Annexe au rapport d'activité 82-83 - Francis KAHN

PALM COMMUNITY IN "TERRA FIRME" FOREST

OF CENTRAL AMAZONIA, BRAZIL

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Fonds Documentaire ORSTOM
010005454

Fonds Documentaire ORSTOM
Cote : B*5454 Ex : M P25

ABSTRACT

Palm community in a "terra firme" forest of central Amazonia is presented. Distribution and abundance of the most important species is related to topography and soil. The palm community of this forest is remarkable for its size, its great diversity, and variety of biological forms.

INTRODUCTION

Palms are an abundant and characteristic component of the terra firme forests of central Amazonia. They are found in all levels of the forest, from the understory to the canopy, on all soils and topographic sites, and exhibit a variety of growth forms. CORNER's marvellous book(1966) and MOORE's authorotative works(1973-a;-b), represent cornerstones in our knowledge of the family. There have been few works,however, dealing specifically with the palm flora of Amazonia. In fact, since the numerous publications of MARTIUS (1875-1907)[1],DRUDE (1876-1908)[1],BARBOSA-RODRIGUES (1928-1956)[1],and BURRET (1928-1956)[1],only MACBRIDE's work(1960) in Peru and WESSELS-BOER's (1965) and (1971) in Suriname and Venezuela respectively,have contributed significantly to the taxonomy of amazonian palms.

Works relating to the ecology of palms are even rarer, and generally only take into consideration one species: ecology of Raphia palm swamps in Costa Rica (ANDERSON and MORI,1967);demography of Astrocaryum mexicanum (PIÑERO et al,1977;1982; PIÑERO & SARUKHÁN,1982);intraspecific competition in Socratea durissima (YEATON,1979);and autoecology of Euterpe globosa of the forests of Puerto Rico (BANNISTER,1970 ; VAN VALEN,1975). Some information of an ecological nature is given in various works concerning South American vegetation (MYERS,1933; DAVIS and RICHARDS,1934; BEARD,1955;OLDEMAN,1974) or concerning useful plants (CAVALCANTE,1977). MOORE (1973-b) regroups the taxons in terms of the main neotropical climax formations. Specifically regarding the Amazon region BOUILLENNE

1.The bibliography of these authors is recapitulated by GLASSMAN (1972).

(1930) describes the *Mauritia* formations on poorly-drained soils; OLDEMAN (1969) tackles the ecology of the *Euterpe oleracea* formations or "pinotières" of French Guiana, and GRANVILLE (1974,1977,1978) presents several studies on the biology and ecology of the palms of French Guiana.

This paper presents the palm community in a "terra firme" forest of central Amazonia and notices the distribution and abundance of the most important species in relation to topography and soils.

METHODS

The survey areas are located in the Tropical Sylviculture Experimental Station of INPA (Instituto Nacional de Pesquisas da Amazônia),60 km from Manaus,between the BR-174 (Manaus-Boa Vista highway) and the Rio Cuieiras, a tributary of the Rio Negro (2°35′-2°40′ latitude S;60°00′-60°20′ longitude W). Rain-fall is about 2,5 m per year.The rainy season extends from December to May; the dry season from June to November. The water deficit is low or nil and the potential evapotranspiration is regularly distributed throughout the year (RIBEIRO,1976).

The survey areas, 6 km apart, are selected,each to include a catena of 5 topographic sites - plateau, crest, slope, a transition zone at the base of the slope, and the seasonal flooded "igarapé" (stream) bed (Figure 1). The first 3 sites are characterised by well-drained soils with high clay content; the transition zone by poorly-drained soils with less clay and more sand, and the "igarapé" bottom by water-logged soils.

Study plots of 1200 m^2 (30 x 40 m) are established in each topographic site in both survey areas, giving a total of 10 plots and a total survey area of 1,2 ha.

All palms, seedlings, juveniles and adults are surveyed. Data are presented by topographic site listing the species encountered and giving their height-class distribution. In multiple-stemmed species, all the stems are counted. Figures from both survey areas are cumulated and therefore total number of palms are given for 2400 m^2.

