Studies of the vegetation of a white-sand black-water igapó (Rio Negro, Brazil)

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INTRODUCTION

Since Takeuchi's preliminary investigation (1962), there have not been any detailed studies dealing with the vegetation structure of central amazonian igapós. The forests studied by Black *et al.* (1950) near Rio Guamá and by Pires and Prance (1977) in the Catú Reserve (both in the vicinity of Belém), though termed igapós, are in fact white-water várzea forests. Similarly, in his paper on igapó forests along the Rio Negro and its tributaries, Takeuchi treated the mixed water várzeas of Lago Janauacá as igapós. To a great extent, this confusion is the result of inconsistent use of terminology for amazonian vegetation types subject to inundation. The correct application of terms to amazonian forest types subjected to inundation was fully discussed by Prance (1979). He suggested that the term "igapó" be restricted to forests inundated by black or clear waters. In the present study, Prance's definition of igapó will be used.

The seasonal igapós in the Amazon basin are flooded annually by the rise of water level of black water rivers. In the case of the Rio Negro, flooding is during the rainy season from December to May (Table 1 & Fig. 1); the water level does not recede until well into August, which is the middle of the dry season (Fig. 2). Although temperature is uniformly high throughout the Amazon basin, soil shows great variety and thereby plays a more important role than climate in the differentiation of vegetation types (Ducke & Black, 1953). Igapó vegetation growing on different soil types exhibits different physiognomies. Some seasonal igapós occur on white-sand podzol and are flooded annually by black water, which ranges in pH from 3.7 to 5.4 (Sioli, 1968). The investigation of amazonian podzol has revealed that it is extremely deficient in nutrients. Rich in white quartz, this soil is highly porous and therefore rapidly leached by the usual heavy tropical rain. Its acidity results in low ion-retention capacity (Klinge, 1965; Stark, 1971; Stark & Jordan, 1978). The poverty of this soil and seasonal flooding act as important edaphic factors which determine the vegetation of igapós. The purpose of this study was to investigate the effect of this environmental stress on the igapó vegetation, and especially to determine the relationship between stress and dominance.

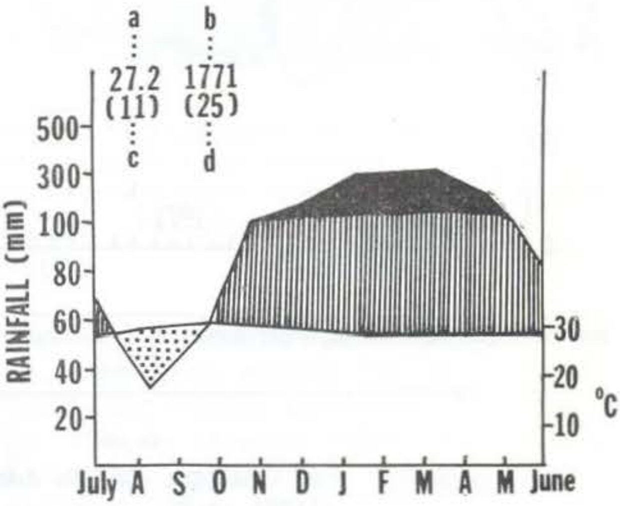

Fig. 1 — Climate diagram for Manaus (adapted from Climate-diagram map of South America. Walter et al., 1975). a: mean annual temperature (°C); b: mean annual precipitation (mm); c: number of years with records of temperature; d: number of years with records of precipitation; dotted area represents dry season; area with vertical hatching represents relatively humid season; shaded area represents monthly precipitation in excess of 100 mm (note the scale is reduced to 1:10 so that one scale interval represents 200 mm).

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The study area, a white-sand, black-water igapó, is located on the north bank of the Rio Negro near Manaus (3° 2'S, 60° 8'W), about 1 km E of the confluence of Igarapé Tarumã and the Rio Negro. The area is relatively undisturbed and has a uniform topography with a gentle slope (a vertical change of 5 m in about 50 m horizontal or 10% slope). During the rainy season, the extent of flooding determines the duration and depth of inundation along the slope. In the present study, the flood level along this slope is treated as a moisture gradient.

