5 Anderson, A.B., Prance, G.T., and Albuquerque, B.W.P. de, Estudos sobre a vegetação das campinas. III. A vegetação lenhosa. Acta amazon. *5* (1975) 225–246.
6 Aubréville, A., Etude écologique des principales formations forestières du Brésil. CTFT, Paris 1961.
7 Araújo, V.C. de, Fenologia de essências florestais amazônicas. Bol. INPA Pesquisas florestais *4* (1970) 1–25.
8 Boulet, R., Chauvel, A., Lucas, Y., Ranzani, G., and Scatolini, F., Transição 'latossolo-podzol' sobre a formação Barreiras na região de Manaus (AM). Comm. 19ª Reunião da Soc. Bras. de Ciência do Solo. Curitiba, Brasil 1982.
9 Braga, P.I.S., Aspectos biológicos das Orchidaceae de uma campina da Amazônia Central. Acta amazon. *7*, Suppl. (1977) 1–89.
10 Braga, P.I.S., Aspectos biológicos das Orchidaceae de uma campina da Amazônia Central. II Fitogeografia das Campinas da Amazônia brasileira. Tese de doutorado, INPA, FUA, Manaus 1982.
11 Ducke, A., Plantes nouvelles ou peu connues de la région amazonnienne. Arq. Jard. Bot. Rio de Janeiro (1922) 2–269.
12 Ducke, A., Notas sobre a fitogeografia da Amazônia brasileira. Bol. Téc. Instit. Agron. N. Belém *29* (1954) 3–62.
13 Granville, J.J. de, Recherches sur la flore et la végétation guyanaises. Thèse de Doctorat Sciences naturelles, Montpellier 1978.
14 Grenand, F., Dictionnaire wayãpi-français – Lexique français-wayãpi (Guyane française). Thèse de 3e Cycle, Paris 1979.
15 Guillaumet, J.L., and Kahn, F., Structure et dynamisme de la forêt *in* Bacia modelo: caracterização ecológica de uma bacia hidrográfica experimental na Amazônia central. Acta amazon. *12*, suppl. (1983) 61–78.
16 Kahn, F., Architecture comparée de forêts tropicales humides et dynamique de la rhizosphère. Thèse doctorat d'état, Montpellier 1983.
17 Lechthaler, R., Inventário das árvores de um hectare de terra firme da Reserva florestal Ducke, Município de Manaus. Publ. INPA: ser. Bot. *3* (1956).
18 Lisbôa, R.C.L., Estudos sobre a vegetação das campinas. V. Brioecologia. Acta amazon. *6* (1976) 171–192.
19 Luizão, F.J., Produção e decomposição da liteira em floresta de terra firme da Amazônia central. Aspectos químicos e biológicos da lixiviação e remoção dos nutrientes da liteira. Dissertação de Mestre em Biologia. INPA-FUA, Manaus 1982.
20 Oldeman, R.A.A., L'architecture de la forêt guyanaise. ORSTOM, Paris 1974.
21 Porto, M.L., Longhi, H.M., Citadini, V., Ramos, R.J., and Mariath, J.E. de A., Levantamento fitossociológico em área de 'mata-de-baixio' na Estação Experimental de Silvicultura Tropical. INPA, Manaus. Acta amazon. *6* (1976) 301–318.
22 Prance, G.T., The origin and evolution on the Amazon flora, Interciência *3* (1978) 207–222.
23 Prance, G.T., and Schubart, H.O.R., Nota preliminar sobre a origem das campinas abertas de areia branca do baixio Rio Negro. Acta amazon. *7* (1977) 567–570.
24 Prance, G.T., and Schubart, H.O.R., Notes on the vegetation of Amazonia. I. A premininary note on the origin of the open white sand campinas of the lower Rio Negro. Brittonia *30* (1978) 60–63.
25 Prance, G.T., Rodrigues, W.A., and Silva, M.F. da, Inventário florestal de um hectare de mata de terra firme km 30 da Estrada Manaus – Itacoatiara. Acta amazon. *6* (1976) 9–35.
26 Projeto Radambrasil. Programa de integração nacional – Levantamento de recursos naturais. Vegetação *8* (1975) and *11* (1976).
27 Richards, P.W., The tropical rain forest, 3rd edn. Camb. Univ. Press, Cambridge, London, New York, Melbourne, 1979.
28 Rodrigues, W.A., Inventário florestal piloto ao longo da Estrada Manaus-Itacoatiara. Estado do Amazonas. Dados preliminares. Atas do Simpósio sobre a Biota amazônica, Belém *7* (1967) 257–267.
29 Rollet, B., L'architecture des forêts denses humides sempervirentes de plaine. CTFT. Nogent-sur-Marne, France (1974) 62–64.
30 Takeuchi, M., A estrutura da vegetação na Amazônia I. A mata pluvial tropical. Bol. Museu Parense Emilio Goeldi, N.S., Bot. *6* (1960) 1–17.
31 Unesco, International classification and mapping of vegetation (Anglais, Français, Espagnol) Ecol. conserv. *6* (1973) 93.
32 Vieira da Silva, J., Introduction à la théorie écologique. Masson, Paris 1979.

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The distribution of palms as a function of local topography in Amazonian terra-firme forests

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Key words. Palms; forest architecture; topography; Amazonia.

Introduction

Ten years ago, Moore[8] lamented our ignorance of the ecology of palms, one of the most conspicuous plant families of the Amazonian forest, and he wrote: 'We need to know much more about water, soils, light and temperature relationships ...' Trying to fill in the gap, we initiated a series of ecological investigations on Amazonian palms in 1980 at the National Institute for Amazonian Research (INPA). Some of the results obtained so far will be discussed in this study.

