Forest areas 1 and 2); while in the Cerrado *sensu stricto* a more rapid method had to be used because of time constraints. A total of 138 species was recorded and the results were analysed using Sørensen and Morisita Indices, TWINSPAN and DCA. In addition, comparisons were made with data from studies undertaken in 1968 in the same area by the Xavantina-Cachimbo Expedition. No species was common to all communities sampled but a seral succession of important species occurs along the transition. The Sørensen and Morisita Indices demonstrate this, with the Cerrado s.s. and Forest 2 at the two extremes showing no species in common (zero similarity) and Cerradão 1 and 2 giving the very high figures of Sørensen 0.64 and Morisita 0.84. The ecotonal cerradão is a very characteristic Dystrophic facies cerradão with Hirtella glandulosa, Emmotum nitens, Sclerolobium paniculatum and Vochysia haenkeana as its typical indicator species. The ecotone studied in the present work represents the comparatively abrupt transition from cerrado to the peripheral form of Amazonian forest (dry forest, mata seca) on flat terrain with a uniform very dystrophic soil. Other workers have suggested that this type of transition may be restricted to the headwaters of the Xingu basin, but one of the present authors has seen similar vegetation at localities in Maranhão, Rondônia, and on the Mato Grosso-Rondônia border. Comparison of the present vegetation with the survey made in 1968 shows that in this area the advancing face of the Amazonian forest has extended about 7 km southwards into the cerrado. However, in the majority of places this process has been obscured by forest clearing for agriculture. The study draws attention to the urgent need for the establishment of conservation areas in this extremely threatened and very little studied ecotone.

Keywords. Amazonian forest expansion, conservation, endangered vegetation, transition, TWINSPAN classification.

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PREFACE

The Royal Society/Royal Geographical Society UK–Brazilian Xavantina-Cachimbo Expedition worked at the invitation of the Brazilian Government from 1967 to 1969 in a then virtually uninhabited area of northeast Mato Grosso. Contacts originally established at that time between British and Brazilian scientists have developed and led to long-term collaboration, particularly in the fields of botany and ecology. The present communication reports a detailed survey of an area of the Cerrado–Amazonian forest transition zone by staff of the Nova Xavantina campus of the State University of Mato Grosso (UNEMAT) and compares the results with data obtained by the Xavantina-Cachimbo Expedition in exactly the same area in 1968. It seems particularly appropriate that this work should continue the publication series of the original expedition.

INTRODUCTION

The line of contact between the Amazonian forest and cerrado biomes is immense, extending for some 4500 km. Despite this, there is a remarkable paucity of studies on the transition zone. Most of the existing data are reported in Ratter (1992) who gives a summary of observations in several parts of Brazil, while Ackerly *et al.* (1989) carried out a survey in some 60 sites covering a mosaic of transitional vegetation types over a large part of Mato Grosso State.

Intensive studies of the vegetation transition were made by the UK-Brazilian Xavantina-Cachimbo Expedition (1967–69) in the area around 12°49'S, 51°46'W in a then virgin region of the Serra do Roncador, Mato Grosso State (Ratter, 1971; Ratter et al., 1973, 1978; Eiten, 1975), and were accompanied by a detailed soil survey (Askew et al., 1970a, 1970b, 1971). The observations on vegetation led to the conclusion that the situation was dynamic, with Amazonian forest expanding rapidly into cerrado through a seral community, termed *Hirtella glandulosa*[†] cerradão, after one of its most important tree species[‡] (Ratter et al., 1973, 1978). This deduction of forest expansion accords well with data from Quaternary pollen records of other southern Amazonian sites obtained since the original fieldwork was carried out in 1968. For instance, Mayle et al. (2000) have shown that the humid evergreen rainforests of eastern Bolivia have been expanding southward over the past 3000 years, and that their present-day limit represents the southernmost extent of Amazonian rainforest for at least the past 50,000 years. While Behling (2002) working in a transition zone at Lagoa de Confusão in Tocantins State at 10°38'S, 49°43'W, some 450 km northeast of our area on the Serra do Roncador, also demonstrated expansion of Amazonian rainforest since the mid-Holocene.

[†] Authorities for all species are given in Table 2.

[‡] Since the most important indicator species varied in other localities, it was termed 'cerradão do tipo distrófico' or 'dystrophic facies cerradão' in later publications (Ratter *et al.*, 1977; Furley & Ratter, 1988). However, we are using the original terminology in the present work.

The object of the present investigation was to resurvey the original transition area studied by the Xavantina-Cachimbo Expedition, which miraculously has survived the past 36 years more or less intact, and now stands as an island of natural vegetation in an ocean of pasture and soya plantations. The area was identified as having exceptional conservation importance by specialists from a range of disciplines at the Workshop *Ações Prioritárias para a Conservação do Cerrado e Pantanal* held in Brasília in 1998 (Cavalcanti, 1999). It was decided, therefore, to make an up-todate and more detailed inventory, using more exacting techniques of analysis than in the original work, hopefully as a first step towards establishment of a reserve.