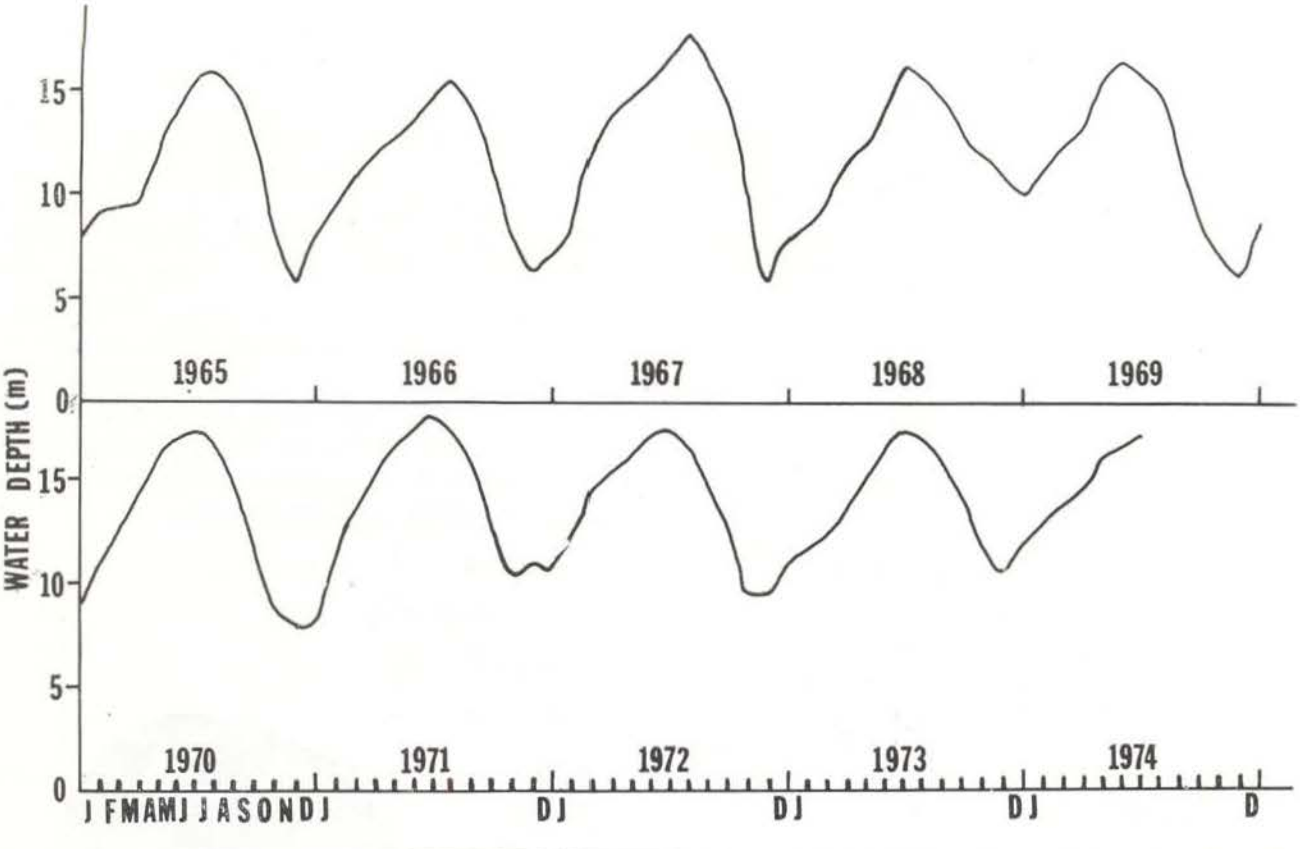

Fig. 2 — The variation of water depth of the Rio Negro at Manaus over a ten-year period (from Prance & Arias, 1975. Fig. 3).

TABLE 1. Climatic data of Manaus (Wernstedt, 1972)

BRAZIL STATION	YRS	ELEV	LAT	LONG	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	ANNUAL
Manaus	30	157	3.08 S	60.01 W	10.87	10.91	11.85	11.30	7.60	3.90	2.40	1.61	2.44	4.41	6.50	8.98	82.72
					79.5	78.6	79.0	79.3	80.2	79.7	79.2	80.2	80.4	81.0	80.8	81.0	79.7

"YR" (Year) represents the number of years of record over which the monthly and annual precipitation values have been computed.
"ELEV" (Elevation) represents the elevation in feet above mean sea level of the reporting station.
"LAT" (Latitude) and "LONG" (Longitude) represent latitudes and longitudes to the nearest degree and minute. "E" (East) or "W" (West) indicate longitudes east or west of the Greenwich Meridian.
The first (or upper) line of data given for each station represents the monthly and annual precipitation in inches and hundredths.
The second (or lower) line of data given for each station represents the average monthly and annual temperatures in degrees and tenths Fahrenheit.

MATERIALS AND METHODS

The field work was carried out in 1977 from October to December. During the dry season, the limit of the igapó can be easily recognized by the attachment of sponges (Photo 1) and flood marks on stems of trees and shrubs. A preliminary study was made to determine an adequate sample area. Figure 3 indicates that numbers of species increase sharply with the initial increase of area. However, the increase levels off after a sample of 1,800 m^2, with 68 species including vines and herbs (54 species excluding vines and herbs).

The igapó vegetation was sampled by means of 12 randomly chosen plots, each 10 x 15 meters. These plots were laid with their longer sides at a right angle to the shore. Within each plot, trees and shrubs higher than 1 m were recorded and their diameters at ground level were measured. The importance

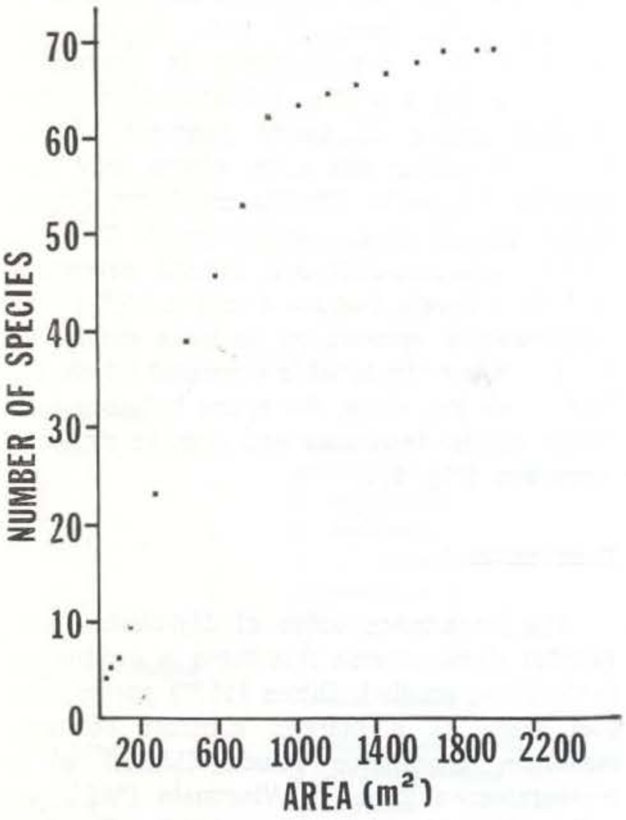

Fig. 3 — Species-area curve for 14 plots of 150 m^2 area. The graph shows the cumulative number of species in relation to the increase in numbers of plots sampled.