The most general assertion that could be made until now is that palms react to vertical patterns of soil drainage. Bouillenne's[1] description of *Mauritia* formations, Moore's[9] survey of the general features of palm ecology, de Granville's[2] ecological analysis of the monocotyledons of the French Guiana, all agree that the distribution of palm species in lowland forests is related to the presence of hydromorphic or well-drained soils (or more exactly non-hydromorphic soils).

Recently Kahn and Castro[6] tracked the distribution of palms along two catenas (technical term for topographic sequence) at the Experimental Station of Tropical Sylviculture (INPA), near Manaus, in a primary forest, and came to the following conclusions (fig. 1):

- On well-drained soils, the vegetation includes arborescent palms which do not reach the forest canopy; arborescent multiple-stemmed palms do not occur; the palm diversity in the understory (under 10 m in height) is particularly high, up to 17 species per plot of 1200 m^2.
- On poorly-drained soils which are waterlogged during the rainy season, arborescent palms are abundant in the forest canopy, reaching 30 m in height, and arborescent multiple-stemmed palms are frequent; the palm diversity

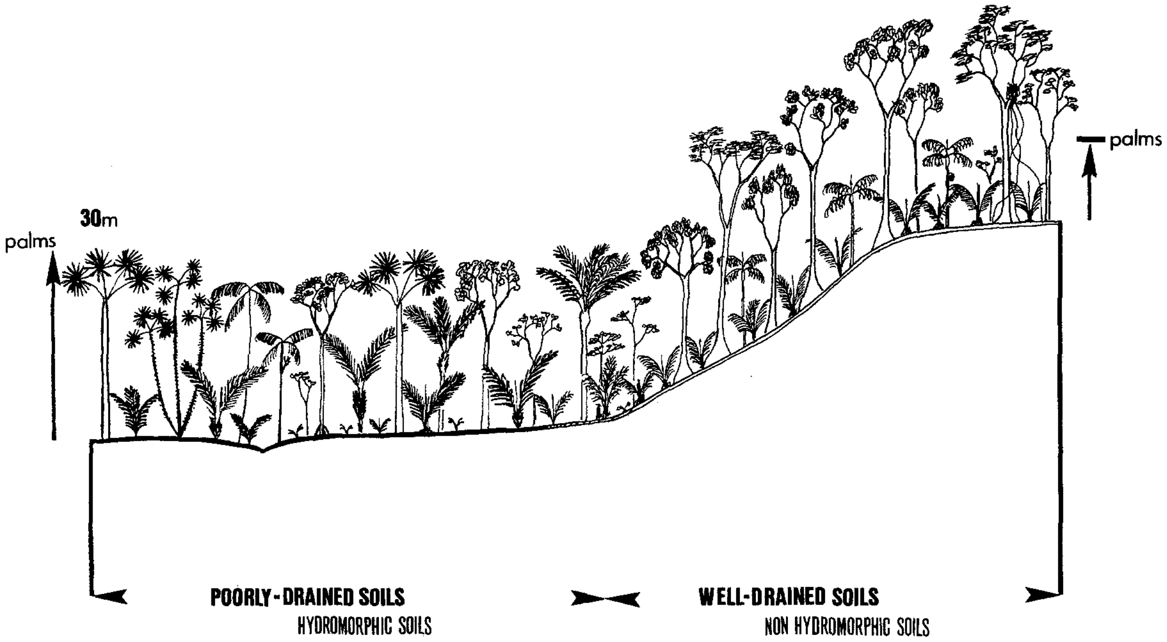

Figure 1. Distribution of palms along the catena in a primary forest of central Amazonia near Manaus[6] located at the Experimental Station of Tropical Sylviculture (INPA).

in the understory is lower, remaining below 6 species per plot.

The purpose of this study is to analyze and discuss the variation of palm populations on well-drained soils in relation to local topography and forest architecture.

Study site

The terra-firme forest studied is located in the valley of the Rio Tocantins, in the state of Pará, east of the city of Tucuruí, on the opposite side of the river (fig. 2). Floristic composition and the relative importance of families constituting the canopy is shown in table 1.

The climate belongs to the tropical humid type with 2500 mm annual rainfall and an average temperature of 26 °C. The rainy season extends from December to May and maximum precipitation occurs from January to April. Minimum rainfall and maximum temperature are registered in September. The soils are classified as 'yellow red latosols' with low fertility and a low level of saturation of bases[10].

Methods

The survey area was selected to include 8 catenas each of which crosses four different topographic sites: plateau, crest, slope and depression with a central gully, 2–3 m wide, with isolated spots of poorly-drained soil (fig. 3). Plots for detailed analysis of 30 × 40 m were established in each of the four topographic sites in each of the eight