MATERIALS AND METHODS

Area of study

The area studied (Fig. 1) lies in the northeast region of the State of Mato Grosso within the municipalities (administrative districts) of Ribeirão Cascalheira and Canarana, and is classified on the Mapa de Vegetação do Brasil (IBGE, 1993) as an area of ecological tension in the contact between savanna (cerrado) and seasonal forest (*floresta estacional*). Five localities in three vegetation types were selected to sample the transition from the cerrado to the Amazonian forest biome (Fig. 1). Unfortunately, since the area of cerrado sensu stricto (s.s.) closest to the ecotonal vegetation has been destroyed for agriculture, a similar area had to be chosen further afield. This was located at 13°37'S, 51°56'W, approximately 90 km south of the other sites, in the large Xavante Indian reserve of Pimentel Barbosa in the Municipality of Canarana. However, a good species list is also available for the original cerrado s.s. lying at the end of the transition (Ratter *et al.*, 1973). This was situated very close to the base camp of the Xavantina-Cachimbo Expedition (see Fig. 1) and was surveyed in 1968. Since it represented the now extinct cerrado s.s. marginal to the vegetation transition it has been included in the comparisons using the Sørensen Index given in Table 3, thus providing a complete suite of comparisons across the ecotone (albeit with one nearly 40 years old). The other study sites are all in the Municipality of Ribeirão Cascalheira, close to the BR-158 highway, and lie within the 20 \times 20 km intensive study square of the Xavantina-Cachimbo Expedition (Ratter et al., 1973). Ecotonal vegetation was sampled in two localities, Cerradão 1 (12°53'S, 51°49'W) and Cerradão 2 (12°50'S, 51°47'W), both lying in the vegetation type designated as *Hirtella* glandulosa cerradão by Ratter (1971) and Ratter et al. (1973). The Amazonian forest sites were Forest 1 ($12^{\circ}47'$ S, $51^{\circ}47'$ W) and Forest 2 ($12^{\circ}45'$ S, $51^{\circ}50'$ W) which lie in dryforest (locally known as *mata seca*, a type of evergreen seasonal forest representing the periphery of the Amazonian forest, and described by Ratter et al. (1973, 1978), Pires (1974), and Pires & Prance (1985)). Cerradão 1, lying further to the south, was of lower structure and less dense than Cerradão 2, while Forest 1 was lower and had more obvious cerradão influence than the more northern Forest 2. The distance between the



FIG. 1. Map to show location of study areas. The square in the centre and as an inset is the 20×20 km intensive study area of the Xavantina-Cachimbo Expedition (XCE), 1967–69. The numbered ringed dots are the study sites of the XCE and its continuation programme: 1, Morro de Fumaça, Torixoreu; 2, Vale de Sonhos; 3, Nova Xavantina; 4, base camp of XCE; 5, Rio Suiá-Missu area; 6, Reserva do Araguaia. Codes: Ce BC, Cerrado *s.s.* (Base Camp); Ce PB, Cerrado *s.s.* (Pimentel Barbosa); Ca 1 & 2, Cerradão 1 & 2; F 1 & 2, Forest 1 & 2.

most southern of these sites (Cerradão 1) and the most northern (Forest 2) is approximately 15 km.

The climate of the region is of type Aw, according to Köppen's classification (Camargo, 1971), and Ratter *et al.* (1973) give the annual rainfall for 1968, the only year for which figures are available, as 1372 mm and mean annual temperature as 24.9°C.

| | pH in H ₂ O | Ca | Mg (mEq/100 g so | K vil) | Extractable P (10 ⁻⁶) |
|---------------------------------|------------------------|------|---------------------|-----------|--------------------------------------|
| Cerrado s.s. | 4.8 | 0.05 | 0.19 | 0.07 | 14 |
| Hirtella glandulosa cerradão | 4.1 | 0.07 | 0.02 | 0.04 | 27 |
| Dry forest | 4.2 | 0.02 | 0.10 | 0.03 | 20 |

TABLE 1. Analytical data for surface horizons (0-10 cm) of cerrado *s.s.*, cerradão, and dry forest of the cerrado-forest ecotonal area

Modified from Ratter et al. (1973), table 4. Information from Askew et al., pers. comm.

Using the detailed soil-map made by Askew *et al.* (1970b) and basing the classification on the recent system proposed by EMBRAPA (1999), the predominant soil of the region is Red-Yellow Dystrophic Latosol with sandy clay texture (*Latossolo Vermelho-Amarelo com textura argilo-arenosa*) and to a lesser extent Quartz-Sand Dystrophic Neosol (*Neossolo Quartzarênico Distrófico*). Table 1 gives soil analytical data obtained by the Xavantina-Cachimbo Expedition for the complete transition (zones of cerrado *s.s.*, *Hirtella glandulosa* cerradão, and dry forest).

Within each of the four areas of cerradão and forest (Cerradão 1 and 2, Forest 1 and 2) five 20×10 m plots were set up in which all individuals ≥ 15 cm cbh (circumference at breast height) were measured and identified. In the area of cerrado *s.s.* five plots were also established, but because of the constraints of working in an Indian reserve time was not available to measure all individuals. Therefore, we carried out a rapid survey by recording the total number of trees of each species estimated as reaching ≥ 15 cm cbh, the qualifying size used for the other areas. This method allowed us, in a much shorter time, to derive figures for absolute and relative density approximately comparable with the other areas. Voucher herbarium collections were made, and where necessary material was sent to specialists for identification. These collections are now lodged in the Coleção Zoobotânica James Alexander Ratter, Campus Universitário de Nova Xavantina, Universidade do Estado de Mato Grosso (NX).

