

## Palm communities in wetland forest ecosystems of Peruvian Amazonia

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### ABSTRACT

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Palm surveys in most representative wetland forest ecosystems were carried out in the lower Ucayali and upper Huallaga River valleys, in the lowland and Andean piedmont regions of Peruvian Amazonia, respectively. These ecosystems are characterized by the species association, density, and vertical distribution of their palm communities. Palms may form almost monospecific stands, e.g., *Mauritia flexuosa* swamps (aguajal), or multispecific communities, e.g., the seasonal swamp forests in upland valleys (bosque de quebrada) which are dominated by *Euterpe precatoria*, *Jessenia bataua*, *Mauritia flexuosa*, and *Socratea exorrhiza*, and the forests on periodically flooded alluvial soils (restinga) dominated by some species of the genera *Astrocaryum*, *Phytelephas*, and *Scheelea*. Palm diversity is very low in the forests which are periodically flooded by blackwater streams (tahuampa); palm density, however, is often high with a characteristic patchy distribution due to clustered species.

### INTRODUCTION

Wetland forest ecosystems cover vast areas in Peruvian Amazonia (Anonymous, 1975; Salo et al., 1986; López Parodi and Freitas, 1990, this volume). In the main river valleys, they are diversified and constitute a complex mosaic (Encarnación, 1985). In upland valleys, they are rather homogeneous, and clearly differ from terra-firme forests on slopes and plateaus by their floristic composition, physiognomy and structure (Oldeman, 1974; De Granville, 1976; Kahn and Castro, 1985).

Palms occur in all forests in the Amazon basin. Large, arborescent palms are frequent and usually constitute dense stands in wetland forests on waterlogged or inundated soils. Some of these species are clearly related to flooding patterns and to water properties (sediment load, acidity) as was early reported by Spruce (1871).

Palm communities of the most representative wetland forest ecosystems are described from two Peruvian regions located in lowland Amazonia and in the eastern Andean piedmont. Species composition and richness, density, and vertical distribution of palms are given for each forest surveyed. Comparison of these data brings out the characteristics of each palm community as elements for definition and identification of wetland forest ecosystems.

## METHODS

### *Study areas*

In the lower Ucayali River valley, near Jenaro Herrera ( $4^{\circ}55'S$ ;  $73^{\circ}40'W$ ), the most representative wetland forest ecosystems are locally called 'tahuampa', 'restinga', 'aguajal', and 'bosque de quebrada' (Encarnación, 1985). The tahuampa forests are periodically flooded by black-water streams. This ecosystem, which rarely covers great areas, is not so clearly defined as the Brazilian igapó forest (Takeuchi, 1962; Prance, 1979; Adis, 1984). The restinga forests are the last stage of a primary succession which starts on sediments deposited by the Ucayali River (white-water). This vegetation corresponds to the Brazilian concept of várzea forest (Prance, 1979). Aguajal formations are swamp forests in permanently flooded depressions which lie parallel to the river bed between ridges. The substratum is clayey, and retains rainfall. River water enters the depressions only at the time of highest flooding. The soil (histosol) is composed of an accumulation of slightly decomposed organic matter, in acidic water (pH 3.5). 'Bosques de quebrada' (i.e., small stream forests) are seasonal swamp forests in upland valleys. The soil (gleysol) is waterlogged and irregularly inundated by rainfall during the rainy season.

In the upper Huallaga valley, near Uchiza ( $8^{\circ}17'S$ ;  $76^{\circ}26'W$ ), bottomland vegetation is dominated by seasonal swamp forests on waterlogged soils inundated by rainfall during the rainy season, and by forests on alluvial soils annually flooded by the Huallaga River.

### *Palm surveys*

In the lower Ucayali River basin, palm communities were inventoried on a 0.4-ha plot in a forest on periodically flooded alluvial soils, and on two 1-ha plots, one located in a *M. flexuosa* swamp and one in a seasonal swamp forest in an upland valley. The palm community in forests periodically flooded by black-water streams was only described qualitatively because of the very low diversity and the patchy distribution of palms. In the upper Huallaga River valley, palms were surveyed on two 0.8-ha plots in the seasonal swamp forest, and on one 0.4-ha plot in the forest on periodically flooded alluvial soils. Counting included all height classes of palms, except that in both 1-ha plots

in the lower Ucayali River valley, palms under 1 m were not considered. For multi-stemmed species, each axis was counted as one palm.