RESULTS

In the 1,2 ha surveyed, 32 species of palms, in 12 genera, are encountered. The distribution of these species is strongly related to soils and three distinct "palm zones" are recognised, on: well-drained soils (plateau, crest, slope), poorly-drained soils (transition zone), and water-logged soils ("igarapé" bottom). Each of these "palm zones" is characterised by a number of typical species, but, there are also a few, less abundant species which appear to be indifferent to the nature of the soil and are common to two or three zones (Table 1).

Palms on well-drained soils (Table 2)

The understory of the forest on well-drained soil is dominated to a height of 5 m by the leaves of two acaulescent species, Astrocaryum cf javarense and Attalea attaleoides.

Numerous species of the genera Bactris and Geonoma are also found here but their frequency varies and their total number per plot is often reduced to a few individuals.

These species form clumps of 2 to 10 axes.

In the upper level of the understory, between 6-10 m, Syagrus inajai, a monoaxial palm with a stem of 4-5 m, is frequent, as are Astrocaryum munbaca and Oenocarpus minor. These latter 2 species form clumps of 2 to 4 axes. Less frequently encountered is Iriartella setigera, a small palm, 7 to 10 m in height, characterised by the production of creeping stolons.

In the forest mid-story, Oenocarpus bacaba reaches a height of 15 m. It is the dominant palm and is only fou nd below discontinuities of the upperstory canopy, indicating that it can only compete in clearings with enough light.

In the 7200 m^2 of forest on well-drained soils we surveyed, 1346 palms between 1-10 m in height were recorded, and of these 676 belong to the two acaulescent species. No palms reach the canopy in forest on well-drained soils.

Palms on poorly soils

In the forest on poorly-drained soil, transition zone between the clay soils of the slope and the water-logged soils of the "igarapé" bottom, two acaulescent palms, Attalea spectabilis and Astrocaryum acaule, dominate the understory (Table 2).They are very abundant and their leaves spread up, funnel-like, to 5 m. These two species are strictly limited to the transition zone at the base of the slope and disappear in the vicinity of the "igarapé" when the soil becomes water-logged. There, they are replaced by juveniles of Jessenia bataua. This transition zone does indeed stand out; in 2400 m^2, 343 acaulescent palms greater than 1 m in height were recorded, of these 259 are Attalea spectabilis and 74 are Astrocaryum acaule.

Also 158 young Jessenia bataua (from 1 to 6 m in height) were found.

Palms on water-logged soils

The forest on water-logged soils is almost devoid of the acaulescent palms (only 19 Attalea spectabilis) but overrun by young Jessenia bataua (472, already defined). One species of Bactris form clumps, its axes not exceeding 5 m in height; Mauritia aculeata are distributed in isolated patches.

Whereas arborescent palms are absent from the forest canopy on well-drained soils, they are an important component of the forest canopy on poorly-drained and water-logged soils: Jessenia bataua, Mauritia flexuosa (not encountered in our plots, although very common in the "igarapé" bottoms), Mauritia aculeata, Euterpe precatoria (Table 3).

Cross topography palms

Some species of the forest on well-drained soils, such as Oenocarpus minor, Iriartella setigera, Bactris simplicifrons and Geonoma sp penetrate the transition zone at the base of the slope; Euterpe precatoria, frequent on water-logged soils, is occasionally found on well-drained soils, but usually only as seedlings and juveniles that have germinated and started their growth in gaps; very few reach maturity here. Iriartea exorrhiza, an arborescent palm with typical stilt roots (BOUILLENNE, 1924; KAHN, 1977; BODLEY and BENSON, 1980), seems quite independant of the nature of the soil but requires light and is only found in openings of the forest canopy.

DISCUSSION

The palm community of the forest of central Amazonia clearly shows 3 zones according to the nature of the soil: well-drained soil of the upland forest, poorly-drained soil of transition zone, and water-logged soil of the seasonal swamp forest. The community is remarkable for its size, its great diversity, its variety of biological forms. The discussion of community size and diversity will be limited due to scarcity of comparable amazonian literature in this field.

Abundance of palms

The forest of central Amazonia are literally overrun by palms, especially in understory. KLINGE and RODRIGUES (1971) established that palms greater than 1,5 m in 2000 m^2 of forest on well-drained soil near Manaus represented 17% of the foliar phytomass.