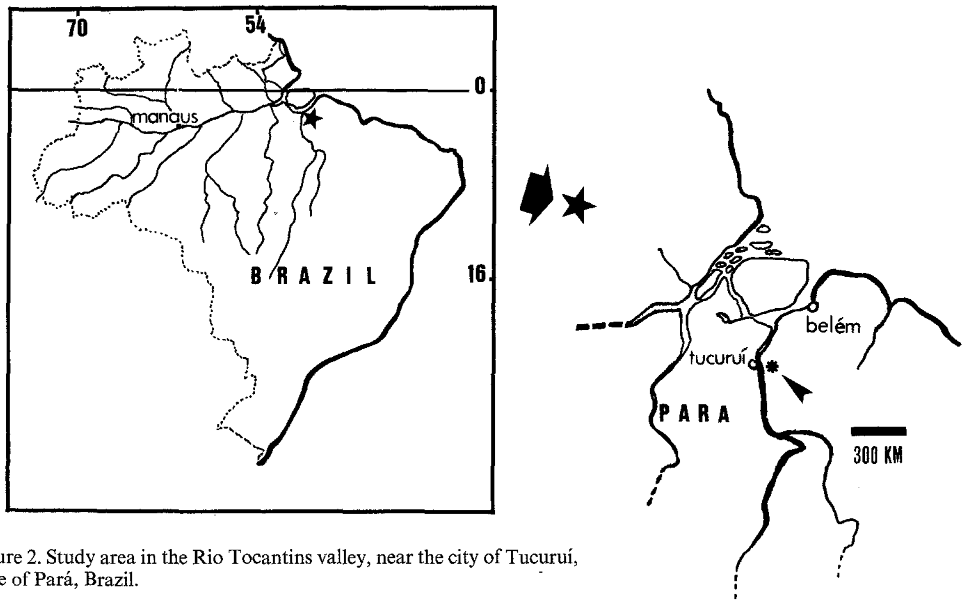

Figure 2. Study area in the Rio Tocantins valley, near the city of Tucuruí, state of Pará, Brazil.

Table 1. Floristic composition of the forest canopy and relative importance of basal area calculated from trees with ⩾ 0.4 m DBH (diameter of tree at breast height). Data from the same 32 plots in which palms were counted

Number of trees with diameter ⩾ 0.40 m	Tree families	Basal area m^2/3.84 ha
76	Leguminosae	26.7
34	Lecythidaceae	23.2
49	Chrysobalanaceae	9.7
16	Burseraceae	4.3
6	Anacardiaceae	3.6
6	Lauraceae	1.5
8	Sapotaceae	1.5
4	Meliaceae	1
1	Bignoniaceae	1
2	Myristicaceae	0.8
3	Tiliaceae	0.5
3	Flacourtiaceae	0.4
1	Melastomataceae	0.4
2	Nyctaginaceae	0.4
1	Bombacaceae	0.25
1	Humiriaceae	0.2
1	Sterculiaceae	0.15
214		75.6 m^2/3.84 ha

catenas, which resulted in a total of 3.84 ha being studied. Why were plots of 30 × 40 m chosen? This area corresponds more or less to the size of the clearings made by the falling of the largest trees (emergents and upper canopy trees). 'Any forest is a mosaic of patches at different stages of maturity' wrote Whitmore[12] (see also references 4 and 13). For this reason, the plots were not chosen at random, but in relation to these stages. Different plots at the same topographic site, however, include different successional stages. For each plot we counted all the palms, and described the vertical forest architecture with regard to the number of distinct layers of tree crowns above 15 m, which corresponded to the strata defined by Richards[11].

Knowing the topographic site and the architecture of each plot we may then attempt to separate the two factors according to their respective influence on the palm populations. The degree of declivity of each topographic site determines the lateral drainage conditions of the soil. Forest architecture determines the light intensity received by the understory plants.

Results

Palm populations and declivity. Twelve species of palms were found on the 3.84 ha surveyed. We shall only consider the seven species with high densities because only these permit quantitative comparison between different topographic sites. The results presented in table 2 are pooled for the eight similar plots for each of the four different topographic sites, which gives a total of 0.96 ha for each. For multiple-stemmed species every stem was counted as one palm. (Herbarium specimens are conserved at INPA, Manaus, with the following references: *Astrocaryum munbaca* Mart. (F.K. 533); *Bactris elegans* Barbosa Rodrigues (F.K. 524); *Bactris humilis* (Wallace) Burret (F.K. 523); *Geonoma deversa* (Poiteau) Kunth. (F.K. 592); *Oenocarpus bacaba* Mart. (F.K. 603); *Syagrus inajai* (Spruce) Beccari (F.K. 604). Adult forms of *Attalea regia* (Mart.) W. Boer were not encountered in the survey area.)

– *Oenocarpus bacaba* and *Attalea regia,* two arborescent and monocaulous palms. These species can reach up to 25 m in height in this forest (Fig. 4a, b).

– *Syagrus inajai,* a monocaulous palm of the understory, of approximately 8 m in height (fig. 4c).