### *Palm identification and collection*

All palm species were collected. Some could not be identified because of the lack of comparative vouchers in the herbaria (BH, K, NY, USM, AMAZ)

TABLE 1

Palm collections and Herbaria (AAU, BH, CAY, K, NY, USM: acronyms follow Holmgren et al., 1987)

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<i>Astrocaryum macrocalyx</i> Burret (Kahn & Mejia 2081, USM)
<i>A. murumuru</i> Martius (K. 1933, CAY)
<i>Bactris acanthocarpoides</i> Barbosa Rodrigues (K. & M. 1827, USM)
<i>B. bifida</i> Martius (K. & M. 1946, USM)
<i>B. concinna</i> Martius (K. & M. 1816, K)
<i>B. maraja</i> Martius (K. & M. 1730, K; K. 1868, K)
<i>B. monticola</i> Barbosa Rodrigues (K. & M. 1824, K)
<i>B. simplicifrons</i> Martius (K. & M. 1980, USM)
<i>Bactris</i> sp. 1 (K. & M. 1749, K)
<i>Bactris</i> sp. 2 (K. 1930, K)
<i>Chamaedorea</i> cf. <i>lanceolata</i> (Ruiz & Pavon) Kunth (K. 1935, USM)
<i>Chelyocarpus ulei</i> Dammer (K. 1838, K)
<i>Desmoncus polyacanthos</i> Martius (M. 643, K)
<i>Desmoncus</i> sp. (K. 1862, USM)
<i>Euterpe precatorea</i> Martius (K. & M. 1778, USM; K. 1852, NY)
<i>Geonoma acaulis</i> Martius (K. & M. 1719, USM; K. 1847, K)
<i>G. brongniartii</i> Martius (K. 1864, K)
<i>G. leptospadix</i> Trail (K. & M. 1900, BH)
<i>G. macrostachys</i> Martius (K. 1845, USM)
<i>G. maxima</i> (Poiteau) Kunth (K. 1938, K)
<i>G. oligoclona</i> Trail (K. & M. 1711, K)
<i>G. piscicauda</i> Dammer (K. & M. 1810, K)
<i>G. spixiana</i> Martius (K. & M. 1808, K)
<i>Iriarteia deltoidea</i> Ruiz & Pavon (K. 1842, NY)
<i>Jessenia bataua</i> (Martius) Burret subsp. <i>bataua</i> (K. & M. 1792, USM; K. 1939, USM)
<i>Lepidocaryum tessmannii</i> Burret (K. & M. 2000, USM)
<i>Mauritia flexuosa</i> L.f. (K. & M. 1784, USM; K. 1940, USM)
<i>Oenocarpus mapora</i> Karsten (K. & M. 1727, NY; K. 1853, K)
<i>Orbignya polysticha</i> Burret (K. & M. 1724, NY)
<i>Phytelephas microcarpa</i> Ruiz & Pavon (K. & M. 1726, AAU; K. 2037, USM)
<i>Scheelea brachyclada</i> Burret (K. & M. 1728, USM)
<i>Scheelea</i> sp. (K. 2033, USM)
<i>Socratea exorrhiza</i> (Martius) Wendland (K. & M. 1702, NY; K. 1941, USM)
<i>Wettinia augusta</i> Poeppig & Endlicher (K. & M. 1767, USM; K. 1843, NY)

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When two voucher numbers are given, the first refers to the lower Ucayali survey, the second to the upper Huallaga survey.

—*Bactris* spp. 1 and 2, and *Scheelea* sp. — or because of the lack of fertile material, e.g., *Desmoncus* sp. Except for *Desmoncus*, all herbarium references correspond to fertile material (Table 1). The following well-known species were not found flowering or fruiting in the plots surveyed in the lower Ucayali River valley: *Geonoma leptospadix*; *G. piscicauda*; *G. spixiana*; *Lepidocaryum tessmannii*; *Orbignya polysticha*; *Socratea exorrhiza*; and *Wettinia augusta*. The herbarium references given for these species correspond to fertile material collected outside of the plots, but in the same locality.