Palm densities reach their maximum on the well-drained soils of the crest: for the combined area of 2400 m^2, 906 individuals were recorded for the crest, as opposed to 700 and 720 for the plateau and slope respectively (Table 3). This is most likely a result of greater exposure to wind and subsequent higher frequency of gap formation. The forest here thus tends to be less well developped architecturally, permitting greater penetration of light, which favours the regeneration of palms.

Species richness

The species richness of palms in this forest is remarkable: 32 species in 1,2 ha. This can be compared with a parallele study in the forests of the Tocantins valley, Para, which recorded 21 species in 10,56 ha (KAHN, following paper).

The total number of species of palms reaches a maximum in upland forest on well-drained soils and decreases into seasonal swamp forest on water-logged soils (Table 4). Even more striking is the variation of the number of understory species which in plots of 1200 m^2 decreased from 14-17 species on well-drained soils to 3 species on water-logged soils.

Variety of forms

The great majority of arborescent palms in the forest of central Amazonia are monocaulous. *Mauritia aculeata* which occurs in seasonal swamp forest is the only species forming clumps.

The absence of arborescent palms of TOMLINSON's architectural model from upland forest was noted and accounted for by GRANVILLE (1978). All arborescent palms require high light levels during the stage of stem growth and thus in the forest their regeneration tends to be restricted to gaps. As a gap closes, palm growth must keep pace with pioneer species (*Cecropia*, *Inga*, *Pourouma*, *Protium*, etc.) in order to compete effectively for light and continue development of its stem. It follows then that such gaps are not suitable for palms of TOMLINSON's growth model, since the second axis initiated at the lower part of the stem will be shaded out from the moment it emerges, by the pioneer species then maturing in gap.

Arborescent multiple-stemmed palms, however, can develop in the seasonal swamp forest on water-logged soils.Here, the forest is more open with fewer trees and ambiant light levels are higher than in upland forest and sufficient to maintain stem growth.

Arborescent palms of CORNER's-model are also more abundant on water-logged soils: 26 palms greater than 10 m in height were recorded in 4800 m^2 on poorly-drained and water-logged soils compared to 4 on well-drained soils in 7200 m^2.

Further, on well-drained soils, arborescent palms are rarely exceed 15 m in height (as also noted by KLINGE and RODRIGUES,1973), whereas on water-logged soils they often reach 25-30 meters.

In understory species, TOMLINSON's growth form is as common as CORNER's (Table 1). Thus,in the case of multiple-stemmed palms, Astrocaryum munbaca and Oenocarpus minor occupy the upper levels of the understory and various species of the Genera Bactris and Geonoma are distributed between 0,5 and 5 m. Similarly, with monopodial palms, Syagrus inajai reaches the upper level of the understory, and between 2 and 5 m the leaves of the 4 acaulescent palms (Astrocaryum cf javarense, A. acaule, Attalea attaleoides, A. spectabilis) constitute an almost continuous cover. While the stem of these acaulescent species are reduced to a short subterranean axis, the leaves maintain significant size and give the understory of these central Amazonian forest its characteristic appearance (Figure 2).

Table 1 - Presence of palm species in relation to soils.

11 of the 12 species of Bactris are found on well-drained soils (WDS). One of these (Bactris simplicifrons Mart.) penetrates the transition zone on poorly-drained soils (PDS). Only one oth species occurs in seasonal swamp forest on water-log soils (WLS). The 6 species of Geonoma are restricted to well-drained soils. Only one of them reaches the transition zone on poorly-drained soils. As the floristic material of all these small species was not completely collected (flowers are especially infrequent) their identification was problematic. We have thus prefered to remain at generic level.

- The architectural models are defined by HALLE et al (1978). TOMLINSON's model corresponds to palms which ramify at the base and may form clumps (multiple-stemmed palms) ; CORNER's corresponds to monocaulous palms with lateral inflorescences.

Table 2 - Population of most abundant palms on well-drained soils. (P=plateau; C=crest; S=slope; TZ=transition zone; IB="igarapé" bottom). For acaulescent species, the two first height-classes correspond to seedlings and juveniles, the third to mature palms. For upper-understory species, an intermediary class is considered corresponding to the phase of stem elaboration, except for Astrocaryum munbaca which fructifies from 3 m in height. For arborescent species, the two first classes correspond to seedlings and acaulescent juveniles, the third to the phase of the stem elaboration, and the fourth to mature palms.