Data analysis

The program FITOPAC 1 (Shepherd, 1994) was used to calculate relative density, relative frequency, relative dominance, and their summation in the Importance Value Index (IVI). The Shannon Index of Species Diversity (H') and the Pielou Evenness Index (J') were calculated following Brower & Zar (1984). The Shannon Index of Cerradão 2 was compared with the two ends of the transition (Cerrado *s.s.* and Forest 2) using the Hutcheson *t*-test (method described in detail by Zar, 1999).

Comparisons between areas were made through FITOPAC 1 (Shepherd, 1994) using the Sørensen Index, based entirely on presence/absence of species, and the

Morisita Index, which also compares species density (Horn, 1966; Mueller-Dombois & Ellenberg, 1974). The areas were also analysed using (a) a divisive hierarchical classification by Two-Way Indicator Species Analysis (TWINSPAN) (Hill, 1979a), and (b) an analysis of gradients using Detrended Correspondence Analysis (DCA) (Hill, 1979b; Hill & Gauch, 1980). These TWINSPAN and DCA analyses were made using the program PC-ORD, version 3.0 (McCune & Mefford, 1997).

RESULTS AND INTERPRETATION

Table 2 gives species lists, with families, and IVIs (or in the Cerrado *s.s.*, relative densities) for all species occurring in the five areas analysed. The most important families were: (a) in the Cerrado *s.s.*, *Myrtaceae* (6 spp.), *Fabaceae* (5 spp.) and *Vochysiaceae* (5 spp.); (b) in Cerradão 1, *Vochysiaceae* (4 spp.) and *Fabaceae* (4 spp.); in Cerradão 2, *Annonaceae* (4 spp.), *Caesalpiniaceae* (4 spp.) and *Fabaceae* (3 spp.); in Forest 1, *Chrysobalanaceae* (4 spp.) and *Burseraceae* (3 spp.); and in Forest 2, *Burseraceae* (4 spp.) and *Lauraceae* (3 spp.). There was no species common to all five areas, but the families *Annonaceae*, *Chrysobalanaceae*, *Connaraceae*, *Myrtaceae* and *Sapotaceae* occurred in them all.

Absolute density was calculated as: 3470 individuals/ha in Cerrado *s.s.*, 2130 individuals/ha in Cerradão 1, 1850 individuals/ha in Cerradão 2, 1080 individuals/ha in Forest 1, and 1320 individuals/ha in Forest 2. Absolute dominance (basal area) figures were respectively 18.05, 13.31, 21.18 and 43.71 m²/ha for Cerradão 1 and 2 and Forest 1 and 2. The species with the greatest relative density in the Cerradão 1 and 2 was the small, shrubby, *Davilla elliptica*. That with the highest IVI in Cerradão 1 and 2 was *Hirtella glandulosa* (with values of 40.11 and 22.17 respectively), which also showed the highest relative densities and frequencies. In Forest 1 the highest IVI was for *Protium pilosissimum* (35.22) which also had a high relative density; in Forest 2 *Trattinickia burserifolia* had the highest IVI (36.74) as the result of the presence of a single tree 5 m in circumference at breast height (the second highest was *Minquartia guianensis* with 23.82).

Values for the Shannon Index (H') and Pielou Evenness Index (J') are given at the end of Table 2. Cerradão 2 gave the highest (H' = 3.5 nats/ind) and Forest 1 the lowest (2.97) species diversity. The greatest evenness was observed in Forest 2 (J' = 0.915) and the lowest in Cerrado *s.s.* (0.819). Comparison of the value of H' for Cerradão 2 with the value from the two extremes of the ecotone showed a statistical difference from Cerrado *s.s.* ($t_{0.05(2)447} = 2.449$, P < 0.05) to Forest 2 ($t_{0.05(2)312} = 2.148$, P < 0.05).

Table 3 shows a comparison of all areas using Sørensen and Morisita Indices. The Sørensen Index ranges from zero (Cerrado *s.s.* at Pimentel Barbosa × Forest 2) to 0.64 (Cerradão 1 × 2); the Morisita Index shows the same two extremes and varies from zero to 0.837. Since only presence/absence records are available for Cerrado *s.s.* at base camp (Ratter *et al.*, 1973), the Morisita Index could not be calculated.

