

The Palm Community in a Forest of Central Amazonia, Brazil¹

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ABSTRACT

The palm community in a forest of central Amazonia clearly shows three zones according to the hydromorphic condition of the soil: well-drained soils of the upland forest, poorly-drained soils of a transition zone, and water-logged soils of the seasonal swamp forest. The community is remarkable in three aspects: its size (with 2122 palms/ha, and the highest density on water-logged soils); its great diversity (32 species/1.2 ha), which also depends on the hydromorphic condition of the soil; and its variety of biological forms with characteristic acaulescent palms in the understory, monocaulous and multiple-stemmed palms in the upper understory, and arborescent palms only reaching the canopy in the seasonal swamp forest.

PALMS ARE AN ABUNDANT and characteristic component of the 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. However, as Moore (1973a) lamented, our ignorance of the biology and ecology of palms is almost complete. Corner's marvelous book (1966) represents the cornerstone of our knowledge of the family in these ways. Several early works dealt specifically with the palm flora of Amazonia. In fact, since the early studies of this subject (Poitezu's (1822) history of palms in French Guiana; Wallace's famous book (1853); Spruce's works (1871, 1908); the numerous publications of Martius (1823–1853)³, Drude (1876–1908)³, Barbosa-Rodrigues (1875–1907)³, and Burret (1928–1956)³, 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. Recently, Balick and de Silva (1982) established the state of systematic collections in regional herbaria and showed the necessity to intensify them.

Works relating to the ecology of palms are even rarer (see Discussion). Thus, we initiated a series of ecological investigations on Amazonian palms in 1980 at the National Institute for Amazonian Research (INPA). This paper presents a community-level study of palms in central Amazonia and describes the distribution and abun-

dance of the most important species in relation to topography and soils.

METHODS

The survey areas were located in the Tropical Sylviculture Experimental Station of INPA, 45 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). Rainfall 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, were selected to include a catena of five topographic sites: plateau, crest, slope, a transition zone at the base of the slope, and the seasonal flooded "igarapé" (stream) bed (Fig. 1). According to Ranzani and de Podestá (1984), the soils of plateau correspond to "Latossolo Amarelo Álico, textura muito argilosa" (heavy yellow clay latosols), the soils of crest and slope to "Podzólico Vermelho Amarelo Álico, textura argilosa" (heavy clay red yellow Podzolic soils), the soils of transition zone to hydromorphic Podzols, and the soils of the "igarapé" bottom to Gley Pouco Húmico (Humic Gley). These works clearly showed that the main variable along the catena is hydromorphic condition. In this paper we shall qualify the latossols of the plateau and the podzolic soils of the slope as well-drained soils, the soils of transition zone as poorly-drained soils and the soils of "igarapé" bottom as water-logged soils. The hydromorphic character is due to the outcrop of the water-table.

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³ The bibliography of these authors is recapitulated by Glassman (1972).



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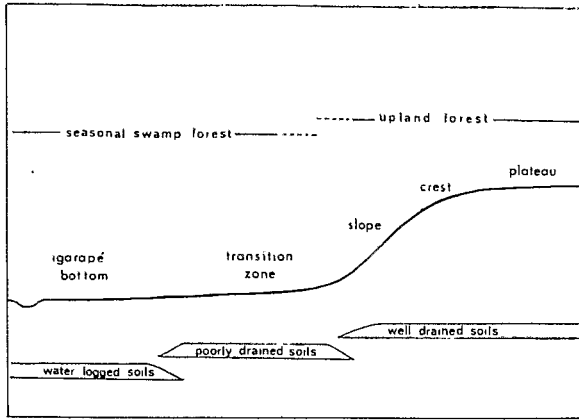


FIGURE 1. Vegetation, topographic sites, and soils

Study plots of 1200 m² (30 × 40 m) were established in each topographic site in both survey areas, giving a total of 10 plots and a total survey area of 1.2 ha. Within each plot, all palm seedlings, juveniles and adults were surveyed. In multiple-stemmed species, all the stems were counted.