## RESULTS

### *Palms in wetland forests in the lower Ucayali valley*

In the forest on alluvial soil (restinga), eleven species were found on the 0.4-ha plot (Table 2). Among them, five represent 98.9% of the community: *Astrocaryum macrocalyx* (37.3%); *Phytelephas microcarpa* (30.8%); *Scheelea brachyclada* (16.9%); *Bactris bifida* (9.9%); and *Geonoma acaulis* (4.0%). Palm density is very low (0.3%) above 10 m in height, and very high between 1 and 10 m (353 palms/0.1 ha; 50.2% of the community). *Astrocaryum macrocalyx* and *P. microcarpa*, a single and a multistemmed species, respectively, dominate the 1–10-m stratum; both species rarely reach more than 10 m in height. Palm density under 1 m in height is high (49.5% of the community) in spite of the 3–4-month annual flooding.

TABLE 2

Species richness, density and vertical distribution of the palm community on 0.4 ha surveyed in a forest on periodically flooded alluvial soils located in the lower Ucayali River valley

	Height classes			Total
	0–1 m	1–10 m	> 10 m	
<i>Astrocaryum macrocalyx</i>	722	328	0	1050
<i>Bactris bifida</i>	183	95	0	278
<i>B. maraja</i>	0	1	0	1
<i>B. monticola</i>	7	5	0	12
<i>Desmoncus polyacanthos</i>	0	1	0	1
<i>Euterpe precatoria</i>	6	2	0	8
<i>Geonoma acaulis</i>	78	34	0	112
<i>Oenocarpus mapora</i>	0	2	0	2
<i>Phytelephas microcarpa</i>	25	841	0	866
<i>Scheelea brachyclada</i>	372	97	7	476
<i>Socratea exorrhiza</i>	0	6	0	6
Total	1393	1412	7	2812

TABLE 3

Species richness, density, and vertical distribution of the palm community on 1 ha in a permanently flooded forest on histosol located in the lower Ucayali River valley

	Height classes			Total
	0-1 m	1-10 m	> 10 m	
<i>Astrocaryum macrocalyx</i>	-	5	0	5
<i>Bactris concinna</i>	-	15	0	15
<i>B. maraja</i>	-	42	0	42
<i>B. monticola</i>	-	26	0	26
<i>Desmoncus polyacanthos</i>	-	20	0	20
<i>Euterpe precatoria</i>	-	16	34	50
<i>Geonoma acaulis</i>	-	252	0	252
<i>Mauritia flexuosa</i>	-	478	167	645
<i>Oenocarpus mapora</i>	-	119	2	121
<i>Scheelea brachyclada</i>	-	1	0	1
<i>Socratea exorrhiza</i>	-	3	4	7
Total		977	207	1184

In the permanently flooded swamp forest (aguajal), eleven species were found on 1 ha surveyed (Table 3). Among these, four represent 90.2% of the palm community (above 1 m in height): *Mauritia flexuosa* (54.5%); *G. acaulis* (21.3%); *Oenocarpus mapora* (10.2%); and *Euterpe precatoria* (4.2%). The canopy of this swamp forest is essentially composed of *M. flexuosa* crowns. Palm density above 10 m in height is high, with 207 individuals per ha. Palm basal area represents 55% of the total basal area ( $31.11 \text{ m}^2 \text{ ha}^{-1}$ ), with 336 trunks, including 230 *M. flexuosa* (138 adults, and 92 trunked juveniles). Palm density in the understory (1-10 m) is 98 palms/0.1 ha; half of these are acaulescent and trunked juveniles of *M. flexuosa*. The density of *Astrocaryum macrocalyx* and *Scheelea brachyclada* is very low, though both are dominant species on the two 'restingas' which bound the *M. flexuosa* swamp depression. *Phytelephas microcarpa*, also abundant in the neighbouring 'restingas', is absent in the swampy depression.