Photo 1 — Sponge attached on the branch of a shrub. This is used as a demarcation of inundated area. The highest point of sponge attachment is used to estimate the flood level at a given area.

value (I.V.) for each species was calculated by summing up relative frequency, relative density and relative dominance. To calculate the Shannon diversity index (H) and the evenness index (e) the following formula was used (Odum, 1971):

$$\overline{H} = -\sum P_i \log P_i$$ (P_i = importance probability for each species = $\frac{\text{importance value for each species}}{\text{total of importance values}}$)

$$e = \frac{\overline{H}}{\log_2 S}$$ (S: number of species)

To investigate the effect of moisture stress on vegetation change, five linear transects, each 50 m long and 50 m apart, were placed at a right angle to the shore. One transect was only 40 m in length because of an abrupt 1 m rise above which terra firme vegetation was present. Trees and shrubs higher than 1 m and within 50 cm on both sides of transect lines were recorded, and their diameters at ground level were measured. The data from each 10 m segment of 5 transects were pooled separately, and the importance values were determined. The flood levels at each 10 m interval of transects were obtained by the highest points of sponge attachment on stems. Vouchers of sterile plant specimens from transects and plots were deposited in INPA, while those of fertile plants were deposited in INPA (Ist set) and NY (3rd set).

RESULTS

The study site is a low, open to closed one-story forest consisting of shrubs 2 — 5 m high as the main life-form. The leading dominant in the area is *Myrciaria dubia* with an I.V. 75.78 (Table 2). The subdominant species are *Pithecellobium adiantifolium* (I. V. = 33.74), *Eugenia cachoeirensis* (I. V. = 30.96), and *E. chrysobalanoides* (I. V. = 19.41). The Shannon diversity index (H), 4.358 bits per individual, is based on samples of 12 plots which contain 54 species of trees and shrubs higher than 1 m with 1028 individuals. This value represents an estimate; the total number of species in the community studied is actually unknown. For this reason, 4.358 bits per individual is a slightly underestimated value (Pielou, 1975). The evenness value of abundance 75.73% indicates that most species have few individuals.

Transect data (Table 3) suggest that species with I.V. ≧ 50 change nearly every 10 m, an arbitrarily dividing unit for segments of transects. The same leading dominant, *Myrciaria dubia* occurs in both the 0 — 10 m and the 10 — 20 m segments, though the species composition of these two segments is very different. *Myrciaria dubia* has a higher I.V. in the 0 — 10 m segment than in the 10 — 20 m segment, where the dominance is shared by *Pithecellobium adiantifolium*. Within the 20 — 30 m segment, *Schistostemon macrophyllum* and *Eugenia chrysobalanoides* are the dominant species with I.V. ≧ 50. The high I.V. of *S. macrophyllum*, a tree, is derived largely from high relative dominance, whereas the high I. V. of *E. chrysobalanoides*, a shrub, is largely the result of high relative density. *Eugenia cachoeirensis* assumes the dominance in the 30 — 40 m segment, whereas *Pera distichophylla* and *E.* cf. *patrisii* are the dominant species in the 40 — 50 m segment.

Although species zonation is obvious, along the moisture gradient boundaries of the zones are not abrupt (Fig. 4). *Myrciaria dubia* occurs only in the segments close to the water (between 0 — 30 m), and its abundance decreases along each subsequent 10 m segment. *Eugenia cachoeirensis* and *E. chrysobalanoides* grow between the area delimited by the second and fourth segment, while *Schistostemon macrophyllum* can be found only up to the third segment. Although *E.* cf. *patrisii* grows from the third to the fifth segment, *Pera distichophylla* is limited to segments four and five. *Pithecellobium adiantifolium* grows in every segment of the transects except the first, where only four species (*M. dubia, Remijia tenuiflora, Tococa subciliata* and *Turnera acuta*) occur. The area covered by the first and second segments, with flood levels that are 4 to 6 m high in the rainy season, appears to be more open with the individual plants widely spaced (Photo 2). Further up the slope, the space between individual plants decreases and species richness increases (Fig. 5).

DISCUSSION

The importance value of *Myrciaria dubia* (75.78) demonstrates that there is dominance in the igapó studied. Dittus (1977) pointed out that there is a marked contrast between maximum importance values (M.I.V.) of a temperatezone forest in Wisconsin (M.I.V. = 228) and equatorial rainforests in Brazil and in Borneo (M.I.V. = 23.42 & 14). The M.I.V. of igapó vegetation is notably higher than those of rainforests which do not have clear-cut