| | | | Cerrado s.s. | Cerradão 1 | Cerrado s.s. Cerradão 1 Cerradão 2 | Forest 1 | Forest 2 |
|-----|--|------------------|--------------|------------|------------------------------------|----------|----------|
| | Species | Family | RD | IVI | IVI | IVI | IVI |
| 1. | Agonandra brasiliensis Miers | Opiliaceae | | 5.89 | | | |
| 5 | Amaioua guianensis Aubl. | Rubiaceae | | | | 2.91 | 18.84 |
| 3. | Anadenanthera colubrina (Vell.) Brenan | Mimosaceae | | | | | 2.28 |
| 4. | Andira cuiabensis Benth. | Fabaceae | 0.8645 | | | | |
| 5. | Annona crassiflora Mart. | Annonacea e | 0.2882 | | | | |
| 6. | Antonia ovata Pohl | Loganiaceae | | 1.57 | | | |
| 7. | Apuleia leiocarpa (Vogel) Macbr. var. | Caesalpiniaceae | | | | 9.44 | |
| | molaris (Spruce ex Benth.) Koeppen | | | | | | |
| 8. | Aspidosperma macrocarpon Mart. | A pocynace a e | 0.5764 | 1.60 | 1.70 | | |
| 9. | Aspidosperma multiflorum A.DC. | Apocynaceae | | 5.04 | 2.13 | | |
| 10. | Aspidosperma tomentosum Mart. | A pocynace a e | 0.8645 | 2.29 | 1.86 | | |
| 11. | Bowdichia virgilioides Kunth | Fabaceae | 0.5764 | | 2.13 | | |
| 12. | Brosimum sp. | Moraceae | | | | | 4.78 |
| 13. | Buchenavia tomentosa Eichl. | Combretaceae | 0.2882 | | 6.20 | | |
| 14. | Byrsonima coccolobifolia Kunth | Malpighiaceae | 2.5936 | | | | |
| 15. | Byrsonima crassa Nied. | Malpighiaceae | 4.8991 | | | | |
| 16. | Byrsonima verbascifolia (L.) Rich. ex | Malpighiaceae | 0.2882 | | | | |
| | A.Juss. | | | | | | |
| 17. | Caryocar brasiliense Cambess. | Caryocaraceae | | | 6.29 | | |
| 18. | Casearia arborea (Rich.) Urban | Flacourtiaceae | | 1.66 | 2.62 | 7.42 | |
| 19. | Chaetocarpus echinocarpus (Baill.) Ducke | Euphorbiaceae | | 17.22 | 6.37 | 13.52 | 3.19 |
| 20. | Cheiloclinium cognatum (Miers) A.C.Sm. | Hippocrateaceae | | | | | 11.42 |
| 21. | <i>Chrysobalanaceae</i> – Indet. | Chrysobalanaceae | | | | 6.54 | |
| 22. | Chrysophyllum sp. | Sapotaceae | | | | | 2.31 |
| 23. | Clusia sellowii Schltdl. | Clusiaceae | | 1.68 | | | |
| 74 | Cosseleba alarianii Lindan | Dolygongoogo | | 706 | 2 40 | 72 0 | |

TABLE 2. Importance Value Index (IVI) of species in Cerradão 1 & 2 and Forest 1 & 2; relative density (RD) figures for Cerrado 3.3. at Pimentel

| | | Cerrado s.s | : Cerradão 1 | Cerrado s.s. Cerradão 1 Cerradão 2 | Forest 1 | Forest 2 |
|--|------------------|-------------|--------------|------------------------------------|----------|----------|
| Species | Family | RD | IVI | IVI | IVI | IVI |
| Connarus perrottetti (DC.) Planch. | Connaraceae | | | 2.32 | 3.22 | 13.10 |
| Connarus suberosus Planch. | Connaraceae | 0.2882 | 1.56 | | | |
| Copaifera langsdorffii Desf. | Caesalpiniaceae | | | 4.11 | | |
| Cordia trichotoma (Vell.) Arráb. ex Steud. | Boraginaceae | | | 3.40 | | 5.23 |
| Couepia grandiflora (Mart. & Zucc.) Benth. & Hook.f. | Chrysobalanaceae | 1.4409 | | | | |
| Croton sp. | Euphorbiaceae | | | | | 2.31 |
| Curatella americana L. | Dilleniaceae | 0.2882 | | | | |
| Davilla elliptica A.StHil. | Dilleniaceae | 15.5619 | | | | |
| Dimorphandra mollis Benth. | Caesalpiniaceae | 0.5764 | | | | |
| Diospyros hispida A.DC. | Ebenaceae | 1.4409 | | | | |
| Diospyros sericea A.DC. | Ebenaceae | | | | 14.90 | |
| Dipteryx alata Vogel | Fabaceae | | | | 2.79 | |
| Duguetia marcgraviana Mart. | Annonaceae | | | | | 2.76 |
| Emmotum nitens (Benth.) Miers | Icacinaceae | 0.2882 | 15.34 | 16.58 | 9.49 | |
| Ephedranthus parviflorus S.Moore | Annonaceae | | | | 4.25 | |
| Eriotheca gracilipes (K.Schum.) A.Robyns | Bombacaceae | 0.2882 | 6.74 | 2.96 | | |
| Erythroxylum engleri O.E.Schulz | Erythroxylaceae | 0.5764 | | | | |
| Erythroxylum squamatum Sw. | Erythroxylaceae | | 2.16 | | | |
| Erythroxylum suberosum A.StHil. | Erythroxylaceae | 1.7291 | | | | |
| Erythroxylum sp. | Erythroxylaceae | | 1.66 | 1.70 | | |
| Eugenia aurata O.Berg | Myrtaceae | 0.8645 | | | | |
| Eugenia dysenterica A.DC. | Myrtaceae | 0.5764 | | | | |
| Ferdinandusa rudgeoides Benth. | Rubiaceae | | | | | 6.20 |
| <i>Guapira graciliflora</i> (Mart. ex J.A.Schmidt) Lund | Nyctaginaceae | | 6.45 | 3.65 | | |
| Guatterionsis hlenharonhvlla (Mart.) R.F.Fr. Annonaceae | Annonaceae | | 1.90 | 1.75 | 2.69 | |