RESULTS

In the 1.2 ha surveyed, 32 species of palms, in 12 genera, were encountered. All species were collected, and vouchers are now deposited at the department of Ecology, INPA, Manaus. Identification was to species, except when floristic material was not completely collected (flowers were especially infrequent). The species (with voucher no.'s) were: *Astrocaryum acaule* Mart. (AC 590), *A. sociale* Barbosa Rodrigues (FK 587), *A. munbaca* Mart. (AC 522), *Attalea attaleoides* (Barbosa Rodr.) W. Boer (AC 615), *A. spectabilis* Mart. (FK 618), *Euterpe precatoria* Mart. (AC 591), *Iriarteia exorrhiza* Mart. (FK 581), *Ir-*

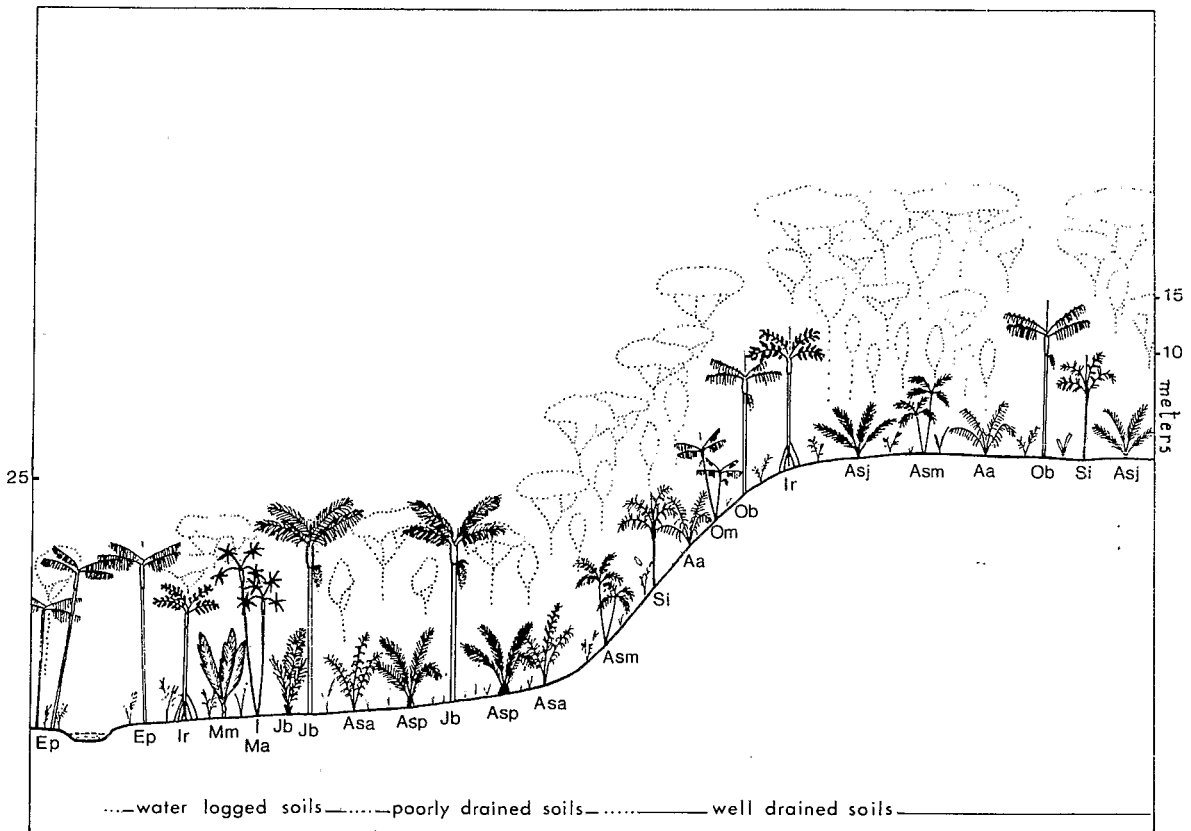


FIGURE 2. Distribution of the palm community along the catena. Aa = *Attalea attaleoides*, Asp = *Attalea spectabilis*, Asa = *Astrocaryum acaule*, Asj = *Astrocaryum sociale*, Asm = *Astrocaryum munbaca*, Ep = *Euterpe precatoria*, Ir = *Iriarteia exorrhiza*, Jb = *Jessenia bataua*, Ma = *Mauritia aculeata*, Mm = *Manicaria mariana*, Ob = *Oenocarpus bacaba*, Om = *Oenocarpus minor*, and Si = *Syagrus inajai*. *Bactris* spp., *Geonoma* spp. and *Iriartella setigera* are not drawn.