Table 3 - Population of most abundant palms on poorly-drained and water-logged soils (see also legend of Table 2).

Table 4 - Number of palms per topographic sites in upland forest on well-drained soils (per 2400 m^2).

Table 5 - Number of palm species per plot (1200 m^2).

Figure 1 - Vegetations, topographic sites, and soils.

Figure 2 - Acaulescent palms in upland forest understory on well-drained soils (Astrocaryum cf javarense).

TABLE I

	WDS	PDS	WLS	mature height	architectural model	reference herbarium ↓
ARBORESCENT PALMS						
Oenocarpus bacaba Mart.	+			15m	CORNER's	
Iriartea exorrhiza Mart.	+	+	+	15m	CORNER's	
Jessenia bataua (Mart.)Burret		+	+	20m	CORNER's	
Mauritia aculeata Mart.		+	+	15m	TOMLINSON's	
Euterpe precatoria Mart.	(+)	+	+	20-25m	CORNER's	
UNDERSTORY PALMS						
Syagrus inajai (Spruce)Beccari	+			8-10m	CORNER's	
Oenocarpus minor Mart.	+	+		8-10m	TOMLINSON's	
Astrocaryum munbaca Mart.	+			3-10m	TOMLINSON's	
Iriartella setigera (Mart.)Wendl.	+	+		7-10m	TOMLINSON's	
Attalea attaleoides (Barbosa Rodr.)W.Boer	+			3-5m	CORNER's acaulescent	
Astrocaryum cf *javarense* Drude ex Trail	+			3-5m	CORNER's acaulescent	
Attalea spectabilis Mart.		+	+	3-5m	CORNER's acaulescent	
Astrocaryum acaule Mart.		+		3-5m	CORNER's acaulescent	
Manicaria martiana Burret			+	5m	CORNER's	
Bactris spp	11	1	1	0,5-5m	TOMLINSON's	
Geonoma spp	6	1		0,5-5m	TOMLINSON's	

TABLE 2

ACAULESCENT PALMS

Astrocaryum cf *javarense* Drude ex Trail

	.P.	.C.	.S.	.TZ.	.IB.
-1 m	45	46	31	-	-
1-3 m	118	122	102	-	-
≥ 3 m	35	38	29	-	-
Total	198	206	162	0	0

Attalea attaleoides (Barbosa Rodr.)W.Boer

	.P.	.C.	.S.	.TZ.	.IB.
-1 m	5	5	10	-	-
1-3 m	65	63	42	-	-
≥ 3 m	16	23	23	-	-
Total	86	91	75	0	0

UPPER-UNDERSTORY PALMS

Oenocarpus minor Mart.

	.P.	.C.	.S.	.TZ.	.IB.
-1 m	-	3	1	1	-
1-3 m	2	18	19	12	-
3-5 m	3	8	4	6	-
≥5 m	1	1	-	1	-
Total	6	30	24	19	0

Syagrus inajai (Spruce)Beccari

	.P.	.C.	.S.	.TZ.	.IB.
-1 m	5	14	1	-	-
1-3 m	10	51	7	-	-
3-5 m	-	-	-	-	-
≥5 m	1	-	-	-	-
Total	16	66	8	0	0

Astrocaryum munbaca Mart.

	.P.	.C.	.S.	.TZ.	.IB.
-1 m	9	10	19	-	-
1-3 m	17	40	23	-	-
≥3 m	11	10	7	-	-
Total	37	60	49	0	0

ARBORESCENT PALMS

Oenocarpus bacaba Mart.