330

| | | | Cerrado s.s. | Cerradão 1 | Cerrado s.s. Cerradão 1 Cerradão 2 | Forest 1 | Forest 2 |
|-----|---|------------------|--------------|------------|------------------------------------|----------|----------|
| | Species | Family | RD | IVI | IVI | IVI | IVI |
| 50. | Hancornia speciosa Gomez | Apocynaceae | 0.2882 | | | | |
| 51. | Heteropterys byrsonimifolia A.Juss. | Malpighiaceae | 0.2882 | | | | |
| 52. | Himatanthus obovatus | Apocynaceae | 0.8645 | | | | |
| | (Müll.Arg.) R.E.Woodson | | | | | | |
| 53. | Hirtella glandulosa Spreng. | Chrysobalanaceae | | 40.11 | 22.17 | 3.05 | |
| 54. | <i>Hirtella</i> sp. | Chrysobalanaceae | | | | | 4.96 |
| 55. | Hymenaea stigonocarpa Mart. ex Hayne | Caesalpiniaceae | 0.2882 | 3.82 | 1.89 | | |
| 56. | Inga heterophylla Willd. | Mimosaceae | | | 3.52 | 4.95 | 2.43 |
| 57. | Indet. | Indet. | | | | | 6.46 |
| 58. | Kielmeyera rubriflora Cambess. | Clusiaceae | 0.2882 | | | | |
| 59. | Lafoensia pacari A.StHil. | Lythraceae | 2.3055 | | | | |
| 60. | Lauraceae – Indet. | Lauraceae | | | | | 4.78 |
| 61. | Licania blackii Prance | Chrysobalanaceae | | | | 28.64 | 2.26 |
| 62. | Licania sclerophylla (Mart. ex Hook.f.) | Chrysobalanaceae | | 4.20 | | | |
| | Fritsch | | | | | | |
| 63. | Licania cf. sprucei (Hook.f.) Fritsch | Chrysobalanaceae | | | | 3.01 | |
| 64. | Luetzelburgia praecox (Harms) Harms | Fabaceae | | 2.01 | | | |
| 65. | Mabea fistulifera Benth. | Euphorbiaceae | | | | 6.65 | |
| 66. | Machaerium acutifolium Vogel | Fabaceae | 0.2882 | 3.68 | | | |
| 67. | Magonia pubescens A.StHil. | Sapindaceae | 0.5764 | | 2.22 | | |
| 68. | Maprounea guianensis Aubl. | Euphorbiaceae | | 15.23 | 13.13 | 6.69 | |
| 69. | Matayba guianensis Aubl. | Sapindaceae | | 1.84 | | | |
| 70. | Mezilaurus crassiramea (Meisn.) Taub. | Lauraceae | | 8.08 | 3.37 | | |
| 71. | Miconia pyrifolia Naud. | Melastomataceae | | | | | 5.67 |
| 72. | Miconia sellowiana Naud. | Melastomataceae | | | 1.80 | | |
| 73. | Miconia tomentosa (Rich.) D.Don | Melastomataceae | | 1.68 | | | |
| 74. | <i>Miconia</i> sp. 1 | Melastomataceae | | 4.84 | 16.75 | | |

| C anoritor | Equility | Cerrado s.s. RD | Cerradão 1 IVI | Cerrado s.s. Cerradão 1 Cerradão 2 RD IVI IVI | Forest 1 IVI | Forest 2 IVI |
|--|-----------------|--------------------|-------------------|--|-----------------|-----------------|
| appula | 1 anniy | | | | | |
| <i>Miconia</i> sp. 2 | Melastomataceae | | 1.60 | | | |
| Micropholis venulosa (Mart. & Eichler) Pierre | Sapotaceae | | | 2.01 | 9.04 | 7.81 |
| Minquartia guianensis Aubl. | Olacaceae | | | | | 23.82 |
| Mouriri apiranga Spruce ex Triana | Memecylaceae | | | | | 7.38 |
| Mouriri pusa Gard. | Memecylaceae | 1.4409 | | | | |
| Myrcia lanuginosa DC. | Myrtaceae | 7.2046 | | | | |
| Myrcia regneliana O.Berg | Myrtaceae | 10.6628 | | | | |
| Myrcia sellowiana O.Berg | Myrtaceae | 0.5763 | | 1.78 | | |
| Myrciaria floribunda O.Berg | Myrtaceae | | 2.13 | 3.48 | 8.18 | 8.05 |
| Myrtaceae - Indet. | Myrtaceae | 0.2882 | | | | |
| Nectandra cuspidata Nees | Lauraceae | | | | 4.65 | 7.08 |
| Ocotea guianensis Aubl. | Lauraceae | | | | | 13.16 |
| Ocotea sp. | Lauraceae | | 3.91 | | | |
| Ouratea castaneaefolia (DC.) Engl. | Ochnaceae | | | | | 5.95 |
| Ouratea hexasperma (A.StHil.) Baill. | Ochnaceae | | 3.14 | | | |
| Peltogyne confertiflora (Hayne) Benth. | Caesalpiniaceae | | | 6.84 | | |
| Pera glabrata (Schott.) Baill. | Euphorbiace ae | | 3.79 | | | |
| Piptocarpha rotundifolia (Less.) Baker | Asteraceae | 0.2882 | | | | |
| Plathymenia reticulata Benth. | Mimosaceae | 0.2882 | | | | |
| Plenckia populnea Reiss. | Celastraceae | 0.8645 | | | | |
| Pouteria ramiflora (Mart.) Radlk. | Sapotaceae | 1.1527 | 2.74 | | | |
| Pouteria sp. | Sapotaceae | | | | 2.69 | |
| Protium heptaphyllum (Aubl.) March. | Burseraceae | | | 13.06 | 3.85 | |
| Protium pilosissimum Engl. | Burseraceae | | 1.55 | 5.53 | 35.22 | 16.55 |
| Protium unifoliolatum Engl. | Burseraceae | | 3.32 | 4.49 | 24.67 | 2.28 |

