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LIFE FORMS AND GROWTH STRATEGIES OF GUIANAN PALMS AS RELATED TO THEIR ECOLOGY

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Abstract

Palm life forms and species found in the main ecosystems of the 3 Guianas (savannahs, herbaceous swampy savannahs, forests) are described and listed respectively. Stems are erect, creeping, climbing or subterranean, and palms are solitary or clustered. Leaf blades are entire, irregularly or regularly divided into pinnae which are regularly disposed in one plane or clustered and oriented in several directions from the rachis. All these characters are considered in relation to habitat. Small, clustered palms with entire or divided leaves predominate in shady understory. Species with creeping rhizomes are mostly found in quickly changing mediums, such as periodically flooded ecosystems, owing to their capacity to spread and to form dense clonal populations. Erect solitary palms are particularly well adapted to fit gaps in the canopy and are therefore more frequent in disturbed forests. Most examples are illustrated. In conclusion, it seems that palms are fairly well adapted to marginal habitats.

Key words: *Arecaceae, Guianas, life forms, growth strategy.*

FORMAS BIOLÓGICAS Y ESTRATEGIAS DE CRECIMIENTO DE LAS PALMAS GUYANESAS EN RELACIÓN CON SU ECOLOGÍA

Resumen

Se describe las formas biológicas de las palmas encontradas en los principales ecosistemas de las tres Guyanas (sabanas, sabanas herbáceas pantanosas y bosques) y se da una lista de las especies. Luego se considera el tipo de estipite en relacion con el hàbitat: estipite erecto, rastrero, trepador o subterráneo, solitario o multiple. De la misma manera se analiza el tipo de ramificación basal y la morfología de las hojas: enteras, disecadas en segmentos de ancho irregular, o divididas en muchas pinnas regularmente distribuidas en un plano, o bien agrupadas y orientadas en diversas direcciones a partir del raquis. Pequeñas palmas cespitos, con hojas enteras o poco divididas, predominan en el sotobosque. Especies con rizomas rastreros se encuentran principalmente en medios rapidamente cambiantes, como los ecosistemas periódicamente inundados, debido a la alta capacidad de dichas palmas para extenderse y formar densas poblaciones clonales. Las palmas erectas, solitarias, particularmente bien adaptadas para llenar los estrechos claros de la copa de los árboles, son por lo tanto más frecuentes en los bosques alterados. Son ilustrados la mayoría de los ejemplos. En conclusión, parece que las palmas están muy bien adaptadas a los hábitats marginales.

Palabras claves: *Arecaceae, Guyanas, formas biológicas, estrategia de crecimiento.*

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FORMES BIOLOGIQUES ET STRATÉGIES DE CROISSANCE DES PALMIERS GUYANAIS EN RELATION AVEC LEUR ÉCOLOGIE

Résumé

Après une description des formes biologiques des palmiers présents dans les principaux écosystèmes des trois Guyanes (savanes, marécages à végétation herbacée, forêts), une liste des espèces est donnée. Les types de stipe sont ensuite considérés en fonction de l'habitat : stipe érigé, rampant, grimpant ou souterrain, solitaire ou multiple. De la même manière sont analysés les types de ramification basale et la morphologie des feuilles : entières, disséquées en segments de largeur variable ou divisées en nombreuses folioles disposées soit régulièrement selon un plan, soit groupées et orientées dans plusieurs directions. Les petits palmiers cespiteux, à feuilles entières ou peu divisées, prédominent dans les sous-bois. Les espèces à rhizomes rampants se trouvent principalement dans les milieux soumis à de brusques changements, tels que les écosystèmes périodiquements inondés, en raison de leur grande aptitude à former de denses populations clonales. Les palmiers érigés et solitaires sont particulièrement bien adaptés pour cicatriser les trouées de la canopée; ils sont plus fréquents dans les forêts perturbées. La majorité des exemples est illustrée. En conclusion, il semble que les palmiers soient parfaitement adaptés aux habitats marginaux.

Mots clés : *Arecaceae, Guyanes, formes biologiques, stratégies de croissance.*

The three Guianas constitute, with part of Venezuela and the Brazilian State of Amapá, the phytogeographic region of the Guianas which is distinct from the Amazon Basin because of the old Precambrian shield and a hydrographic network independent of those of the Amazon and Orinocco rivers. The major Guianan rivers flow directly into the ocean. For practical reasons, the international program "Flora of the Guianas", which started in 1983, deals with an area limited to the political boundaries of the three Guianas. Consequently, this short analysis concerns only the palms growing in Guyana, Surinam and French Guiana.

The different vegetation types found in the Guianas are:

- Forests, including the mangrove, the montane and the lower montane moist forests, the inundated forest types (marsh and swamp forest), the low transition forest on granite outcrops, the liana forest on lateritic crusts, and the upland moist forests on ferrallitic soils which are found everywhere on gently undulating terrain (Granville, 1988).

- Open vegetation types, including the different categories of herbaceous swamps restricted to the coastal plain, the dry savannas, the epipetric low lying plant communities on granite outcrops, and the montane scrub and swamps found on the highest tops of the Guayana Highland (Granville, 1991; 1992).