	.P.	.C.	.S.	.TZ.	.IB.
-1 m	185	161	130	-	-
1-6 m	24	68	75	-	-
6-10m	-	-	-	-	-
10-15m	2	2	-	-	-
Total	211	231	205	0	0

TABLE 3

ACAULESCENT PALMS

	Astrocaryum acaule Mart.					*Attalea spectabilis* Mart.				
	.P.	.C.	.S.	.TZ.	.IB.	.P.	.C.	.S.	.TZ.	.IB.
-1 m	-	-	-	68	-	-	-	-	126	-
1-3 m	-	-	-	40	-	-	-	-	161	11
≥3 m	-	-	-	34	-	-	-	-	98	8
Total	0	0	0	142	0	0	0	0	385	19

ARBORESCENT PALMS

	Euterpe precatoria Mart.					*Jessenia bataua* (Mart.)Burret				
	.P.	.C.	.S.	.TZ.	IB.	.P.	.C.	.S.	.TZ.	.IB.
-1 m	9	18	22	210	794*	-	-	-	122	1092*
1-6 m	2	-	9	40	20	-	-	-	158	472
6-10m	-	-	-	5	1	-	-	-	5	13
10-22m	-	-	-	-	5	-	-	-	6	15
Total	11	18	31	255	820	0	0	0	291	1592

* estimated number from 200 m^2 surveyed.

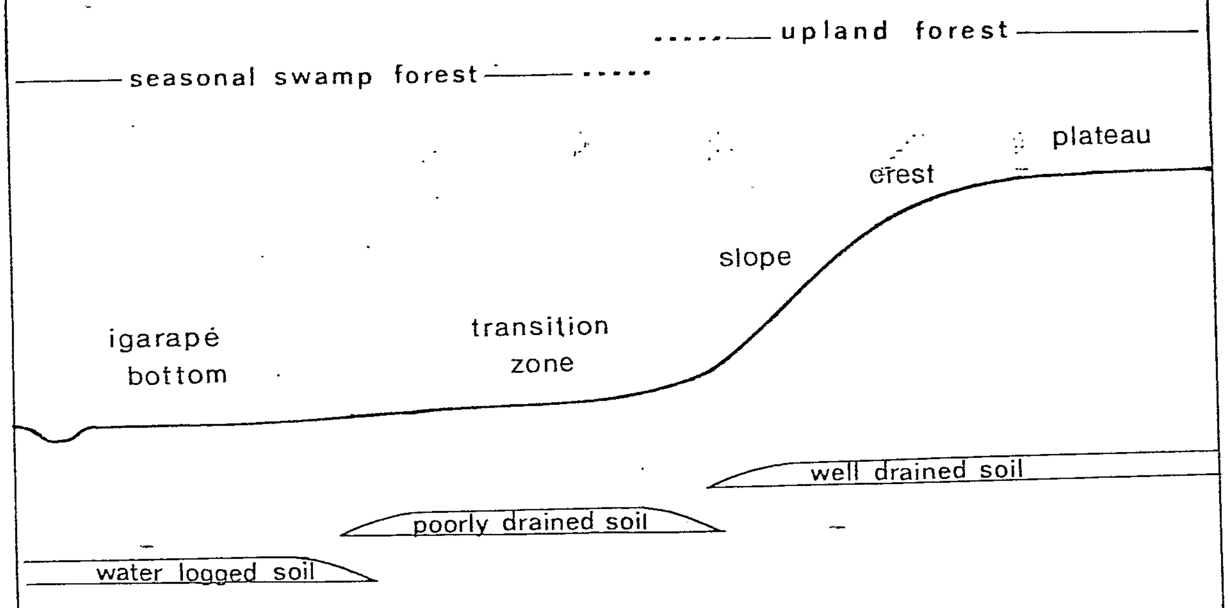
TABLE 4

	Plateau	Crest	Slope
Astrocaryum cf *javarense* Drude ex Trail	198	206	162
Astrocaryum munbaca Mart.	86	91	75
Attalea attaleoides (Barbosa Rodr.)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	146	222	197
Total number	700	906	710

TABLE 5

	catena 1	catena 2
Plateau	16	16
Crest	19	20
Slope	19	19
Transition zone	5	10
"Igarapé" bottom	8	6

FIG. 1


upland forest
seasonal swamp forest
plateau
crest
slope
igarapé
bottom
transition
zone
well drained soil
poorly drained soil
water logged soil

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ACKNOWLEDGEMENTS

This study was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Instituto Nacional de Pesquisas da Amazônia (INPA) and by the Projeto Multilateral "Ecologia da Floresta Tropical" of the Organisation of the American States (OAS/OEA). We specially thank Catherine Mackenzie for her helpful assistance on the English manuscript. We would further like to thank Charles Clement for providing valuable comments upon critical reading of the manuscript. We also thank José Palheta for his assistance during field work.