332

| | | | Cerrado s.s. | Cerradão 1 | Cerrado s.s. Cerradão 1 Cerradão 2 | Forest 1 | Forest 2 |
|------|--|-----------------|--------------|------------|------------------------------------|----------|----------|
| | Species | Family | RD | IVI | IVI | IVI | IVI |
| 100. | Pseudobombax longiflorum (Mart. & Zucc.) A.Robvus | Bombacaceae | 0.2882 | | 1.70 | | |
| 101. | Pseudolmedia laevigata Tréc. | Moraceae | | | | | 13.47 |
| 102. | Pterodon pubescens (Benth.) Benth. | Fabaceae | 0.2882 | 11.13 | 13.08 | 21.83 | |
| 103. | Qualea grandiflora Mart. | Vochysiace ae | 4.0346 | 5.75 | | | |
| 104. | Qualea multiflora Mart. | Vochysiaceae | 4.3227 | 2.38 | 1.77 | | |
| 105. | Qualea parviflora Mart. | Vochysiaceae | 5.4755 | 1.66 | 3.60 | | |
| 106. | Quiina sp. | Quiinaceae | | | | | 2.26 |
| 107. | Roupala montana Aubl. | Proteaceae | | 11.24 | 4.13 | | |
| 108. | Rourea induta Planch. | Connaraceae | 1.4409 | | | | |
| 109. | <i>Rubiaceae</i> – Indet. | Rubiaceae | | | 1.72 | | |
| 110. | Sacoglottis guianensis Benth. | Humiriaceae | | | 10.18 | 30.47 | |
| 111. | Salacia elliptica (Mart.) G.Don | Hippocrateaceae | 1.7291 | | | | |
| 112. | Salvertia convallariaeodora A.StHil. | Vochysiace ae | 3.4582 | | | | |
| 113. | Sclerolobium aureum (Tul.) Benth. | Caesalpiniaceae | 0.2882 | | | | |
| 114. | Sclerolobium paniculatum Vogel | Caesalpiniaceae | | 25.46 | 11.80 | | |
| 115. | Simarouba amara Aubl. | Simaroubaceae | | 4.34 | 8.45 | | |
| 116. | Siparuna guianensis Aubl. | Monimiaceae | | 4.85 | 3.02 | | |
| 117. | Sloanea sinemariensis Aubl. | Elaeocarpaceae | | 1.59 | | | 8.09 |
| 118. | Strychnos pseudoguina A.StHil. | Loganiaceae | 2.0173 | | | | |
| 119. | Strychnos sp. | Loganiaceae | | | | | 6.20 |
| 120. | Syagrus comosa (Mart.) Becc. | Arecaceae | 4.3227 | | 3.53 | | |
| 121. | Syagrus flexuosa L. | Arecaceae | 5.4755 | | | | |
| 122. | Tabebuia aurea (Silva Manso) Benth. & | Bignoniaceae | 0.2882 | | | | |
| | Hook.f. ex S.Moore | | | | | | |
| 123. | Tabebuia ochracea (Cham.) Standl. | Bignoniaceae | 0.2882 | | | | |
| 124. | Tapirira guianensis Aubl. | Anacardiaceae | | 2.38 | 12.68 | 3.81 | 6.45 |

TABLE 2. (Cont'd).

THE CERRADO-AMAZONIAN FOREST ECOTONE IN BRAZIL 333

| | | | Cerrado s.s | s. Cerradão | Cerrado s.s. Cerradão 1 Cerradão 2 | Ц | Forest 2 |
|------|---|-----------------|-------------|-------------|------------------------------------|-------|----------|
| | Species | Family | RD | IVI | IVI | IVI | M |
| 25. | Tapura amazonica Poepp. & Endl. | Dichapetalaceae | | | 2.16 | | |
| 126. | Terminalia argentea Mart. & Zucc. | Combretaceae | 0.2882 | | | | |
| 127. | Tetragastris altissima (Aubl.) Swart. | Burseraceae | | | | | 11.42 |
| 28. | Trattinnickia burserifolia Mart. | Burseraceae | | | | | 36.74 |
| 29. | Trichilia micrantha Benth. | Meliaceae | | | | 4.38 | 2.26 |
| 30. | Unonopsis lindmanii R.E.Fr. | Annonaceae | | | 3.57 | | 2.98 |
| 31. | Vatairea macrocarpa (Benth.) Ducke | Fabaceae | 0.8645 | 9.13 | 5.43 | | |
| 132. | Virola sebifera Aubl. | Myristicaceae | | 7.97 | 13.54 | 3.49 | |
| 33. | Vitex polygama Cham. | Verbenaceae | | | | 3.03 | |
| 134. | Vochysia haenkeana Mart. | Vochysiaceae | | 14.35 | 10.00 | | |
| 35. | Vochysia rufa Mart. | Vochysiaceae | 2.0173 | | | | |
| 136. | Xylopia amazonica R.E.Fr. | Annonaceae | | | | | 10.59 |
| 137. | Xylopia aromatica (Lam.) Mart. | Annonaceae | | 5.72 | 12.15 | | |
| 138. | Xylopia sericea A.StHil. | Annonaceae | | 4.36 | 6.19 | 11.77 | 8.48 |
| | Total | | 100 | 300 | 300 | 300 | 300 |
| | Number of species | | 55 | 49 | 51 | 32 | 37 |
| | Number of genera | | 43 | 40 | 44 | 27 | 34 |
| | Number of families | | 27 | 30 | 33 | 21 | 22 |
| | Absolute density (individuals/ha) | | 3470 | 2130 | 1850 | 1080 | 1320 |
| | Absolute dominance (m ² /ha) | | I | 18.05 | 13.31 | 21.18 | 43.71 |
| | Shannon Index (H') | | 3.28 | 3.38 | 3.50 | 2.97 | 3.31 |
| | Pielou Evenness Index (J') | | 0.819 | 0.870 | 0.891 | 0.849 | 0.915 |



