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Species Richness and Density of Palms in Terra Firme Forests of Amazonia[1]

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ABSTRACT

The characteristics of the palm community in Amazonian terra firme forests are defined from three inventories carried out in the lower Tocantins (east), the lower Rio Negro (center), and the lower Ucayali (west) valleys. At all sites, most of the palms are small, understory species; the palm community is mainly under 10 m in height (99.8 to 99.9%); and adult arborescent palms occur at very low densities. Species richness and diversity are clearly higher in the western and central forests. The difference in density seen in the latter sites reflects a difference in dominant life forms. Spatial occupation of the understory by palms is almost complete at both sites: in the western forest by a large number of small axes from rhizomatous species, and in the central forest by a lower density of subterranean-trunked palms with larger leaves.

RESUMEN

Las características de la comunidad de palmeras en bosques de altura de la Amazonía están definidas a partir de tres inventarios hechos respectivamente en el Bajo Tocantins (Este), en el Bajo Río Negro (Centro) y en el Bajo Ucayali (Oeste). En los tres bosques, la mayoría de las palmeras son especies pequeñas del sotobosque; la communidad está concentrada debajo de 10 m de altura (99.8 a 99.9%), y los adultos de las especies arborescentes están presentes con densidades bajas. Riqueza específica y densidad son claramente más altas en los bosques de las regiones occidental y central. La diferencia de densidad entre estas dos últimas corresponde a una diferencia entre las formas de vida dominantes. La ocupación del sotobosque por las palmeras es casi total en ambos casos: en el bosque de la región Oeste, son especies rizomatosas que producen una alta densidad de ejes pequeños; en el bosque de la región central, son especies en densidad más baja, pero que son caracterizadas por su tronco subterráneo y sus hojas de gran tamaño.

PALMS ARE ONE OF THE MOST characteristic components of Amazonian landscapes. Travelling throughout the Amazon basin, most of the earlier naturalist-explorers were attracted by palms. D'Orbigny, Wallace, Martius, Drude, Barbosa Rodrigues, Poiteau, Spruce, and Trail left basic studies on the taxonomy of palms, with numerous notes on their ecology and use by the natives. Although these studies reflect their enthusiasm, the early explorers provided little quantitative data on species richness and density of palms in Amazonian forests. Most forestry and botanical inventories that include plants with ≥10 cm DBH take into account the trunked palms (Black *et al.* 1950; Pires *et al.* 1953; Lechthaler 1956; Takeuchi 1960; Prance *et al.* 1976; Gentry 1982, 1985; Boom 1986a, b), but they do not consider the majority of smaller palms.

To define and compare the characteristics of the palm community in terra firme forests, we present here a synthesis of three palm inventories at different locations in the Amazon basin.

STUDY AREAS

The three forests studied were located in the eastern, central, and western Amazon basin.

EASTERN AMAZONIA.—The first site was located in the lower Rio Tocantins valley on the east bank of the river near the city of Tucuruí (3°30'S, 49°0'W). A total of 3.84 ha on ferralitic soils was surveyed. This area was part of a more extensive inventory (10.56 ha) that included ferralitic, sandy, and waterlogged soils (Kahn 1986a).

CENTRAL AMAZONIA.—The second site was located in the lower Rio Negro valley, 60 km north of Manaus (2°35'–2°40'S, 60°00'–60°20'W), at the Experimental Station of Tropical Sylviculture (National Institute for Amazonian Research, INPA). The relationship between palms, soils, and topography was investigated on 1.2 ha (Kahn & Castro 1985). We consider here only the 0.72 ha on well-drained, clayey, ferralitic soils.