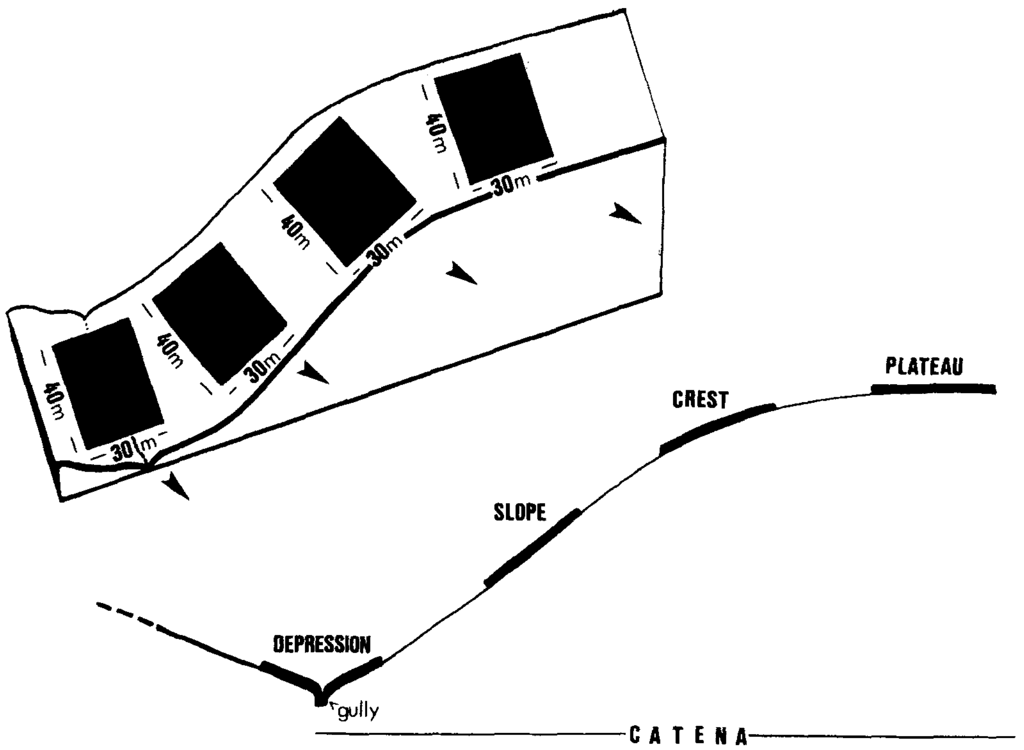

Figure 3. Distribution of the four plots along the catena in the Tucuruí forest (there is no seasonal swamp forest in the survey areas).

– *Astrocaryum munbaca, Bactris humilis, Bactris elegans, Geonoma deversa* are four multiple-stemmed palms in the understory. The first reaches 7–10 m, the other three remain below 3 m (fig. 4d, e, f, g).

Figure 5 shows cumulative densities of these seven species in the four topographic sites. With the exception of *Geonoma deversa* all species are less numerous on the slopes and in the depressions than on the plateaus and the crests. *Astrocaryum munbaca, Bactris humilis* and *Oenocarpus bacaba* appear in all plots, whereas the frequencies of the other four species change as a function of local topography (table 3).

Five species with low densities have not been considered. *Iriartea exorrhiza* Mart. occurred mainly along gullies where clearings are frequent; *Euterpe oleracea* Mart. was found in the rare and limited areas with poorly-drained soils in the depression. *Bactris* sp. *Bactris simplicifrons* Mart. and *Geonoma maxima* (Poiteau) Kunth. were encountered in a few plots only 7, 3 and 2 respectively).

Figure 4. The 7 species with high densities. A) *Oenocarpus bacaba* B) *Attalea regia*, (these two species reach 25 m in height), C) *Syagrus inajai*, adult form with pinnate leaves (8 m in height) and juvenile form with entire leaves 2 m in height), D) *Astrocaryum munbaca* (8 m in height), E) *Bactris humilis* (3 m in height), F) *Bactris elegans* (3 m in height), G) *Geonoma deversa* (3 m in height).

Table 2. Population size of the 7 species with high densities in relation to topography (0.96 ha surveyed for each topographic site)

	Plateau	Crest	Slope	Depression
Understory palms*				
Astrocaryum munbaca Mart.				
–1 m	100	101	64	57
1–3 m	173	134	71	149
⩾3 m	108	92	54	79
	381	327	189	285
Bactris elegans Barbosa Rodrigues				
–1 m	38	81	22	9
1–3 m	87	161	42	7
⩾3 m	34	31	12	1
	159	273	76	17
Bactris humilis (Wallace) Burret				
–1 m	19	20	11	6
1–3 m	51	63	19	26
⩾3 m	19	15	13	16
	89	98	43	48
Syagrus inajai (Spruce) Beccari				
–1 m	6	6	4	1
1–3 m	30	15	3	4
⩾3 m	5	5	–	1
	41	26	7	6
Geonoma deversa (Poiteau) Kunth.				
–1 m	14	39	30	72
1–3 m	34	54	56	118
⩾3 m	1	4	8	29
	49	97	94	219
Arborescent palms**				
Oenocarpus bacaba Mart.				
– 1 m	113	133	70	41
1– 6 m	74	51	19	21
6–10 m	–	4	1	–
10–20 m	2	1	–	–
	189	189	90	62
Attalea regia (Mart.) W. Boer				
–1 m	11	18	24	5
1–8 m	56	31	24	12
	67	49	48	17

* For understory species the first height class corresponds to seedlings and juveniles, the second to a transition between juveniles and adults and the third to adult palms (or axes for multiple-stemmed palms). With de Granville[2] we define the adult stage in palms by the fructifying capacity.
** For arborescent palms the first height class corresponds to seedlings, the second to acaulescent juveniles, the third to caulescent juveniles and the last to potential fructifying palms. We noticed that there are no adults of *Attalea regia*.

Table 3. Number of plots in which the 7 palm species were encountered (8 plots surveyed in each topographic site)

	Plateau	Crest	Slope	Depression
Astrocaryum munbaca Mart.	8	8	8	8
Bactris humilis (Wallace) Burret	8	8	8	8
Oenocarpus bacaba Mart.	8	8	8	8
Bactris elegans Barb. Rodr.	8	8	8	4
Syagrus inajai (Spruce) Beccari	8	6	4	3
Attalea regia (Mart.) W. Boer	7	7	6	3
Geonoma deversa (Poiteau) Kunth.	6	5	5	8

Palm populations and forest architecture. We can classify our observations of the forest into three types of canopy architecture (figs 6, 7 and 8): a) 6 plots had only a single layer of foliage above 15 m in height, b) 12 plots had two layers and c) 14 plots showed three layers which were well developed and separated.