In the seasonal swamp forest in an upland valley (bosque de quebrada), eighteen species were found on 1 ha surveyed (Table 4). Among these, seven were located on a  $\pm 500\text{-m}^2$  area of dryer soils within the wetland parcel. These species, which are very common in uplands (Kahn and Mejia, 1990), cannot be considered representative of this swamp community. Six species represent 89.2% of the palm community (above 1 m in height): *Bactris monticola* (36.4%); *Jessenia bataua* (15.2%); *Euterpe precatoria* (10.5%); *Mauritia flexuosa* (10.5%); *Geonoma acaulis* (10.0%); and *Socratea exorrhiza* (6.7%). Palm basal area represents 36.3% of the total basal area ( $26.34 \text{ m}^2 \text{ ha}^{-1}$ ),

TABLE 4

Species richness, density, and vertical distribution of the palm community on 1 ha in a seasonal swamp forest in an upland valley located in the lower Ucayali River valley

	Height classes			Total
	0-1 m	1-10 m	> 10 m	
<i>Astrocaryum macrocalyx</i>	-	13	0	13
<i>Bactris acanthocarpoides</i> <sup>1</sup>	-	3	0	3
<i>B. monticola</i>	-	866	0	866
<i>B. simplicifrons</i>	-	18	0	18
<i>Bactris</i> sp. 1 <sup>1</sup>	-	5	0	5
<i>Euterpe precatoria</i>	-	205	45	250
<i>Geonoma acaulis</i>	-	237	0	237
<i>G. leptospadix</i> <sup>1</sup>	-	1	0	1
<i>G. oligoclona</i>	-	10	0	10
<i>G. piscicauda</i> <sup>1</sup>	-	1	0	1
<i>G. spixiana</i> <sup>1</sup>	-	4	0	4
<i>Jessenia bataua</i>	-	313	48	361
<i>Lepidocaryum tessmannii</i> <sup>1</sup>	-	151	0	151
<i>Mauritia flexuosa</i>	-	218	32	250
<i>Oenocarpus mapora</i>	-	39	1	40
<i>Orbignya polysticha</i> <sup>1</sup>	-	9	0	9
<i>Socratea exorrhiza</i>	-	113	46	159
<i>Wettinia augusta</i>	-	2	0	2
Total		2208	172	2380

<sup>1</sup>These species are common in terra firme forests. They occur here on  $\pm 500\text{-m}^2$  island of dryer soil.

with 279 trunks of which 172 reach more than 10 m in height. Their crowns constitute a major component of the forest canopy. *Bactris monticola* is the dominant species in the understory on the waterlogged soil (while *Lepidocaryum tessmannii* reaches a very high density on the small 'island' of dryer soil).

In forests periodically flooded by blackwater streams (tahuampa), palm species richness is very low. The most common species are *Astrocaryum jauari*, an arborescent, multistemmed palm which can reach up to 20 m in height, and *Bactris concinna*, and *B. maraja*, both small, multistemmed palms, up to 10 m in height. These clustered species constitute dense, monospecific patches on small areas.

#### *Palms in the wetland forests in the upper Huallaga valley*

In the seasonal swamp forest, the 15 species found were present in each of the two 0.8-ha plots surveyed (Table 5; density for each species is lumped on

TABLE 5

Species richness, density, and vertical distribution of the palm community on 1.6 ha surveyed in a seasonal swamp forest located in the upper Huallaga River valley

	Height classes			Total
	0-1 m	1-10 m	> 10 m	
<i>Astrocaryum murumuru</i>	10	22	0	32
<i>Bactris maraja</i>	2	15	0	17
<i>Bactris</i> sp. 2	32	50	0	82
<i>Chamaedorea</i> cf. <i>lanceolata</i>	0	2	0	2
<i>Desmoncus</i> sp.	0	7	0	7
<i>Euterpe precatoria</i>	239	88	1	328
<i>Geonoma acaulis</i>	10	23	0	33
<i>G. brongniartii</i>	103	320	0	423
<i>G. macrostachys</i>	152	147	0	299
<i>Iriartea deltoidea</i>	153	104	0	257
<i>Jessenia bataua</i>	231	160	7	398
<i>Mauritia flexuosa</i>	22	85	22	129
<i>Oenocarpus mapora</i>	109	184	0	293
<i>Socratea exorrhiza</i>	206	57	9	272
<i>Wettinia augusta</i>	127	42	4	173
Total	1396	1306	43	2745