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TABLE 1. *Species richness in the three terra firme forests.*

Genera	Number of species		
	Lower Ucayali (0.71 ha)	Lower Rio Negro (0.72 ha)	Lower Tocantins (3.84 ha)
Astrocaryum	1	2	1
Bactris	10	11	4
Chelyocarpus	1	—	—
Desmoncus	1	—	—
Euterpe	1	1	1
Geonoma	5	6	2
Hyospathe	1	—	—
Iriartella	1	1	—
Jessenia	1	—	—
Lepidocaryum	1	—	—
Maximiliana	1	—	1
Oenocarpus	1	2	1
Orbignya	1	—	—
Pholidostachys	1	—	—
Scheelea	—	1	—
Socratea	1	1	1
Syagrus	—	1	1
Wettinia	1	—	—
Total species	29	26	12

WESTERN AMAZONIA.—The third site was located in the lower Rio Ucayali valley near the village of Jenaro Herrera (4°55'S, 73°40'W) at the Center for Research and Development (CID-JH) of the Research Institute of Peruvian Amazonia (IIAP). A survey of 0.71 ha is selected from a larger inventory (Kahn & Mejia, in press).

The climate of the three regions is humid, with an average annual rainfall from about 2 m (center) to 2.5 m (east and west) and an average temperature of 25–26°C.

METHODS

For each inventory, all palms were counted in delimited areas. In the case of multistemmed species, each axis was considered as a separate plant.

In the eastern and central forests, 0.12-ha plots were distributed along a topographic gradient: on plateau, crest, slope, and in the lowest part of the slope (only in the eastern forest). In the western forest, contiguous 0.02-ha plots were distributed along a transect from the plateau to the lowest part of the slope.

Species names and voucher numbers can be found in the publications cited above. Brazilian palms were deposited at INPA, and Peruvian palms at USM, BH, K and NY. Most of these latter were identified by J. Dransfield (K). Several species of *Bactris* and *Geonoma* were not identified because of either the lack of fertile material or the lack of comparable specimens in the herbaria; the latter was especially the case in *Bactris*. Distinguishing palm species in the field, however, was possible after assembling a collection from seedling to adult of each species involved and working with palms in these forests for several months (eastern Amazonia) or years (central and western Amazonia).

RESULTS

SPECIES RICHNESS.—We found 12 species in 8 genera on the 3.84 ha surveyed in eastern Amazonia, 26 in 9 genera on 0.72 ha in central Amazonia, and 29 in 16 genera on 0.71 ha in western Amazonia. In the central and western sites, 2 genera were especially diversified: *Bactris* with 11 and 10 species, respectively, and *Geonoma* with 6 and 5 species, respectively (Table 1).

DENSITY AND VERTICAL DISTRIBUTION.—Palm density was lowest at the eastern Amazonian site with 3446 palms on 3.84 ha (90 per 0.1 ha). The central Amazonian forest presented 2326 palms on 0.72 ha (323 per 0.1 ha). The highest density was encountered in the western forest, with 7004 palms on 0.71 ha (986 per 0.1 ha). In the three forests studied, the great majority of palms (99.8 to 99.9%) were under 10 m in height (Table 2).

LIFE FORMS.—Most of the palms counted belonged to understory, small species (Table 3). Multistemmed palms were predominant at both eastern and western sites, with respectively 72.3 and 84.0 percent of the palm community density. This life form is characteristic of most species of *Bactris* and *Geonoma,* and of *Astrocaryum munbaca* Mart., *Hyospathe* cf. *weberbaueri* Dammer ex Burret, *Iriartella setigera* (Mart.) Wendl., *Lepidocaryum tessmannii* Burret, *Oenocarpus minor* Mart. (generally single-stemmed with new shoots from the base), and *Wettinia augusta* Poepp. et Endl. Understory, single-stemmed palms were fewer: *Chelyocarpus repens* F. Kahn & K. Mejia, *Syagrus inajai* (Spruce) Becc., *Geonoma poeppigiana* Mart., and *Pholidostachys synanthera* (Mart.) H. E. Moore. Lianescent palms and acaulescent palms with small leaves were found only at the western site, represented by *Desmoncus* sp. and

TABLE 2. *Density and vertical distribution of palms in the three terra firme forests.*

	Lower Ucayali (0.71 ha)	Lower Rio Negro (0.72 ha)	Lower Tocantins (3.84 ha)
>10 m height	5 (0.07%)	4 (0.17%)	4 (0.12%)
<10 m height	6999 (99.93%)	2322 (99.83%)	3442 (99.88%)

TABLE 3. *Palm life forms in the three terra firme forests. Density (%) is given for each life form with the number of species (in parentheses).*