FIG. 2. (A) Classification of sites derived from the TWINSPAN analysis. Ce, Cerrado *s.s.* (Pimentel Barbosa); Ca 1 & 2, Cerradão 1 & 2; F 1 & 2, Forest 1 & 2. (B) Results of the first two DCA ordinations of the 25 ecotone plots.

However, the Sørensen Index shows a much higher similarity between this site and Cerradões 1 and 2 and Forest 1 than that shown by the Cerrado *s.s.* at Pimentel Barbosa. This is to be expected as the base camp was only a few kilometres from the present ecotone sites, whereas the site at Pimentel Barbosa is c.90 km more distant. However, despite the differences they show in degree of similarity to the ecotone, the two cerrado *s.s.* sites have a very strong floristic relationship to each other, demonstrated by a high Sørensen Index of 0.59.

The TWINSPAN classification produced two floristic groups at the first division, separating the five plots of Cerrado *s.s.* from the others (Fig. 2A). At this division *Byrsonima coccolobifolia*, *B. crassa*, *Davilla elliptica*, *Diospyros hispida*, *Lafoensia pacari* and *Myrcia lanuginosa* are amongst the preferential species of the Cerrado *s.s.*, occurring in at least four of the five plots of this vegetation sampled. The Cerrado *s.s.* group is clearly a natural one, and was not further subdivided by the second division of the analysis. The remaining 20 plots were of forest and cerradão, and at the next division they were split into two groups (Fig. 2A), the first of which comprised eight plots of dry forest (from Forest 2 and 1) and one of Cerradão 2 (amongst the preferential species of this group are *Amaioua guianensis*, *Cheiloclinium cognatum*, *Connarus perrottettii*, *Minquartia guianensis*, *Pseudolmedia laevigata* and *Tetragastris altissima*), whilst the other consisted of the remaining nine plots of Cerradão 1 and 2 and three plots of Forest 1. At the next division the Forest and Cerradão plots of the latter group were separated (Fig. 2A). Amongst the



FIG. 3. Substitution of species along the cerrado–Amazonian forest ecotone. For complete species names see Table 2.

preferential species of the three plots of Forest 1 were Apuleia leiocarpa, Diospyros sericea, Licania blackii, Protium pilosissimum, P. unifoliolatum and Sacoglottis guianensis, and amongst those of Cerradão 1 and the four plots of Cerradão 2 were Hirtella glandulosa, Emmotum nitens, Pterodon pubescens, Roupala montana, Sclerolobium paniculatum and Vochysia haenkeana.

Figure 2B shows the results of the DCA ordination. The first axis (eigenvalue = 0.8677) shows a clear separation between the two ends of the ecotone (Cerrado *s.s.* and Forest 2) with Cerradão 1 and 2 and Forest 1 in intermediate positions clearly following the gradient Cerrado *s.s.* \leftrightarrow Cerradão \leftrightarrow Forest 1 \leftrightarrow Forest 2. The second axis separates less strongly (eigenvalue = 0.4091) plots of Cerrado *s.s.* and is probably related to species richness and absolute density (Fig. 2B).

The principal species of each area sampled (those with higher IVIs or, in the case of Cerrado *s.s.*, relative density) were plotted according to their occurrence along the ecotone from Cerrado *s.s.* to Forest 2 (Fig. 3). The figure demonstrates the seral change of important species along the ecotone.

TABLE 3. Sørensen and Morisita Indices for the sites studied. The data from Cerrado *s.s.* (BC = Base Camp) come from Ratter *et al.* (1973, table 6, stations 6, 7 & 8) and cover only presence/absence of species, hence the Morisita Index could not be included. Cerrado *s.s.* (BC), Base Camp; (PB), Pimentel Barbosa

| | | | | Morisita | | |
|----------|----------------------|----------------------|------------|------------|----------|----------|
| | | Cerrado s.s. (PB) | Cerradão 1 | Cerradão 2 | Forest 1 | Forest 2 |
| | Cerrado s.s. (PB) | — | 0.034 | 0.043 | 0.002 | 0.000 |
| | Cerradão 1 | 0.250 | _ | 0.837 | 0.193 | 0.068 |
| Sørensen | Cerradão 2 | 0.283 | 0.640 | _ | 0.320 | 0.144 |
| | Forest 1 | 0.046 | 0.346 | 0.458 | _ | 0.451 |
| | Forest 2 | 0.000 | 0.162 | 0.250 | 0.376 | _ |
| | Cerrado s.s. (BC) | 0.591 | 0.422 | 0.360 | 0.109 | 0.000 |

DISCUSSION

The present study and those of Ratter *et al.* (1973, 1978) in the same area are, as far as we know, the only detailed plot-based studies of the vegetation transition between the Cerrado and Amazonian forest biomes carried out in southern Amazonia. The two communities forming the ends of the transition, Cerrado *s.s.* and Forest 2, represent floristically typical Brazilian planalto cerrado and characteristic dry forest (*mata seca*), as the peripheral Amazonian evergreen forest is called in southern Amazonia. The species encountered vary in their floristic affinities from *Qualea* grandiflora, the most widespread tree species of the cerrado core area, to Amazonian species such as *Tetragastris altissima* and *Xylopia amazonica*, together with widespread forest and cerradão generalists such as *Tapirira guianensis*, *Amaioua* guianensis and *Chaetocarpus echinocarpus*.

