Life Forms of Amazonian Palms in Relation to Forest Structure and Dynamics[1]

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ABSTRACT

Two Amazonian *terra firme* forests present contrasting structures and palm compositions: one is characterized by tall and broad-trunked trees up to 50 m in height and 2.5 m in DBH, and by tall arborescent palms; the other by more modest-sized trees up to 40 m in height and 1.3 m in DBH, and by abundant acaulescent and smaller arborescent palms.

This comparison strongly suggests that forest structure and dynamics influence life forms, palm size, and species diversity.

Gap size, which mainly depends on the size of upper-canopy trees, determines the intensity of light reaching the understory and thus influences the development of arborescent palms. In this analysis, acaulescent forms are regarded as an adaptation to forests with small trees and resultant small gaps.

Palms offer a great variety of life forms (Holttum 1955; Bondar 1964; Corner 1966; Mangenot 1969, 1973; Moore 1973; Moore & Uhl 1973; Whitmore 1973; Hallé *et al.* 1978). Most of them occur in tropical rain forests, but as Dransfield (1978) concluded, "In most instances . . . so little is known about the interactions of palms and their environment that no obvious correlations can be indicated."

A successful approach considers the relationship between forest dynamics and palm communities. For example, population sizes of several palm species are larger in the first stage of sylvigenesis (Granville 1978, Martinez 1980), and in one case, a palm distribution pattern is conditioned by the pattern of fallen trees (Richards & Williamson 1975).

I shall suggest here that because two forests differ in dynamics and structure, they are characterized by different palm life forms, palm sizes, and palm species diversity.

FOREST STRUCTURE AND DYNAMICS

General data.—An important factor influencing forest dynamics is the death and fall of trees and the consequent formation of gaps in the canopy (Cousens 1965; Poore 1968; Oldeman 1974a, b, 1979, 1983; Whitmore 1975, 1978, 1982; Brokaw 1982a). Gap size influences light availability, soil temperature, and humidity—factors which determine colonizer composition (Vasquez-Yanes 1974, Holthuijzen & Boerboom 1982). Large gaps are most suitable for colonization by pioneer trees, as shown by Kramer's early experiments (1933) and other numerous studies summarized and discussed by Hartshorn (1978, 1980), Denslow (1980), Whitmore (1982, 1983), and Brokaw (1982b, 1985a, b). Sizes of the largest gaps are related to sizes of the largest trees, and gap frequency depends on declivity, microrelief, and soil structure (Oldeman 1974a, Nierstraz 1975, Huttel 1977, Hartshorn 1978, Bonnis 1980, Kahn 1983), as well as on storm frequency.

Study areas.—The eastern forest is located in the Tocantins valley between the towns of Tucuruí and Itupiranga (3°30′–5°S, 49°–49°30′W). The central Amazonian forest is near Manaus, at the Experimental Station of Tropical Sylviculture of the National Institut for Amazonian Research (INPA) (2°35′–2°40′S, 60°00′–60°20′W).

Both areas are in a tropical humid climate with 2.5 m annual rainfall and an average temperature of 25°C. Both have single, annual wet and dry seasons, but the distinction is more marked in the Tocantins region. Storms are more frequent in central Amazonia, according to Nieuwolt (1977).

The Tocantins forest is characterized by the great size of its trees relative to those in other Amazonian forests. Trees up to 50 m are frequent, with DBH up to 2.5 m (Table 1). Three distinct layers of foliage above 15 m in height correspond to three strata (*sensu* Richards 1952). Prominent species are *Bertholletia excelsa* Humb. and Bonpl., *Astronium lecointei* Ducke, *Anacardium giganteum* Hancock ex Engl., and *Alexa grandiflora* Ducke. The "giant" species develop large crowns, and their progressive death creates the many complex clearings seen from the air. A complex clearing, up to 0.12 ha in area, is the result of a series of successive falls of branches, each breaking small trees and shrubs in the understory, followed by the fall of the trunk, usually with a semiregenerated crown.

The forest of central Amazonia is composed of smaller trees, rarely reaching 40 m in height and 1.3 m in DBH

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TABLE 1. *Structure of the two forests and their palm communities.*

Forest structure	Tocantins valley	Central Amazonia
DBH class distribution of trees[a]:		
0.15 m ≤ DBH < 0.6 m	189	384
0.6 m ≤ DBH < 1.3 m	13	11
1.3 m ≤ DBH	5–6	—
Largest DBH	2.5 m	1.25 m
Mean height of upper-canopy trees	45 m	30 m
Largest size of clearings	0.12 ha	0.060 ha
Palm community		
Area surveyed	10.56 ha	1.2 ha
Mean density of palms/ha h ≥ lm	602	2122
Number of understory species	12	27
Number of acaulescent species	0	4
Number of acaulescent palms	0	1345
Number of arborescent species in upland forest	5	2
Height of arborescent species	25–30 m	15 m

[a] Mean number of stems/ha in three DBH classes obtained from 2.4 ha surveyed in Tocantins forest and from 1.44 ha surveyed in this study and Prance *et al.*'s data (1976) on 1 ha in a central Amazonian forest.