TABLE 2. Data of vegetation analysis from 12 plots

Family	Species	Relative Frequency	Relative Density	Relative Dominance	Importance Value
Annonaceae	**Duguetia uniflora**	0.662	0.098	0.337	1.097
Apocynaceae	**Anacampta rupicola**	2.649	1.944	0.480	5.073
	Himatanthus attenuatus	3.974	1.453	0.900	6.327
	Apocynaceae I	0.662	0.098	0.005	0.765
	Apocynaceae II	0.662	0.098	0.005	0.765
Arecaceae	**Bactris** sp.	0.662	0.193	0.0097	0.865
	Leopoldinia pulchra	5.298	5.550	5.937	16.785
Chrysobalanaceae					
	Couepia paraensis ssp. **paraensis**	1.325	0.298	0.058	1.681
	Licania apetala	1.325	0.196	0.126	1.647
Euphorbiaceae					
	Hevea sp.	1.987	0.385	0.136	2.508
	Mabea occidentalis	0.662	0.298	0.058	1.018
	Pera distichophylla	0.662	0.098	0.337	1.097
	Euphorbiaceae I	0.662	0.098	0.005	0.765
Flacourtiaceae					
	Casearia cf. **commersoniana**	1.325	0.875	0.108	2.308
Humiriaceae	**Schistostemon macrophyllum**	1.987	0.298	1.378	3.663
Leguminosae					
Fabaceae	**Dalbergia inundata**	1.325	2.521	1.431	5.277
	Dipteryx cf. **oppositifolia**	1.325	0.193	1.724	3.242
	Sweetia nitens	1.987	0.298	0.036	2.321
Caesalpiniaceae					
	Campsiandra comosa	4.636	1.068	4.075	9.779
	Hymenaea courbaril var. **subsessilis**	0.662	0.098	0.862	1.622
	Macrolobium multijugum	0.662	0.193	0.0097	0.865
	Peltogyne venosa	0.662	0.193	0.031	0.886
Mimosaceae					
	Parkia auriculata	0.662	0.098	0.862	1.622
	Pithecellobium adiantifolium	6.623	15.181	11.931	33.735*
	P. amplissimum	0.662	0.098	0.005	0.765
	P. claviflorum	0.662	0.098	0.005	0.765
	P. cf. **glomeratum**	1.325	0.193	0.031	1.549
	Leguminosae I	0.662	0.098	0.005	0.765
	Leguminosae II	0.662	0.098	0.005	0.765
Melastomataceae					
	Tococa subciliata	1.325	0.193	0.031	1.549
Myrtaceae	**Eugenia cachoeirensis**	7.948	6.899	14.563	30.959*
	E. chrysobalanoides	5.961	8.562	4.883	19.406*
	E. inundata	0.662	0.098	0.026	0.786
	E. longiracemosa	1.987	9.140	1.228	12.355
	E. cf. **patrisii**	1.987	0.770	1.055	3.812
	E. cf. **teffensis**	0.662	0.098	0.121	0.881
	Eugenia sp.	1.987	0.683	0.331	3.001

TABLE 2 (continued)

Family	Species	Relative Frequency	Relative Density	Relative Dominance	Importance Value
	Myrcia sp.	0.662	0.098	0.026	0.786
	Myrciaria dubia	7.948	30.449	37.38	75.777**
	Myrciaria sp.	0.662	0.193	0.0097	0.865
Polygonaceae	**Coccoloba excelsa**	0.662	0.098	0.026	0.786
	Ruprechtia tenuiflora	1.987	1.261	3.186	6.434
Proteaceae	**Roupala obtusa**	0.662	0.298	3.035	3.995
Rubiaceae	**Remijia tenuiflora**	1.325	0.298	0.174	1.797
Sapotaceae	**Franchetella crassifolia**	1.325	0.193	1.483	3.001
	Manilkara amazonica	1.325	0.098	0.820	2.243
	Sapotaceae I	0.662	0.193	0.242	1.097
	Sapotaceae II	0.662	0.098	0.005	0.765
Simaroubaceae	Simaroubaceae I	0.662	0.098	0.121	0.881
	Simaroubaceae II	0.662	0.098	0.005	0.765
	Simaroubaceae III	0.662	0.098	0.005	0.765
Solanaceae	**Solanum** sp.	2.649	0.771	0.039	3.459
Sterculiaceae					
	Buettneria obliqua	0.662	0.098	0.005	0.765
Turneraceae	**Turnera acuta**	7.286	5.831	0.313	13.43

Shannon Diversity Index: $\overline{H}$ (bits per individual) = 4.258

Evenness Index: $e = \frac{\overline{H}}{\log_2 S}$ = 75.73% (S: number of species = 54)

** leading dominant

* subdominants

dominant species. However, the dominant and subdominant species in this study site, *Myrciaria dubia*, *Pithecellobium adiantifolium*, *Eugenia cachoeirensis*, and *E. chrysobalanoides*, do not necessarily characterize all white-sand igapós along the Rio Negro. The forest inventories throughout Amazonia have revealed that characteristic species of forests differ from area to area within a short distance. Thus, to define the forest by characteristic species is often misleading (Pires & Prance, 1977).

The change of species distribution occurs along transects. About 10 m from the shore, the area is overwhelmingly dominated by *Myrciaria dubia*. Beyond 10 m, *Pithecellobium adiantifolium*, *Schistostemon macrophyllum*, *Eugenia chrysobalanoides*, *E. cachoeirensis* and *Pera distichophylla* appear and increase in their relative importance sequentially. The rapid change of dominant species within a short distance in a homogeneous substrate (white-sand) points to the influence of other important environmental factors, e.g. flood level. The physiological basis of flood tolerance has been discussed by Crawford (1976). McMannon & Crawford (1971) demonstrated that in anaerobic conditions flood-intolerant species accumulate ethanol, whereas flood-tolerant species undergo a metabolic change, accumulating malate rather then ethanol. To overcome the lack of O_2, flood tolerant species use more effectively nitrate as an alternate electron acceptor (García-Noro *et al.*, 1973) Since the area has a gentle 10% slope, vegetation near the shore is water-logged longer and deeper than that in the upper area. Thus the change of species along the moisture gradient probably reflects the difference of physiological ability to flood tolerance.