TABLE 1. Presence of palm species in relation to soils.

	WDS	PDS	WLS	Mature height	Architectural model
Arborescent palms					
<i>Oenocarpus bacaba</i>	+			15 m	Corner
<i>Iriarteia exorrhiza</i>	+	+	+	15 m	Corner
<i>Jessenia bataua</i>		+	+	20-25 m	Corner
<i>Mauritia aculeata</i>		+	+	15 m	Tomlinson
<i>Euterpe precatoria</i>	(+) ^a	+	+	20-25 m	Corner
Understory palms					
<i>Syagrus inajai</i>	+			8-10 m	Corner
<i>Oenocarpus minor</i>	+	+		8-10 m	Tomlinson
<i>Astrocaryum muncaba</i>	+			3-10 m	Tomlinson
<i>Iriartella setigera</i>	+	+		7-10 m	Tomlinson
<i>Attalea attaleoides</i>	+			3-5 m	Corner (acaulescent)
<i>Astrocaryum sociale</i>	+			3-5 m	Corner (acaulescent)
<i>Attalea spectabilis</i>		+	+	3-5 m	Corner (acaulescent)
<i>Astrocaryum acaule</i>		+		3-5 m	Corner (acaulescent)
<i>Manicaria martiana</i>			+	5 m	Corner
<i>Bactris</i> spp. ^b	11	1	1	0.5-5 m	Tomlinson
<i>Geonoma</i> spp. ^b	6	1		0.5-5 m	Tomlinson

^a Only seedlings and juveniles of *Euterpe precatoria* were found on well-drained soils.

^b 12 species of *Bactris* were found on well-drained soils (WDS). One of these (*Bactris simplicifrons* Mart., FK 518) penetrated the transition zone on poorly-drained soils (PDS). Only one other species (FK 621) occurred in seasonal swamp forest on water-logged soils (WLS). The 6 species of *Geonoma* were restricted to well-drained soils. Only one of them (AC 525) reached the transition zone on poorly-drained soils.

Iriartella setigera (Mart.) Wendl. (FK 598), *Jessenia bataua* (Mart.) Burret (FK 505), *Manicaria martiana* Burret (FK 519), *Mauritia aculeata* Mart. (FK 648), *Oenocarpus bacaba* Mart. (FK 645), *O. minor* Mart. (FK 612), *Syagrus inajai* (Spruce) Beccari (FK 601), *Bactris* spp. (FK 621), (AC 548), (AC 552), (FK 585), (AC 549), (AC 547), (FK 518), (FK 624), (FK 626), (FK 627), (FK 613), (FK 597), *Geonoma* spp. (AC 599), (AC 535), (FK 628), (FK 589), (AC 524), (AC 525).

The distribution of these species was strongly related to soils and three distinct "palm zones" are recognized (Fig. 2): well-drained soils (plateau, crest, slope), poorly-drained soils (transition zone), and water-logged soils ("igarapé" bottom). Each of these "palm zones" was characterized by a number of typical species, but there were also a few, less abundant species which were common to two or three zones (Table 1).

Quantitative data are presented by topographic site, listing the most important species. Figures from both survey areas are cumulated and therefore total number of palms are given for 2400 m² (Table 2).

PALMS ON WELL-DRAINED SOILS (PLATEAU, CREST, SLOPE).—In the 7200 m² of forest on well-drained soils we surveyed, 1346 palms between one and ten meters in height were recorded, and of these 676 belong to two acaulescent species. No palms reached the canopy in forest on well-drained soils which we studied. The understory of the forest on well-drained soils was dominated to a height of

5 m by the leaves of two acaulescent species, *Astrocaryum sociale* and *Attalea attaleoides*. Eleven and six species, respectively, of the genera *Bactris* and *Geonoma* were also found here but their frequency varied and their total number per plot was often reduced to a few individuals. These species formed clumps of two to ten axes.

In the upper level of the understory, between six and ten meters, *Syagrus inajai* (a monoaxial palm with a stem of 4-5 m) was frequent, as were *Astrocaryum muncaba* and *Oenocarpus minor*. The latter two species formed clumps of two to four axes. Less frequently encountered was *Iriartella setigera*, a small palm, seven to ten meters in height, characterized by the production of creeping rhizomes. In the forest mid-story, *Oenocarpus bacaba* reached a height of 15 m. It was the dominant palm in height and was only found below discontinuities of the upperstory canopy, indicating that it competes only in clearings with enough light.