TABLE 6

Species richness, density, and vertical distribution of the palm community on 0.4 ha surveyed in a forest on periodically flooded alluvial soils located in the upper Huallaga River valley

	Height classes			Total
	0-1 m	1-10 m	> 10 m	
<i>Astrocaryum murumuru</i>	230	352	0	582
<i>Bactris</i> sp. 2	4	12	0	16
<i>Chamaedorea</i> cf. <i>lanceolata</i>	5	7	0	12
<i>Chelyocarpus ulei</i>	8	10	0	18
<i>Euterpe precatoria</i>	176	67	1	244
<i>Geonoma acaulis</i>	3	4	0	7
<i>G. macrostachys</i>	35	19	0	54
<i>G. maxima</i>	1	2	0	3
<i>Iriartea deltoidea</i>	0	8	0	8
<i>Jessenia bataua</i>	1	2	1	4
<i>Mauritia flexuosa</i>	1	2	3	6
<i>Oenocarpus mapora</i>	37	93	0	130
<i>Phytelephas microcarpa</i>	2	34	0	36
<i>Scheelea</i> sp.	9	11	0	20
<i>Socratea exorrhiza</i>	16	16	3	35
Total	528	639	8	1175

1.6 ha). Nine of these represent 93.7% of the community: *Geonoma brongniartii* (15.4%); *Jessenia bataua* (14.5%); *Euterpe precatória* (11.9%); *Geonoma macrostachys* (10.9%); *Oenocarpus mapora* (10.7%); *Socratea exorrhiza* (9.9%); *Iriartea deltoidea* (9.4%); *Wettinia augusta* (6.3%); and *Mauritia flexuosa* (4.7%). Palm density above 10 m in height is low (1.6% of the community) with 43 trunks, of which 22 belong to *M. flexuosa*. Many palms had been cut down, and a lot of decomposing trunks of *J. bataua* and *M. flexuosa* lie on the forest floor.

In the forest on periodically flooded alluvial soils, fifteen species were found on the 0.4-ha plot surveyed (Table 6). Of these, four constitute 86.0% of the community: *Astrocaryum murumuru* (49.5%); *Euterpe precatória* (20.8%); *Oenocarpus mapora* (11.1%); and *Geonoma macrostachys* (4.6%). *Astrocaryum murumuru* is the dominant species in the understory. Palm density above 10 m in height is low (0.7% of the community).

#### DISCUSSION

Many palm species were found in several inventories, indicating a rather high floristic similarity between these ecosystems. In the lower Ucayali River valley, the six species which are common to the three inventories represent 26.6, 38.9 and 65.8% of the palm communities (above 1 m in height) in the forest on periodically alluvial soils, in the *M. flexuosa* swamp, and in the seasonal swamp forest, respectively. These two last forests have in common seven species which constitute 93.4 and 76.3% of their palm communities, respectively. In the upper Huallaga River valley, 11 of the 18 species are common to both ecosystems, and represent 77.4 and 93.4% of the communities in the seasonal swamp forest and in the forest on periodically flooded alluvial soils, respectively. Palm community characteristics of each of the wetland forest ecosystems are, nevertheless, very distinct:

(i) Swamp forests in permanently flooded depressions are mainly composed of *Mauritia flexuosa*, which reaches very high densities (Table 3; and see González Rivadeneyra, 1971; Salazar and Roessl, 1977). Juvenile and adult plants dominate the understory and the canopy, respectively. Aguajal, the local name of these swamp forests, is derived from 'aguaje', the local name of the palm. The close relationship of *M. flexuosa* to water is suggested by Spruce's comments (1871, p. 78): "The prevalent opinion, or rather superstition, throughout Amazonia and Guyana, is that the *Mauritia* has the power of attracting water to itself wherever planted".