The transects cover only sandy areas exposed in the dry season. There are permanent water-logged areas with sparse vegetation stretching out from the shore into the water (Photo 3). Due to limited time available for field work, they were not subjected to the transect analysis. *Eugenia inundata, Sphinctanthus striiflorus* and *Securidaca longifolia* are most frequent in the water. Takeuchi (1962) indicated that *E. inundata* is a dominant

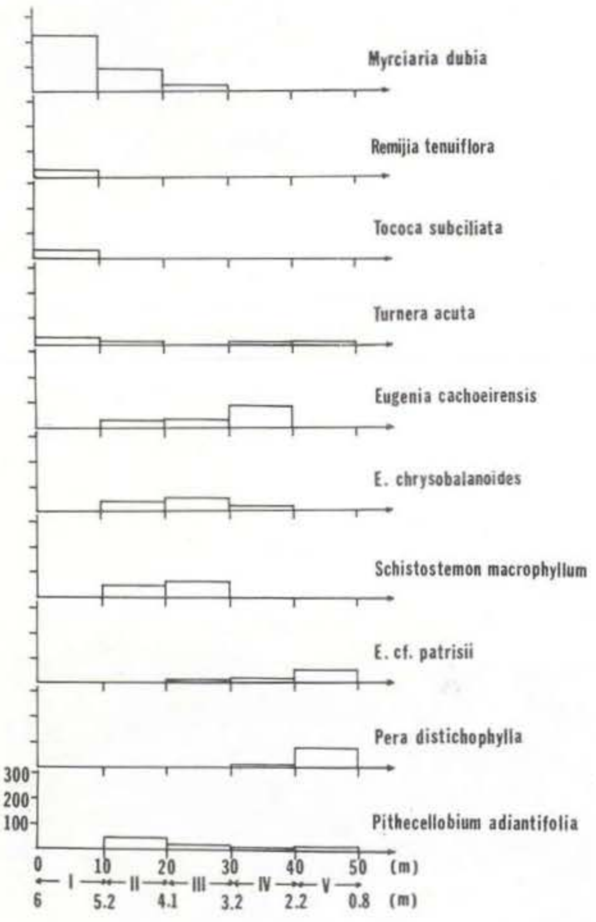

Fig. 4 — Schematic diagram of change in species distribution along the transects. Ordinate: Importance Value. Abscissa: upper Arabic Numerals represent distance from the shoreline; middle Roman Numerals represent segments of transect; lower Arabic Numerals represent estimated flood level at each 10 m transect segment. The flood level along a 10% slope is here used as a moisture gradient. See text for the explanation of change in species distribution.

of igapó forests along river shores and permanently inundated islands. However, according to the authors' observation, this species is mainly restricted to the permanent water-logged area regardless of whether the water is of black or white type. Along sandy beaches which become dry annually for a period of time, different dominant species, such as *Myrciaria dubia*, occur.

The various adaptive strategies of igapó vegetation to seasonal inundation and drought merit further investigation. The study a a woody swamp in Suriname has shown that some trees survived during high water periods by becoming partly deciduous in the crowns or by corky breathing roots (pneumatophores) which bend down sometimes during low water period and develop as prop roots. Others, felled by the flood, regenerate vegetatively with root suckers (Teunissen, 1976). In the area studied, pneumatophores are seen on the trunk of an unknown tree. The vegetation change during the rainy season remains to be investigated. Prance (1979) indicated that some igapó vegetation displays xeromorphic adaptation to seasonal dryness with sclerophyllous leaves. Since no plant with sclerophyllous leaves or other morphological adaptation was noted, the drought effect on vegetation in this igapó may not be very severe. However, the studies of sap tension of flooded trees and shrubs along the Rio Negro near Manaus showed that many plants such as *Ruprechtia* sp., *Parkia auriculata*, *Eugenia* sp., etc. reached zero turgor without wilting at the peak of hot days (Scholander & Perez, 1968). It may well be possible that this physiological property contributes to the tolerance to drought during the dry season.

The species list (Table 4) provides preliminary information about the plants of the igapó studied. Many plants have been identified on the basis of sterile material. In the dry season many seedlings and saplings are found in open canopy areas. They have been excluded from this study because of the difficulties in identifying them. However, if their identification should become possible, their abundance can serve as an indication of the reproductive potential of the area.