The Sørensen and Morisita Similarity Indices (Table 3) demonstrate exactly the series expected along the ecotone, with Cerrado *s.s.* and Forest 2 at the extremes showing zero similarity, and Cerradão 1 and 2 giving the very high figures of Sørensen 0.64 and Morisita 0.84. The figures for the Shannon Index of Species Diversity (H') for Cerradão 1 and 2 are slightly higher than those for the other areas, and this follows the normal pattern in ecotones and is brought about by the edge effect.

The vegetation of Cerradão 1 and 2 is the *Hirtella glandulosa* cerradão, the ecotonal community described and discussed by Ratter (1971) and Ratter *et al.* (1973, 1978), and recognized by them, as the 'advancing front' of the Amazonian forest. This community was described from surveys carried out in 1968 as having *Hirtella glandulosa, Emmotum nitens, Vochysia haenkeana* and *Sclerolobium paniculatum* as its characteristic indicator species. It is interesting that the TWINSPAN analysis of the present study, carried out more than 30 years later,

confirmed this by selecting the same four as its preferential species, and the phytosociological studies showed *Hirtella glandulosa* to be the most important species. Oliveira-Filho & Ratter (1995, 2000) also mention *Hirtella glandulosa*, *Emmotum nitens* and *Vochysia haenkeana* as species characterizing the connection between gallery forests, cerradões and transitional rainforests of southern Amazonia and have mapped their distribution.

It would be interesting to know the extent of the occurrence of the relatively abrupt type of ecotonal transition between cerrado and Amazonian forest we have described here. Ackerly et al. (1989), who conducted a survey over a wide area of Mato Grosso in 1985, consider that it is probably rare and of restricted geographical occurrence. In general, they found a mosaic of vegetation types consisting of a varying mixture of Amazonian, planaltine and widespread taxa in the areas they sampled, rather than a progressive seral transition. However, these authors did report a transition between cerrado and forest in the region south of Sinop (11°43'S, 55°30'W) similar to ours on the Serra do Roncador and noted the presence of cerradão with Hirtella glandulosa. But they concluded on the basis of their own surveys, and the aerial photography and ground truthing of Projeto RADAMBRASIL (1980, 1981a, 1981b, 1982), that 'the narrow band of cerradão transition vegetation is apparently limited to the headwaters of the Xingu basin ... and may not be a feature of the transition in other areas'. Nevertheless, one of us (J.A.R.) has observed similar vegetation in other localities. This included a stand of cerradão in a much disturbed area near Carolina, Maranhão State (7°21'S, 47°22'W), dominated by all four indicator species, and with many Amazonian species in the remnants of the adjacent forest. While near Iquê on the Mato Grosso-Rondônia border (c.12°12'S, 59°40'W), there is a wide belt of cerradão about 10-15 m tall dominated by Sclerolobium paniculatum in the transition between cerrado and Amazonian forest (Ratter, 1992). Rather similar transitional cerradão, again dominated by Sclerolobium paniculatum, was also seen near Colorado do Oeste, Rondônia State (12°54'S, 60°22'W).

As already mentioned, the ecotone described here on the Serra do Roncador is a rather abrupt transition from cerrado to the peripheral form of Amazonian forest (dry forest, *mata seca*) on flat terrain with a uniform, very dystrophic soil (Ratter *et al.*, 1973, 1978 – and see Table 1). Ratter *et al.* (1973, 1978) suggested, on the evidence of presence of isolated giant relict cerrado trees in the dry forest and young saplings of forest trees in the cerradão, that the forest was expanding at considerable speed into the cerrado vegetation. The present study carried out 35 years later in the same locality provides further information. During this period forest has encroached on cerrado and the process would no doubt have been more rapid without the disturbances caused by human occupation. The base camp of the Xavantina-Cachimbo Expedition was situated at $12^{\circ}49'S$, $51^{\circ}46'W$ (determined by traditional survey methods and now confirmed by GPS), and in 1968 was at the transition of *Hirtella glandulosa* cerradão, representing the advancing face of the Amazonian forest, now

extends south to at least 12°53'S (the latitude of study site Cerradão 1), i.e. 4' further south than in 1968. This represents an expansion of c.7 km in about 35 years and confirms previous observations. As already mentioned, this also accords well with new studies based on Quaternary pollen records indicating recent expansion of Amazonian forest along its southern periphery (Mayle *et al.*, 2000; Behling, 2002).

Enormous destruction of both cerrado vegetation and southern peripheral Amazonian forest has occurred during the last three decades (Ratter *et al.*, 1997, 2006). In the ecotonal area it is so drastic and complete that Ackerly *et al.* (1989) emphasized that observations may soon have only a historic interest! Whitmore (1987) points out 'that in past times of drier climate transition forest became much more extensive ... yet this forest is poorly known and is today the one most rapidly disappearing at the hand of man'. It is therefore extremely important to preserve as a living laboratory this superb fragment of the ecotone miraculously surviving on the Serra do Roncador.

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