For the following evaluation of the palm populations as a function of forest architecture we consider only the three palm species which were found in all of the 32 plots: *Astrocaryum munbaca, Bactris humilis, Oenocarpus bacaba*. These species behave in different ways.

Astrocaryum munbaca is the palm with the highest density. The number of stems is relatively lower in areas with the third type of architecture than in the two former, with only one or two canopy layers. The overall mean of the number of *A. muncaba* per plot is 37. The relative number of plots that contain more palms than this average is higher in areas with the first type of architecture with one layer (table 4). In areas with the first and second types of architecture there also tends to be a larger number of stems above 3 m in height which are potential adults.

The density of *Bactris humilis* is higher when the forest architecture is well developed. This palm forms clumps of 2–3 axes, but 82% of stems are single.

Oenocarpus bacaba, too, is more frequent in the third type of architecture. However, the population consists essentially of seedlings and juveniles. Adult individuals were found exclusively amongst pioneer trees underneath discontinuities of the upper canopy.

The variation of the populations of the other four species which do not occur in all plots cannot be interpreted in relation to forest architecture. Nevertheless, we can make the observation that *Bactris elegans* occupies relatively more plots in the type of architecture with three developed foliage layers than in the other two (14/14 as against 11/12 and 3/6 for the first and second types of architecture respectively).

Declivity and forest architecture. Plots with three canopy layers are less frequent on slopes and in depressions (table 5). This is due to a lower frequency of large trees in these topographic sites (table 6) which has been correlated in previous work[5] with the declivity of the slope and the micro-relief of the gullies.

As table 4 shows, *A. munbaca* is more frequent in the types of architecture with only one or two strata. Consequently one would expect larger populations of this species on the slopes and in the depressions. However, this is

Table 4. Palm population and forest architecture (one, two or three layers of tree foliage above 15 m in height)

	Forest architecture with One layer	 Two layers	 Three layers
Number of plots	6	12	14
Astrocaryum munbaca Mart.			
Cumulative palm number	245/0.72 ha (340/ha)	493/1.44 ha (342/ha)	444/1.68 ha (264/ha)
Number of stems above 3 m in height	80/0.72 ha (111/ha)	136/1.44 ha (94/ha)	117/1.68 ha (70/ha)
Mean number of palms per plot	41	41	31
Number of plots with palm number > mean of 32 plots (N = 37)	5/6	7/12	4/14
Bactris humilis (Wallace) Burret			
Cumulative palm number	36/0.72 ha (50/ha)	109/1.44 ha (76/ha)	134/1.68 ha (80/ha)
Oenocarpus bacaba Mart.			
Cumulative palm number	56/0.72 ha (78/ha)	172/1.44 ha (119/ha)	302/1.68 ha (178/ha)

Table 5. Forest architecture and topography[5]. Number of plots of each architecture at each topographic site

	Plateau	Crest	Slope	Depression
Number of plots with				
1 layer of tree foliage	2	0	2	3
2 layers of tree foliage	2	3	3	3
3 layers of tree foliage	4	5	3	2

not the case. On the contrary, the number of stems is lower in these two topographic sites than on the crests and on the plateaus. From this we conclude that declivity determines the magnitude of the palm populations. That is, the effect of declivity dominates over the presumed effect of forest architecture. In the depressions, attenuation of the declivity and a relative openness of the canopy have a cooperative effect on the regeneration of *Astrocaryum munbaca* as shown by a higher number of stems below 3 m in height. The relatively more frequent clearings in the depressions are due to the falling of large trees from the slopes.

In the case of *Oenocarpus bacaba* the two effects, i.e. of declivity and of forest architecture, cannot be separated because they act in the same direction: the populations of this species are less abundant in less developed types of architecture as well as on the slopes and in the depressions.