(Table 1). The average height of the upper-canopy trees is about 30 m. There are no particularly abundant species, although most frequent are *Manilkara surinamensis* (Miq.) Dub., *Hevea guianensis* Aubl., *Scleronoma micranthum* Ducke, *Caryocar villosum* (Aubl.) Pers., and *Dinizia excelsa* Ducke (Lechthaler 1956, Takeuchi 1960, Aubreville 1961, Prance *et al.* 1976, Alencar *et al.* 1979). Although these species can develop large branches, "giant" trees overlooking this forest are rare (J. M. Rankin, pers. comm.). The falls of the biggest trees knock down others, causing multiple clearings (Florence 1981), the areas of which do not exceed 0.06 ha.

LIFE FORMS OF PALMS IN RELATION TO FOREST STRUCTURE AND DYNAMICS

NOTABLE DIFFERENCES IN PALM LIFE FORMS BETWEEN THE TWO FORESTS.—Twenty-seven understory species were found on 1.2 ha in the central Amazonian forest, lumping acaulescent, single-, and multistemmed palms together (Kahn & Castro 1985) (Table 1). Four acaulescent (no stems above ground) species are abundant: *Astrocaryum acaule* Mart., *A. sociale* Barb. Rodr., *Attalea attaleoides* (Barb. Rodr.) W. Boer, and *A. spectabilis* Mart. Their leaves spread up, funnel-like, to 5 m and constitute an almost continuous cover. A short trunk, up to 0.5 m in length and 0.15 m in diameter, develops in soil up to 1 m in depth. Such acaulescent forms are totally absent from the Tocantins forest, where only 12 understory species—single- and multistemmed palms—were found on 10.56 ha surveyed (Kahn 1986).

Only two arborescent palm species frequently occur in the upland forest of central Amazonia, *Oenocarpus bacaba* Mart. and *Iriartea exorrhiza* Mart. A third arborescent species, *Euterpe precatoria* Mart., is only occasionally found in the upland forest, although abundant in the neighboring seasonal swamp forest. Five arborescent species are frequent in the Tocantins upland forest: *Oenocarpus bacaba* Mart., *O. distichus* Mart., *Iriartia exorrhiza* Mart., *Attalea regia* (Mart.) W. Boer, and *A. speciosa* Mart. There they reach 25–30 m in height; by contrast, *O. bacaba* Mart. and *I. exorrhiza* Mart. do not exceed 15 m in height in central Amazonia. In both forests, these species were

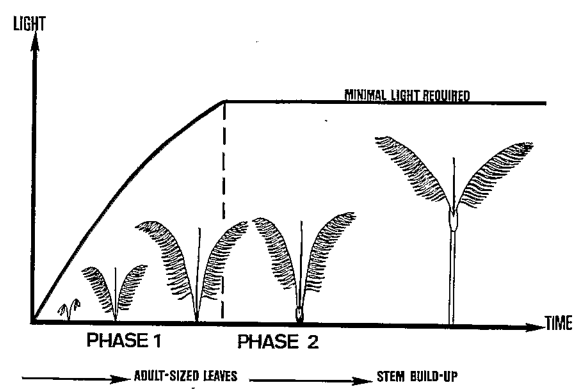

FIGURE 1. Arborescent palm growth and light requirements (after Granville 1978). Minimal light required increases with leaf size (phase 1). With adult-sized leaves, the palm needs a consistently high light intensity level for building its stem (phase 2).

consistently found below discontinuities of the upper canopy, indicating that they can compete only in clearings with enough light.

Arborescent forms in the light of gaps.—Light intensity levels required by forest palms are described by Granville (1978). Two growth phases are distinguished (Fig. 1). The first, which corresponds to the elaboration of adult-sized leaves, requires progressively higher levels of light intensity. The second phase corresponds to the elaboration of the stem and requires a consistently high light intensity level. In fact, this second phase occurs only when the palm stands in full sunlight, *i.e.,* under gaps in the forest canopy.