PALMS ON POORLY-DRAINED SOILS (TRANSITION ZONE).—Two acaulescent palms, *Attalea spectabilis* and *Astrocaryum acaule*, overran the understory of the forest. They were very abundant and their leaves spread up, funnel-like, to five meters. These two species were strictly limited to the transition zone at the base of the slope and disappeared in the vicinity of the "igarapé" when the soil becomes waterlogged. There, they were replaced by stemless juveniles of *Jessenia bataua*. This transition zone does indeed stand out; in 2400 m², 343 acaulescent palms

TABLE 2. Population of most abundant palm species (per 2400 m²) (P: plateau; C: crest; S: slope; TZ: transition zone; IB: "igarapé" bottom).

Form Species	DRY			MOIST	
	P	C	S	TZ	IB
Acaulescent					
<i>Astrocaryum sociale</i>	198	206	162	0	0
<i>Attalea attaleoides</i>	86	91	75	0	0
<i>Astrocaryum acaule</i>	0	0	0	142	0
<i>Attalea spectabilis</i>	0	0	0	385	19
Upper understory					
<i>Oenocarpus minor</i>	6	30	24	19	0
<i>Syagrus inajai</i>	16	66	8	0	0
<i>Astrocaryum munbaca</i>	37	60	49	0	0
Arborescent					
<i>Oenocarpus bacaba</i>	211	231	205	0	0
<i>Euterpe precatoria</i>	11	18	31	255	820 ^a
<i>Jessenia batana</i>	0	0	0	291 ^b	1592 ^b
Other species (22)	135	204	166	28	92
Total/2400 m ²	700	906	720	1120	2523

^a With 5 palms above 10 m in height.

^b With respectively 6 and 15 palms above 10 m in height. In "igarapé" bottom, the number of seedlings and juveniles below 1 m in height was estimated from 200 m² surveyed.

greater than one meter in height were recorded; of these, 259 were *Attalea spectabilis* and 74 were *Astrocaryum acaule*. Also, 158 young *Jessenia batana* (from one to six meters in height) were found.

PALMS ON WATER-LOGGED SOILS ("IGARAPÉ" BOTTOM).—The forest on water-logged soils was almost devoid of the acaulescent palms (only 19 *Attalea spectabilis*), but overrun by young *Jessenia batana* (472, already defined). One species of *Bactris* formed clumps, its axes not exceeding five meters in height; *Mauritia aculeata* were distributed in isolated patches. Whereas arborescent palms were absent from the forest canopy on well-drained soils, they were an important component of the forest canopy on poorly-drained and water-logged soils: *Jessenia batana*, *Mauritia flexuosa* (not encountered in our plots, although very common in the "igarapé" bottoms), *Mauritia aculeata*, *Euterpe precatoria*.

CROSS TOPOGRAPHY PALMS.—Some species of the forest on well-drained soils (such as *Oenocarpus minor*, *Iriartella setigera*, *Bactris simplicifrons*, and *Geonoma* spp.) penetrated the transition zone at the base of the slope. *Euterpe precatoria*, frequent on water-logged soils, was occasionally found on well-drained soils, but usually only as seedlings and juveniles that have germinated and started their growth in gaps; very few reached maturity in the transition zone. *Iriartea exorrhiza*, an arborescent palm with typical stilt roots (Bouillenne 1924, Kahn 1977, Bodley

and Benson 1980), seems quite independent of the nature of the soil, but requires light and was only found below openings of the forest canopy.

DISCUSSION

The palm community of the forest of central Amazonia clearly shows three zones according to the hydromorphic condition of the soil: well-drained soils of the upland forest, poorly-drained soils of the transition zone, and water-logged soils 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. Works relating to the ecology of palms 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 and 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, Anderson 1978, Balick 1981). Moore (1973b) regroups the taxa in terms of the main neotropical climax formations. Specifically regarding the Amazon region, Bouillenne (1930) describes the *Mauritia* formations on poorly-drained soils; Oldeman (1969) tackles the ecology of the *Euterpe oleracea* formation or "pinotières" of French Guiana, and Granville (1974, 1977, 1978) presents several studies on the biology and ecology of the palms of French Guiana. In fact, quantitative data on palms were found in studies relating to structural analysis of vegetations, phytomass evaluations, and floristic inventories.