(ii) Seasonal swamp forests in upland valleys (bosque de quebrada) are dominated by four species, *Euterpe precatória*, *Jessenia bataua*, *Mauritia flexuosa*, and *Socratea exorrhiza*, which together constitute an important component of the canopy. *Jessenia bataua* is very characteristic of seasonal swamp forests on waterlogged soils; this species was rarely found in other wet-



land ecosystems. Three other species particularly common in this ecosystem in the Andean piedmont are *Iriartea deltoidea*, *Oenocarpus mapora*, and *Wettinia augusta*. Structural data from the upper Huallaga valley are biased by the high degree of disturbance of the forest, and cannot be considered representative. The density of trunked palms of the three arborescent species, *E. precatoria*, *J. bataua*, and *M. flexuosa*, is particularly low. All three provide useful products, such as palm heart, oil, edible fruit, and building materials (Kahn, 1988; Mejia, 1988). They have been extensively cut down by the numerous new inhabitants who have settled in this valley, attracted by job prospects at a 4500-ha African oil-palm plantation.

(iii) Forests on periodically flooded alluvial soils (restinga) are characterized by the association of several species of three genera: *Astrocaryum* (*A. macrocalyx* and *A. murumuru*, two closely related species, both locally called 'huicungo'), *Phytelephas* (*P. microcarpa*, 'yarina'), and *Scheelea* (several species, all locally called 'shapaja'). In contrast to other wetland forests, arborescent palms are not dominant in the canopy of restinga forests. On the other hand, palms are the major component of the understory because of the abundance of *Astrocaryum* spp. and/or *Phytelephas microcarpa*. Dense populations of the latter, known as 'yarinal', are usually said to indicate good soils. The association of these three palm genera also occurs in an Ecuadorean floodplain forest on alluvial soils (Balslev et al., 1987).

(iv) Forests which are periodically flooded by black-water streams (tahuampa), are characterized by riparian palms such as *A. jauari* and *Bactris maraja*, the fruit of which is disseminated by fishes (Gottsberger, 1978; Goulding, 1980). These species also occur on the banks of most Amazonian rivers throughout the basin. *Desmoncus polyacanthos*, a lianescent palm, is commonly found in tahuampa forests, as well as in most wetlands, in low vegetation, and in open forests.

Palm diversity in each of the wetland forests in the lower Ucayali River valley is not sharply different: 11 species (9 genera) on 0.4 ha on periodically flooded alluvial soils; 11 species (9 genera) on 1 ha in an *M. flexuosa* swamp; 18 species (11 genera) on 1 ha in the seasonal swamp forest (but in this case, 7 species and 2 genera, which are restricted to a small area on dryer soil, must be excluded). Palm diversity is slightly higher in wetland forests in the upper Huallaga River valley: 15 species (13 genera) on 0.4 ha on periodically flooded alluvial soils; 15 species (12 genera) in each of both 0.8-ha plots surveyed in a seasonal swamp forest. Palm diversity in the neighbouring terra-firme forests is clearly higher: 29 species (16 genera) on 0.71 ha, and 34 species (21 genera) on 0.5 ha were inventoried (Kahn and Mejia, 1990). In central Amazonia (lower Rio Negro valley), palm species richness is also lower in a seasonal swamp forest than in the neighbouring terra-firme forest on slopes and plateaus (Kahn and Castro, 1985). In eastern Amazonia, the differences of

species richness between wetland and upland forest ecosystems are not so noticeable because of the rather low diversity of palms in the latter (Kahn et al., 1988).

Most of wetland palms which are very common in Peruvian Amazonia occur throughout the Amazon basin: *Astrocaryum jauari*, *A. murumuru*, *Bactris concinna*, *B. maraja*, *B. monticola*, *Desmoncus polyacanthos*, *Mauritia flexuosa*, and *Socratea exorrhiza*, which is as frequent in wetlands as in uplands (Kahn and de Castro, 1985). Other species not found in the eastern region, but which are frequent in both central and western Amazonia, include *Astrocaryum macrocalyx*, *Euterpe precatoria*, *Geonoma acaulis*, and *Jessenia bataua* ssp. *bataua* (*J. bataua* ssp. *oligocarpa* occurs in the Guyanas). Western species are *Oenocarpus mapora*, *Phytelephas microcarpa*, *Scheelea* spp., and *Geonoma brongniartii*, *G. macrostachys*, *Iriartea deltoidea* and *Wettinia augusta*, which are particularly frequent in the Andean piedmont.

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