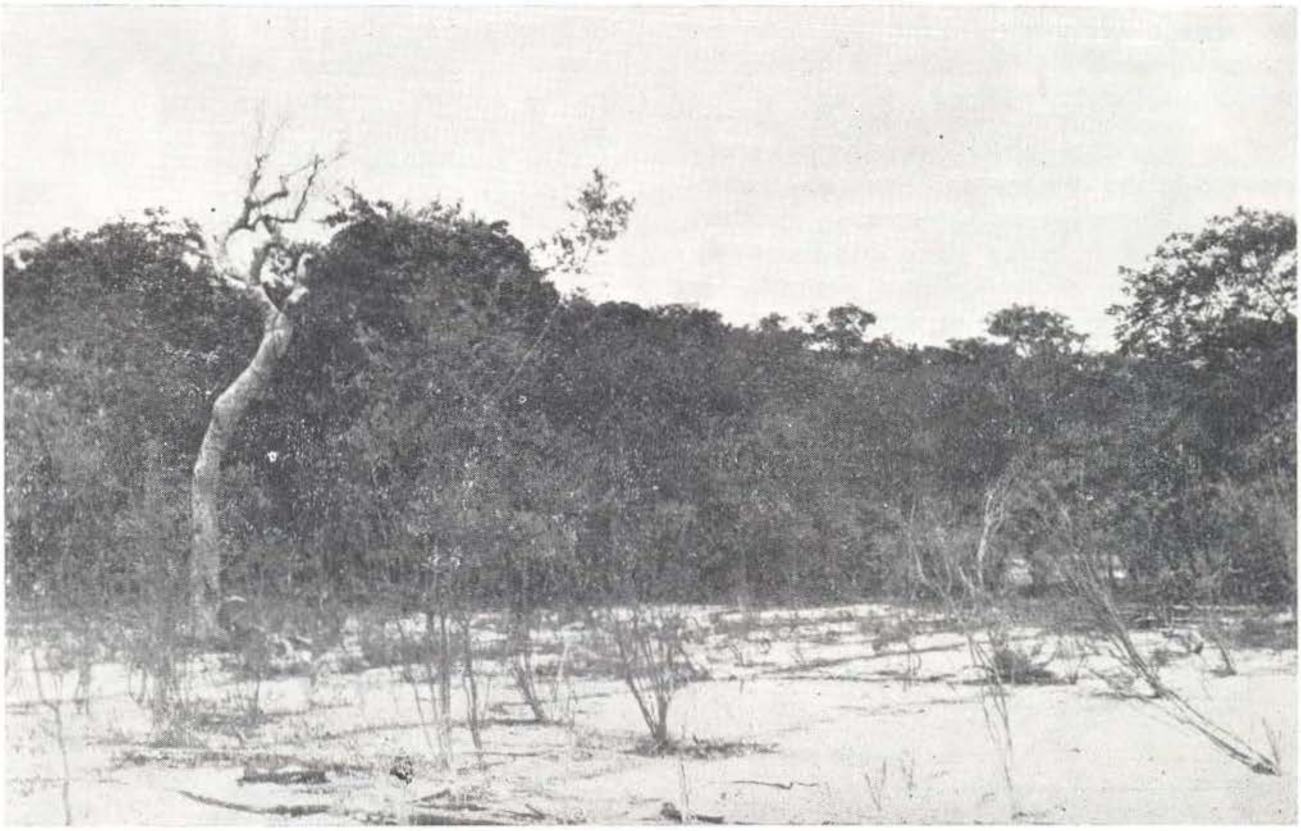

Photo 2 — Open canopy area with individual plants widely spaced and lower species diversity.

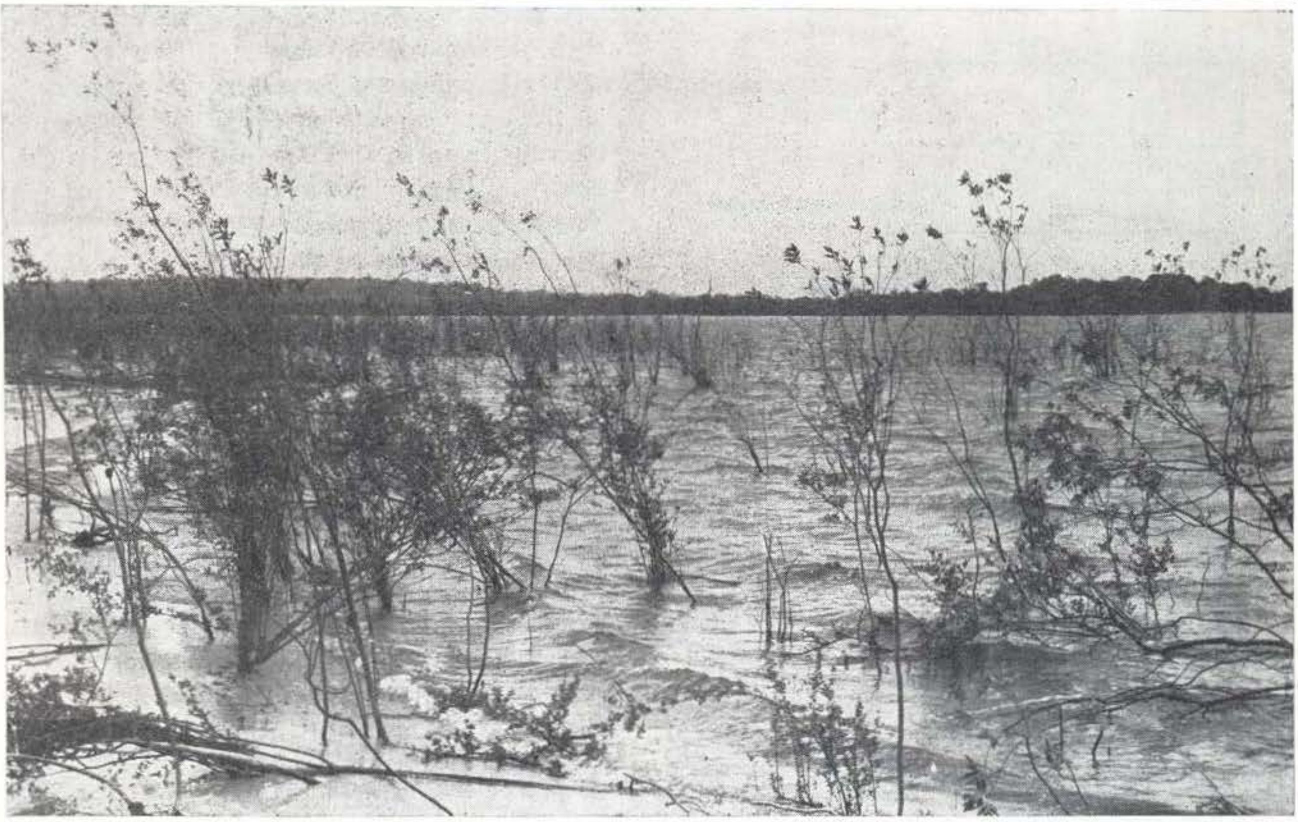

Photo 3 — Permanent water-logged area with plants growing in the water throughout the year.