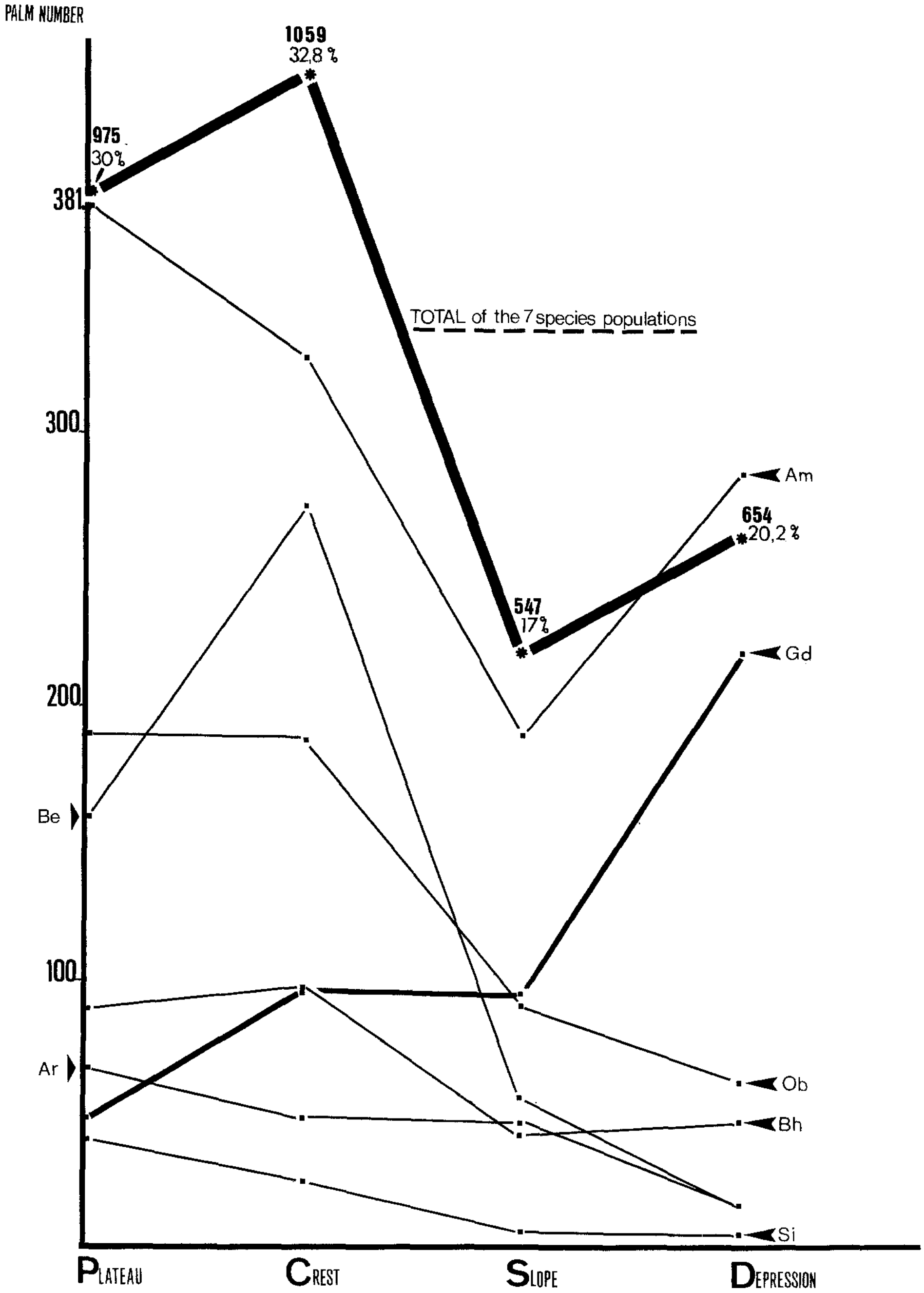

Figure 5. Palm densities and topography. Am, *Astrocaryum muncaba;* Be, *Bactris elegans;* Bh, *Bactris humilis;* Gd, *Geonoma deversa,* Ar, *Attalea regia;* Ob, *Oenocarpus bacaba;* Si, *Syagrus inajai.*

Table 6. Distribution of trees with ⩾ 0.15 m DBH and topography[5]. 0.96 ha surveyed for each topographic site

Tree diameters	Plateau	Crest	Slope	Depression	Plateau + crest (1.92 ha)	Slope + depression (1.92 ha)
0.15 ⩽ Ø < 0.4 m	187	194	204	180	381	384
0.4 ⩽ Ø < 0.8 m	53	52	42	34	105	76
0.8 ⩽ Ø < 1.2 m	9	6	4	2	15	6
1.2 ⩽ Ø < 1.6 m	2	3	–	4	5	4
Ø < 1.6 m	1	2	–	–	3	–

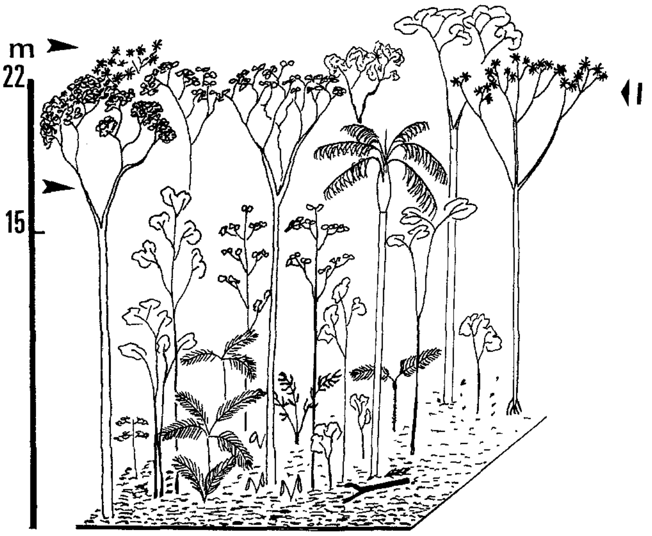

Figure 6. Forest architecture with only one layer of tree foliage above 15 m in height.

The two effects are also concordant with respect to *Bactris elegans,* but in the opposite sense; it appears with peak frequency on the crests and in all plots with three canopy layers which, in turn, are especially frequent on the crests.

Discussion

Comparing this analysis of the Tucuruí forest with a previous study in a central Amazonian forest[6] we may now try to isolate the basic factors which influence density and distribution of Amazonian palms.

In this last forest, the most frequent species show a clear peak of density on the crests (table 7) and in contrast to the situation in Tucuruí forest almost equal density on the plateaus and the slopes. Hence declivity appears to have no effect. The puzzle can only be resolved by considering topographic factors in more detail. In the central Amazonian region the transition from the plateau to slope is abrupt whereas in the Tucuruí forest this transition is smooth and gradual which allows the canopy to be well developed. Hence Central Amazonian trees on crests are more exposed to winds and falls are more frequent, and therefore the forest architecture on crests is open. The intensity of light reaching the understory is higher; firstly, more light penetrates vertically, and secondly light passes laterally through the rupture between plateau and slope. A higher light penetration favors regeneration in the majority of palm species, as has also been shown in the forests of French Guiana[2] and Mexico[7].