ABUNDANCE AND DIVERSITY OF PALMS.—As are the forests of Malaya—on which Whitmore (1973) wrote: "Nowhere in the primary jungles which cover much of the country is one far from a palm"—the forest of central Amazonia is literally overrun by palms, especially in understory. Klinge and Rodrigues (1971) established that palms greater than 1.5 m in 2000 m² of forest on well-drained soil near Manaus represented 17 percent of the foliar phytomass. Takeuchi (1960) counted 112 palms per 1600 m² on high "terra firme" forest and 176 per 2200 m² on low "terra firme" forest. Lechtaler's (1956) and Aubréville's (1961) surveys in Ducke Reserve near Manaus, and Prance *et al.* (1976) inventory of one hectare at kilometer 30 on the Manaus-Itacoatiara road showed, also, the importance of palm populations in the Amazonian forests.

TABLE 3. Number of palm species per plot (1200 m²).

Habitat	Catena 1	Catena 2
Plateau	16	16
Crest	19	20
Slope	19	19
Transition zone	5	10
"Igarapé" bottom	7	6

Palm densities were highest on the well-drained soils of the crest: for the combined area of 2400 m², 906 individuals were recorded for the crest, as opposed to 700 and 720 for the plateau and slope, respectively (Table 2). 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 developed architecturally, permitting greater penetration of light, which favours the regeneration of palms.

Physical and chemical differences exist between the soils of the plateau and those of the slope. Slope soils have a higher density of macropores and a lower organic matter content than plateau soils (Ranzani and de Podestá 1984). These differences, however, do not appear to affect the size of the palm population on these two distinct topographic sites.

Hydromorphic condition affects the population density of palms. We counted 3643 palms on 4800 m² (or 7590·ha⁻¹) on poorly-drained and water-logged soils, and 2326 palms on 7200 m² (or 3231·ha⁻¹) on well-drained soils. The greater size of palm populations on hydromorphic soils is essentially due to greater intensity of light which penetrates into the understory of the open seasonal swamp forest.

The mean of all plots gives 2122 palms (above one meter in height) per hectare. In the forests of Tocantins Valley, Pará, Kahn (1983) counted a mean of 602 palms (above one meter in height) per hectare, from 10.56 ha surveyed. The abundance of palms in this central Amazonian forest is particularly high.

The species richness of palms in this forest is also high: 32 species in 1.2 ha. This can be compared with the parallel study in the forests of the Tocantins Valley which recorded 21 species in 10.56 ha (Kahn, 1983). The total number of species of palms reaches a maximum in upland forest on well-drained soils and decreases in seasonal swamp forest on water-logged soils (Table 3). Even more striking is the variation of the number of understory species which in plots of 1200 m² decreased from 14–17 species on well-drained soils to three species on water-logged soils.

VARIETY OF FORMS.—The great majority of arborescent palms in the forest of central Amazonia are monocaulous.



FIGURE 3. Acaulescent palms in upland forest understory on well-drained soils (*Astrocaryum javarense*).

Mauritia aculeata, which occurs in seasonal swamp forest, is the only species forming clumps.

The absence of arborescent multiple-stemmed palms 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 (defined by Halle *et al.*, 1978: basal ramification and possible formation of clumps), 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 ambient light levels are higher than in upland forest and sufficient to maintain stem growth. Arborescent palms of Corner's model (monocaulous palms with lateral inflorescences, see Halle *et al.*, 1978) are also more abundant on water-logged soils: 26 palms greater than ten meters in height were recorded in 4800 m² on poorly-drained and water-logged soils compared to four on well-drained soils in 7200 m². Further, on well-drained soils, arborescent palms are rarely exceeding 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 form (Table 1). Thus, in the case of multiple-stemmed palms, *Astrocaryum munbaca* and *Oenocarpus minor* occupy the upper levels of the under-

story and various species of the genera *Bactris* and *Genoma* are distributed between 0.5 and five meters. Similarly, with monocaulous palms, *Syagrus inajai* reaches the upper level of the understory, and between two and five meters the leaves of the four acaulescent palms (*Artrocaryum sociale*, *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 (Fig. 3).

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QUERY

For a review of current research on tropical forest clearings (gaps) for the *Annual Review of Ecology and Systematics*, I would appreciate receiving reprints of papers published or in press.

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