In the complex clearings of the Tocantins forest, of 0.10–0.12 ha in area, pioneer trees close gaps, whereas closing by development of the tree crowns from the border is negligible. Palm growth must keep pace with pioneer trees in order to compete effectively for light and, thereby, receive the sunlight necessary for the elaboration of the stem (Fig. 2A). Arborescent palms are suitably adapted for regeneration in these sites.

In the smaller gaps of the central Amazonian forest, areas of which do not exceed 0.06 ha, closing from the border tree crowns is relatively effective in producing a continuous layer of foliage. The light intensity that penetrates the understory layers consequently decreases. Arborescent palm species can reach the first growth phase, but they do not receive enough light for building their stems (Fig. 2B). Arborescent palms are found in the central Amazonian forest, but they occur only on plateaus where gap areas are greater because of a higher frequency of larger trees than on other topographic sites (Guillaumet & Kahn 1982), and on the crests where gaps are more frequent because of wind and declivity effects.

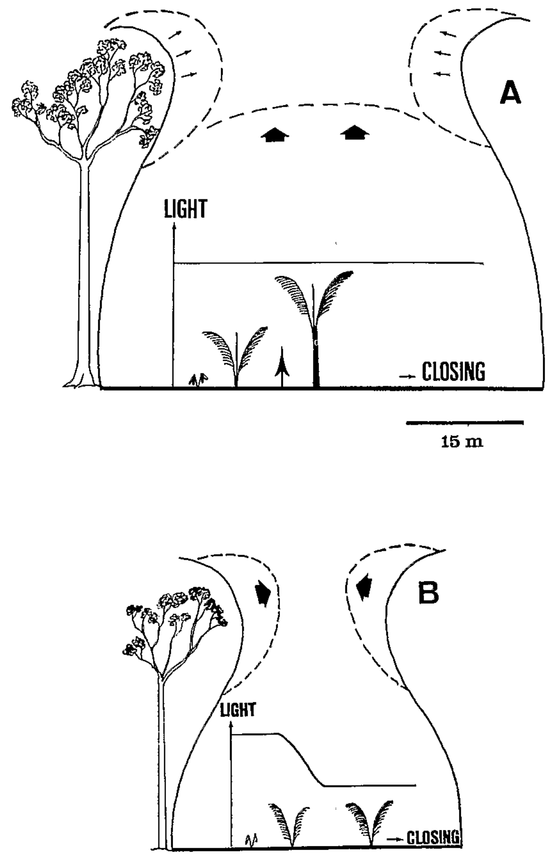

FIGURE 2. Arborescent palm growth in relation to gap size, gap closing, and available light. A. Large gap (up to 0.12 ha) in the Tocantins forest. Pioneer trees close gaps, and closing by the tree crowns from the border is negligible. Palms receive the sunlight necessary for the elaboration of the stem. B. Smaller gap (not exceeding 0.06 ha) in the central Amazonian forest. Closing by the tree crowns from the border is relatively effective, producing a continuous layer of foliages. Consequently, light intensity is decreasing in understory layers where palms do not receive enough light for building their stems.

Adaptive value of the acaulescent forms in tropical rain forest.—The high diversity of understory species in the central Amazonian forest, where trees and gaps are smaller, emphasizes a strong adaptive tendency in palms to colonize low-light layers. The acaulescent forms, in particular, must be regarded as an adaptation to this forest with small trees and small gaps: when gaps close from the tree crowns of the border, palms do not receive the required light intensity to build their stems. They remain at a low light intensity level and can only elaborate a small subterranean axis. Such life forms, which dominate the understory of this forest, do not occur in the Tocantins forest characterized by "giant" trees and resultant large gaps. Some are present but not abundant in forests with intermediate sized trees, such as *Astrocaryum huicungo* Dammer in the Peruvian forest of Jenaro Herrera near Iquitos described by Marmillod (1982), and *Astrocaryum paramaca* Mart., *A. attaleoides* (Barb. Rodr.) W. Boer, and *Attalea sagotii* (Trail ex Im Thurn) W. Boer in the forests of French Guyana described by Granville (1976, 1978) and Lescure (1983).

In tropical rain forests, this adaptation must be related to the light intensity through forest structure and dynamics. However, acaulescent species occur in very open and drier vegetation such as the *campos cerrados* in southern Brazil (Bondar 1964, Medeiros-Costa & Panizza 1983). In this case, acaulescent palms receive constant intense light. The main ecological constraint is water, and the acaulescent form is likely to represent an adaptation to dry conditions as suggested by Rawitscher and Rachid (1946). This indicates that acaulescent forms have different adaptive values in relation to habitats.

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