	Lower Ucayali (0.71 ha)	Lower Rio Negro (0.72 ha)	Lower Tocantins (3.84 ha)
Understory palms:			
Multistemmed	84.0% (16)	29.8% (20)	72.3% (7)
Single-stemmed	6.5% (4)	3.9% (1)	2.3% (1)
Acaulescent with small leaves	1.0% (1)	—	—
"Acaulescent" with tall leaves and subterranean trunk	2.7% (1)	35.2% (2)	—
Lianescent	0.0% (1)	—	—
Arborescent palms:			
Multistemmed	—	—	0.1% (1)[a]
Single-stemmed	5.7% (6)	31.2% (3)	25.2% (3)

[a] Only seedlings.

Geonoma acaulis Mart. "Acaulescent," subterranean-trunked palms with long leaves were common (35.2%) at the central Amazonian site: *Astrocaryum sociale* Barb. Rodr. and *Scheelea* sp. (identified as *Attalea attaleoides* in Kahn & Castro [1985], using Wessels Boer's nomenclature). This life form was less abundant (2.7%) in the western forest—*Orbignya polysticha* Burret—and totally absent in the eastern forest.

Six arborescent, single-stemmed species were largely or exclusively represented by seedlings and juveniles: *Oenocarpus bacaba* Mart., *Socratea exorrhiza* (Mart.) Wendl., *Euterpe precatoria* Mart., *Jessenia bataua* (Mart.) Burret, *Maximiliana maripa* (Corrêa de Serra) Drude, and *Astrocaryum chambira* Burret. Only the first two species were represented by adults (>10 m), which accounted for a mere 0.2 percent of palm community density (Table 2). Arborescent, multistemmed palms were encountered only at the eastern site, limited to a few seedlings of *Euterpe oleracea* Mart.

DISCUSSION

Palm species richness is clearly higher in the lower Ucayali (west) and Rio Negro (center) than in the Rio Tocantins forest (east). This conclusion is corroborated by data from French Guiana, where Sist (1985) found 7 species on 0.5 ha of ferralitic soils, and Granville (1986) encountered 10 species on 1.26 ha on the slopes of the Galbao mountains, between 320 and 660 m in altitude. Generic richness is also highest in the western part of the Amazon Basin.

Species richness is higher in terra firme forests where understory species in particular are more numerous than in seasonal swamp forests. In central Amazonia, for instance, 0.12-ha plots on waterlogged soils contained 6 to 7 species, 2 to 3 of which were limited to the understory; in the neighboring terra firme forest, 16 to 20 species were found on similar areas, with 14 to 17 understory palms (Kahn & Castro 1985).

Palm density is lowest in the Rio Tocantins forest (east) and is also low in French Guiana. The difference in density between central and western forests (Table 2) reflects a difference in dominant life forms. The very high density of the palm community in the Ucayali forest (west) is due to multistemmed palms in the understory. One species, *L. tessmannii* Burret, is especially abundant, with 3801 axes on 0.71 ha (54.3% of the palm community). In Peruvian Amazonia, this species proliferates by rhizomatous propagation (Kahn & Mejia 1987). This is not the case in the Rio Negro forest (center) where the most abundant life form is subterranean-trunked palms with large, funnel-like leaves (5–6 m in length). Here 676 acaulescent palms were found on 0.72 ha. This life form is interpreted as an adaptation to forests with modest-sized trees and small gaps (Kahn 1986b). Although life forms are highly variable, spatial occupation of the understory by palms is almost complete at both sites: in the western forest by a large number of small axes and in the central forest by a lower density of palms with larger leaves.

Adult arborescent palms are very uncommon in terra firme forests. The opposite is true of seasonal swamp forests, which are characterized by a high density of tall palms such as *Mauritia flexuosa* L.f., *J. bataua* (Mart.) Burret, and *Euterpe* spp. (Bouillenne 1930; Oldeman 1969; Gonzales 1971; Kahn 1988). Whereas arborescent, single-stemmed species occur in both ecosystems, multistemmed species, which are frequent in seasonal swamp forests, are virtually absent in terra firme forests (Granville 1978).

Palms are generally depicted with the arborescent, single-stemmed form. The largest and one of the most diversified palm communities of the world is, however, mainly represented by small, understory species.

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