The Central Amazonian study emphasizes the importance of light for the palm populations. We noted in particular the higher frequency of *Oenocarpus bacaba* on the crests. In the Tucuruí forest, however, this species was less frequent under the canopy with a single stratum and, hence,

Figure 7. Forest architecture with two layers of tree foliage above 15 m in height.

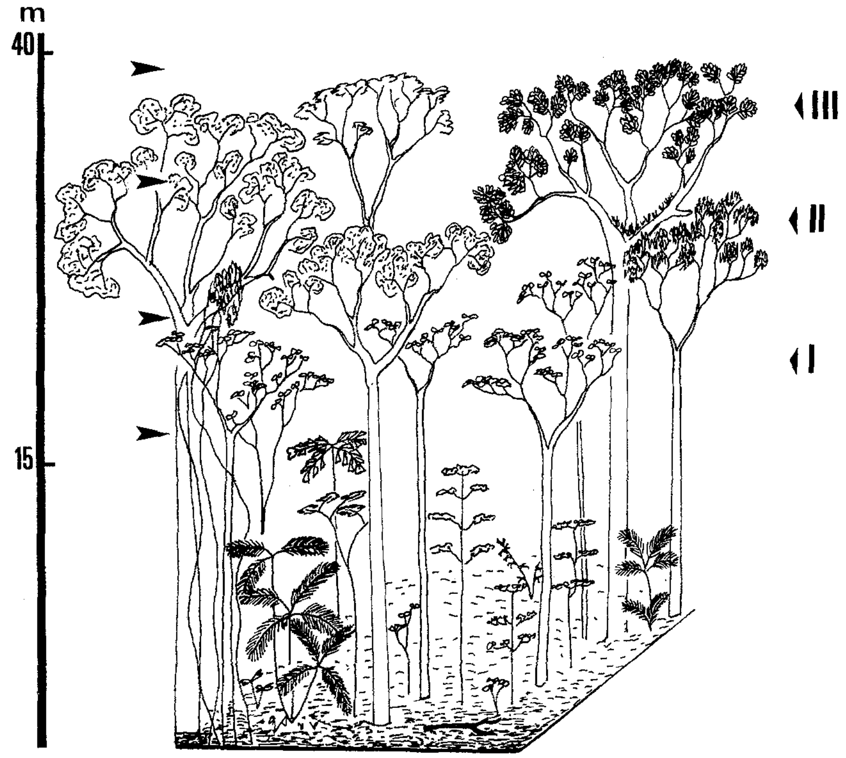

Figure 8. Forest architecture with three layers of tree foliage above 15 m in height.

with a relatively high light intensity. However, this architecture was more frequent on slopes and in depressions. The pattern in the Tucuruí forest, therefore, calls for a different interpretation, namely that effects of a stronger declivity counteract the favorable factor of light penetrating through the understory. We have shown such an effect due to declivity for *Astrocaryum munbaca*.

On the whole, the influence of light dominates in the Central Amazonian forest. However, on the slopes – where forest architecture is low, with one or two layers of tree foliages, as found on the crests[3,5] – the effects of light and declivity seem to neutralize each other as shown by the fact that the frequency of palms on the slopes is equal to that on the plateaux with their fully developed canopy (fig. 9A, table 7). In the Tucuruí forest (fig. 9B) the effect of declivity on drainage is dominant and leads to a low frequency of the majority of the palm species on the slopes and, to a certain extent, in the depressions. This effect is not compensated by the higher light intensities in the understory on these topographic sites.

Table 7. Palm distribution as a function of local topography in a Central Amazonian forest[6]. 0.24 ha surveyed for each topographic site

	Plateau	Crest	Slope
Astrocaryum sociale Barb. Rodr.	198	206	162
Astrocaryum munbaca Mart.	86	91	75
Attalea attaleoides (Barbosa Rodrigues) W. Boer	37	60	49
Syagrus inajai (Spruce) Beccari	16	76	8
Oenocarpus minor Mart.	6	30	24
Oenocarpus bacaba Mart.	211	231	205
Other species (21)	146	222	197
Total number	700	906	720

The comparison of the two studies thus supports the conclusion that the pattern of palm populations on well-

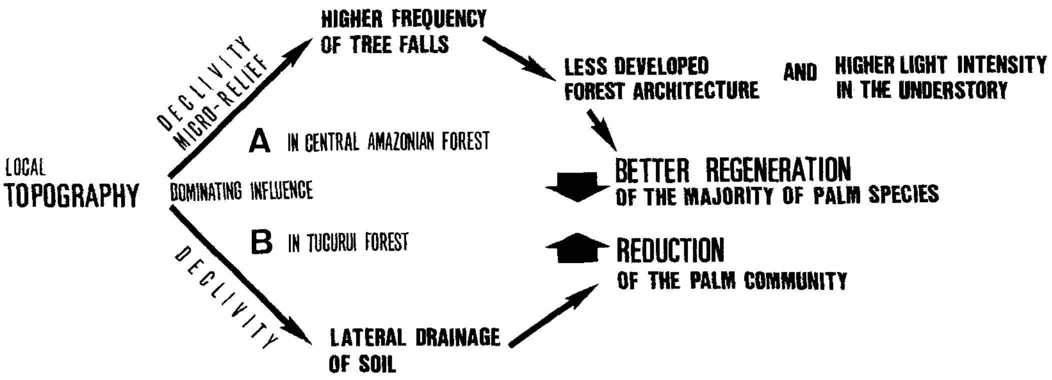

Figure 9. Effect of local topography on the distribution of palms in Amazonian terra-firme forests.

drained soil of the terra-firme forest is largely dependent on the following two factors: 1) the declivity which determines lateral drainage of the soil, 2) the forest architecture which conditions the intensity of the light that is received by understory plants. However, the two factors are mutually dependent. Local topography not only determines declivity, but also interferes with the pattern of forest architecture. It plays an immediate role in the modification of drainage and thus of water supply, and affects forest architecture by influencing the frequency of tree falls.