TABLE 3. Data of vegetation analysis from 5 transects

Distance from the shore	Species	Relative Frequency	Relative Density	Relative Dominance	Importance Value
0-10 m	**Myrciaria dubia**	50.00	75.00	99.287	224.287*
	Remijia tenuiflora	16.67	8.333	0.238	25.241
	Tococa subciliata	16.67	8.333	0.238	25.241
	Turnera acuta	16.67	8.333	0.238	25.241
10-20 m	**Eugenia cachoeirensis**	13.333	14.286	3.235	30.854
	E. chrysobalanoides	20.000	19.048	2.391	41.439
	Lasiadenia rupestris	6.667	4.762	0.013	11.442
	Leopoldinia pulchra	6.667	4.762	0.848	12.277
	Myrciaria dubia	13.333	19.048	49.353	81.734*
	Pithecellobium adiantifolium	20.000	19.048	10.917	49.965*
	Schistostemon macrophyllum	6.667	9.524	33.217	49.408
	Solanum sp.	6.667	4.762	0.013	11.442
	Turnera acuta	6 667	4.762	0.013	11.442
20-30 m	**Anacampta rupicola**	9.091	8.571	1.302	18.964
	Casearia cf. **commersoniana**	4.545	2.857	1.341	8.743
	Eugenia cachoeirensis	9.091	8.571	16.754	34.416*
	E. chrysobalanoides	18.182	34.286	3.688	56.156*
	E. cf. **patrisii**	4.545	2.857	0.054	7.456
	E. cf. **teffensis**	4.545	2.857	0.054	7.456
	Himatanthus attenuatus	4.545	2.857	0.215	7.617
	Inga sp.	4.545	2.857	2.384	9.786
	Leopoldinia pulchra	4.545	5.714	1.469	11.728
	Myrciaria dubia	4.545	5.714	12.633	22.892
	Ormosia excelsa	4.545	2.857	0.006	7.408
	Pithecellobium adiantifolium	9.091	8.571	0.053	17.715
	P. claviflorum	4.545	2.857	0.381	7.783
	P. corymbosum	4.545	2.857	0.024	7.426
	Proteaceae I	4.545	2.857	0.054	7.456
	Schistostemon macrophyllum	4.545	2.857	59.589	66.991*
30-40 m	**Anacampta rupicola**	11.538	17.949	0.616	30.103
	Bactris sp.	3.846	2.564	22.808	29.218
	Campsiandra comosa	3.846	2.564	0.004	6.414
	Eugenia cf. **anastomosans**	3.846	2.564	0.175	6.585
	E. cachoeirensis	15.385	12.821	63.699	91.905*
	E. chrysobalanoides	7.692	12.821	3.656	24.169*
	E. cf. **patrisii**	7.692	7.692	1.002	16.386
	E. cf. **teffensis**	3.846	2.564	0.014	6.424
	Himatanthus attenuatus	3.846	2.564	0.089	6.499
	Leguminosae II	3.846	5.128	0.185	9.159
	Leopoldinia pulchra	3.846	5.128	1.825	10.799
	Macrolobium angustifolium	3.846	2.564	4.366	10.776
	Myrtaceae I	3.846	2.564	0.014	6.424
	Pera distichophylla	3.846	2.564	0.228	6.638
	Pithecellobium adiantifolium	3.846	2.564	0.089	6.499
	P. claviflorum	7.692	10.256	1.212	19.16
	Simaroubaceae II	3.846	2.564	0.004	6.414
	Turnera acuta	3.846	2.564	0.014	6.424
	Anacampta rupicola	13.34	12.50	0.078	25.918
	Byrsonima sp.	6.67	6.25	0.147	13.067

TABLE 3 (continued)

Distance from the shore	Species	Relative Frequency	Relative Density	Relative Dominance	Importance Value
40-50 m**	**Eugenia** cf. **omissa**	6.67	6.25	2.071	14.991
	E cf. **patrisii**	6.67	6.25	43.419	56.339*
	E. cf. **teffensis**	6.67	6.25	0.147	13.067
	Eugenia sp.	6.67	6.25	4.824	17.744
	Leguminosae I	6.67	6.25	0.012	12.932
	Myrcia sp.	6.67	6.25	0.075	12.995
	Pera distichophylla	13.34	18.75	48.545	80.635*
	Pithecellobium adiantifolium	6.67	6.25	0.003	12.923
	P. claviflorum	6.67	6.25	0.003	12.923
	Sweetia nitens	6.67	6.25	0.003	12.923
	Turnera acuta	6.67	6.25	0.027	12.947