* Botanist at the O.R.S.T.O.M. (Institut Français de Recherche Scientifique pour le Développement en Coopération). This study was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (C.N.Pq) and the Instituto Nacional de Pesquisas da Amazônia (INPA) through the 'Projeto Tucuruí', I.N.P.A./Eletronorte. – I am indebted to Dr I. Walker for her helpful assistance with the English manuscript. I should further like to thank Dr F. Hallé and Dr A.B. Rylands for providing valuable comments upon critical reading of the manuscript.

1 Bouillenne, R., Un voyage botanique dans le Bas-Amazone. Archs Inst. bot. Univ. Liège *8* (1930) 1–185, pls 1–34.

2 Granville, J.J. de, Recherche sur la flore et la végétation guyanaises. Thèse Doctorat d'Etat, Univ. Montpellier, France, 1978.

3 Guillaumet, J.-L., and Kahn, F., Structure et dynamisme de la forêt. Acta amazon. suppl. 12, *3* (1982) 61–77.

4 Hallé, F., Oldeman, R.A.A., and Tomlinson, P.B., Tropical trees and forests. An architectural analysis. Springer Verlag, Berlin/Heidelberg/New York 1978.

5 Kahn, F., Architecture comparée de forêts tropicales humides et dynamique de la rhizosphère. Thèse Doctorat d'Etat, Univ. Montpellier, France, 1983.

6 Kahn, F., and Castro, A. de, Palm community in a forest of central Amazonia, Brazil. Biotropica *17* (1985) 210–216.

7 Martinez, M., Aspectos sinecológicos del proceso de renovación natural de una selva alta perennifolia. Tesis profisional UNAM Mexico, 1980.

8 Moore, H.E. Jr, The major groups of palms and their distribution. Gentes Herb. *11* (1973) 27–141.

9 Moore, H.E. Jr, Palms in the tropical forest ecosystems of Africa and South America, in: Tropical Forest Ecosystems of Africa and South America: a Comparative Review, pp. 63–88. Eds B.J. Meggers, E.S. Ayensu and W.D. Duckworth. Smithsonian Institution Press, Washington, D.C. 1973.

10 Ranzani, G., and Podesta, J.A. Fo., Projeto Tucuruí, Convênio INPA/Eletronorte, relatório 1982.

11 Richards, P.W., The Tropical Rain Forest. Cambridge University Press, Cambridge 1952.

12 Whitmore, T.C., Gaps in the canopy, in: Tropical Trees as Living Systems, pp. 639–655. Eds P.B. Tomlinson and M.H. Zimmermann. Cambridge University Press, Cambridge 1978.

13 Whitmore, T.C., On pattern and process in forests, in: The Plant Community as a Working Mechanism, pp. 49–59. Ed. E.I. Newman. Blackwell Sci. Publ. 1982.

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Litter production and decomposition in a terra-firme forest of Central Amazonia

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Summary. Chemical and biological aspects of litter production and decomposition were studied in three distinct areas of the Central Amazon. Litter production was measured during three years, employing the litter trap technique, with adapted conical collectors. Leaf litter decomposition was studied in experiments over five-month-periods with repetitions for the dry and wet seasons, using the nylon-mesh bag technique. The greatest litter production took place during the drier period of the year, mainly from June to October, while decomposition processes were more accentuated in the wet season: in the plateau site, one-half of the litter disappears, according to a mathematical model, in about 218 days under dry season conditions as against 32 days in the wet season. In the rainy season, weight reduction and mineral losses from decomposing leaves occurred more rapidly, owing to the intense biological activity on the material during this period. Particularly noticeable was the intense activity of termites in organic matter breakdown and mineral removal, and the extensive root penetration in the decomposing leaves, which removed some minerals but increased the amounts of others. Leaching effects were also quite noticeable in this period. During the rainy season, in the latosol sites, termites were responsible for more than 40% of the removal of decomposing leaves. While intense biological activity appears to be the major factor responsible for weight reduction and loss of many minerals, as well as for the accumulation of some other minerals (mainly zinc, iron and aluminium) in the decomposing material, leaching seems to be the major factor responsible for the loss of certain minerals such as potassium, boron and copper.

Key words. Litter; litter decomposition; nutrients cycle.

Introduction

Organic material represents a component of vital importance for the majority of the functional processes occurring in the soil of forest ecosystems[16]. The greatest contribution to the soil humus layer is litter, that is the detritus falling from the forest onto the soil surface.

Litter plays a fundamental role in the cycling of nutrients and in the transfer of energy between plants and soil[31], functioning as a fuel source for the nutrient cycles in the uppermost layers of the soil. It is particularly important in the nutrient budgets of forest ecosystems on nutrient-