** Data based only on 4 transects.
* Species discussed in the text.

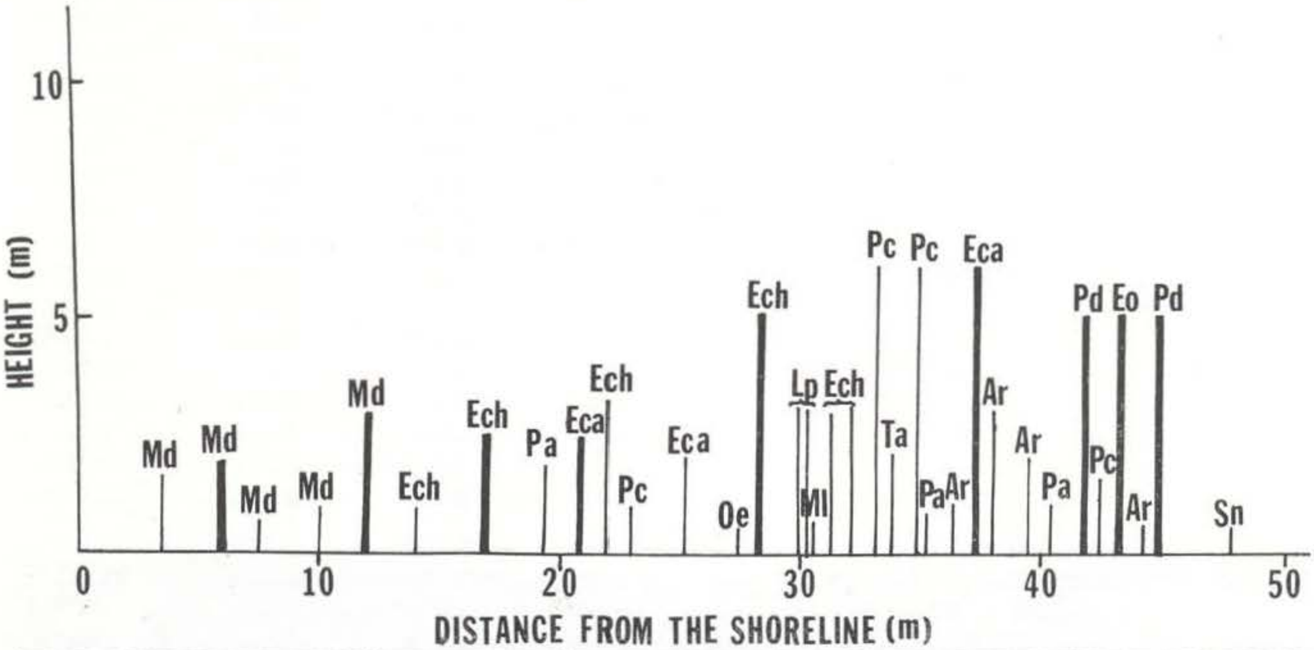

Fig. 5 — A simplified profile of a transect of 1 x 50 m². Thin line indicates basal diameter of stem < 10 cm; trick line indicates basal diameter of stem ≧ 10 cm but < 30 cm; Ar: **Anacampta rupicola;** Eca: **Eugenia cachoeirensis;** Ech: **E. chrysobalanoides;** Eo: **E.** cf. **omissa;** Lp: **Leopoldinia pulchra;** Md: **Myrciaria dubia;** Ml: **Myrtaceae I;** Oe: **Ormosia excelsa;** Pa: **Pithecellobium adiantifolium;** Pc: **P. claviforum;** Pd: **Pera distichophylla;** Sn: **Sweetia nitens;** Ta: **Turnera acuta**.

ACKNOWLEDGMENTS

The authors wish to thank Dr. Eduardo Lleras, Director of the Botany Courses of INPA (Instituto Nacional de Pesquisas da Amazônia, Manaus), for providing the facilities for field work. We are also grateful to Mr. José Guedes, José F. Ramos, Luís F. Coelho, and Osmarino P. Monteiro for assistance with the field work, to Dra. Marlene F. da Silva, Dr. Richard Cowan, Dr. Charles R. Gunn and Dr. Mary K. Arroyo for identifying fruit and sterile material. The authors are greatly indebted to Mr. Peter O'Connor for his suggestions and critical review of the manuscript, and to Dr. María Lebrón-Luteyn many valuable comments.

Field work was supported by NSF Grant INT75-19282, awarded to Dr. Ghillean T. Prance.

Resumo

A vegetação de um igapó de água preta na Amazônia é estudada, mostrando a dominância da espécie **Myrciaria dubia** (Myrtaceae) com valor de importância máxima de 75. O índice de diversidade Shannon desta vegetação foi 4.358 "bits" por indivíduo, de que 75,38% foi devido ao valor de igualdade. As espécies se mudam ao longo do gradiente de umidade que ocorre entre o rio e a mata ao longo dos transectos feitos. Ainda que muitas espécies tenham uma distribuição zonal, os limites não são muito bem delimitados. Esta distribuição zonal das espécies é provavelmente devido aos diferentes requerimentos de luz e diferentes tolerâncias à inundação das diversas espécies. Uma lista completa das 54 espécies da área em estudo é apresentada, acrescida de dados sobre a freqüência, densidade, dominância e importância de cada espécie.

SUMMARY

The vegetation analysis of a Central Amazonian igapó, a forest under severe environmental stress — poor soil and seasonal flooding, reveals the existence of the dominant species **Myrciaria dubia** with a M.I.V. 75. The Shannon diversity index of this forest is 4.358 bits per individual, of which 75.73% is attributable to the evenness value. Species distributions change along the moisture gradient. Though many species exhibit the tendency of zonal distribution, the boundaries of zones are not abrupt. The authors suggest that species distribution is the result of physiological difference to flood tolerance. Further research should be directed to the comparison of flood tolerance of the plants which occur in the following three areas: permanent waterlogged area, beach area with open canopy and upper area with closed canopy. The various adaptive strategies to seasonal inundation and drought, and the reproductive potential of the forest also merit further studies.

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(Aceito para publicação em 26/7/79)