So far, 81 species of palms are known from the Guianas in the following genera (tab. 1): *Acrocomia* (1 sp.), *Asterogyne* (1 sp.), *Astrocaryum* (7 sp.), *Bactris* (27 sp.), *Desmoncus* (3 sp.), *Dictyocaryum* (1 sp.), *Elaeis* (1 sp.), *Euterpe* (2 sp.), *Geonoma* (17 sp.), *Hyospathe* (1 sp.), *Iriartella* (1 sp.), *Jessenia* (1 sp.), *Leopoldinia* (1 sp.), *Lepidocaryum* (1 sp.), *Manicaria* (1 sp.), *Mauritia* (1 sp.), *Mauritiella* (1 sp.), *Maximiliana* (1 sp.), *Oenocarpus* (1 sp.), *Orbignya* (3 sp.), *Scheelea* (4 sp.), *Socratea* (1 sp.) *Syagrus* (3 sp.).

A. OPEN VEGETATION TYPES

Single-stemmed palms:

Acrocomia lasiospatha
Geonoma appuniana
Geonoma fusca
Mauritia flexuosa
Maximiliana maripa
Syagrus cocoides

Multi-stemmed palms:

Astrocaryum jauari
Astrocaryum vulgare
Bactris campestris
Bactris cruegeriana
Bactris major
Bactris pallidispina
Desmoncus orthacanthos
Leopoldinia pulchra
Mauritiella martiana

B. FOREST CANOPY

Single-stemmed palms:

Astrocaryum rodriguesii
Euterpe precatoria
Jessenia bataua
Socratea exorrhiza
Maximiliana maripa
Oenocarpus bacaba
Orbignya phalerata

Multi-stemmed palms:

Euterpe oleracea
Syagrus stratincola

C. FOREST UNDERSTORY

Single-stemmed erect palms:

Asterogyne guianensis
Astrocaryum sciophilum
Geonoma appuniana
Geonoma bartlettii
Geonoma poiteauana
Geonoma umbraculiformis
Manicaria saccifera
Syagrus cocoides
Syagrus inajai

Single-stemmed procumbent palms:

Elaeis oleifera

Subterranean stemmed palms:

Astrocaryum paramaca
Orbignya polysticha
Orbignya sagotii
Scheelea sp. 4
Scheelea sp.1
Scheelea sp.2
Scheelea sp.3

Multi-stemmed palms:

Astrocaryum munbaca
Astrocaryum murumuru
Bactris acanthocarpoides
Bactris aubletiana
Bactris balanophora
Bactris capinensis
Bactris constanciae
Bactris elegans
Bactris floccosa
Bactris gastoniana
Bactris gaviona
Bactris geonomoides
Bactris humilis
Bactris maraja
Bactris oligocarpa
Bactris oligoclada
Bactris pectinata
Bactris penicillata
Bactris rhaphidacantha
Bactris simplicifrons
Bactris trailiana
Bactris turbinocarpa
Bactris sp. 1
Bactris sp. 2
Bactris sp. 3
Desmoncus macroacanthos
Desmoncus polyacanthos
Dictyocaryum ptariense
Geonoma arundinacea
Geonoma baculifera
Geonoma deversa
Geonoma euspatha
Geonoma leptospadix
Geonoma maxima
Geonoma oldemanii
Geonoma pinnatifrons
Geonoma piscicauda
Geonoma stricta
Geonoma sp.1
Geonoma sp.2
Hyospathe elegans
Lepidocaryum guianense

Table 1 - Palm species of the Guianas.

The distributions of these palms depends on the different biotopes, vegetation types, and sylvigenetic phases of the forest and reflects narrow correlations between life forms, growth strategy, and habitat. Growth forms of palms in rain forests of Asia and Africa and their relation with habitat have been discussed by Dransfield (1978). The purpose of my discussion is to describe the life forms of Guianan palms and provide estimates of the proportion of different life forms among palm species found in forests on the one hand and in open vegetation types on the other hand. Only the vegetative features, which are much more diverse than floral variation, will be analyzed. As a matter of fact, all Guianan palms have axillary inflorescences and are pleionanthic. Nevertheless, inflorescences vary in size, branching (spicate or branched), habit (erect or pendent)... In contrast, more significant variations are observed in the type of stem (either solitary or clumped; erect, climbing, procumbent or subterranean) and the morphology of leaves (either pinnate, costapalmate or entire, with narrow or broad leaflets, regularly spaced in one plane or distributed in groups in all directions).

LIFE FORMS AND HABITAT

1. Single-stemmed palms (Fig. 1 A-G)

These palms belong to Corner's model (Hallé & Oldeman, 1970; Hallé *et al.*, 1978) and represent 34% of the Guianan palms (28 species). This model can be divided into the following three growth habits depending on the orientation of the stem: erect, procumbent or subterranean.

Erect trunk. Seventy four percent of these palms are found in forests (17 species) whereas only 26% grow in open vegetation (6 species) like *Mauritia flexuosa* (Fig. 1G, Fig. 2A):

- The forest palm species are equally distributed between the canopy (8 species) and the understory (9 species). Species of palms reaching the canopy are represented by tall palms with the crown fully exposed to the sun (Fig. 1A, tab. 2). They may have a stout trunk like *Maximiliana maripa* or a slender trunk like *Euterpe precatoria*. They are sometimes provided with stilt-roots at the base (*Socratea exorrhiza*) or with internodes armed with spines (*Astrocaryum rodriguesii*).

	FOREST			OPEN VEGETATION
	Canopy	Understory	Total	
SINGLE-STEMMED				
erect	7	9	18	6
procumbent	0	1	1	0
subterranean	0	7	7	0
MULTI-STEMMED				
erect	2	40	42	8
climbing	0	2	2	1

Table 2 - Number of palm species per life form.

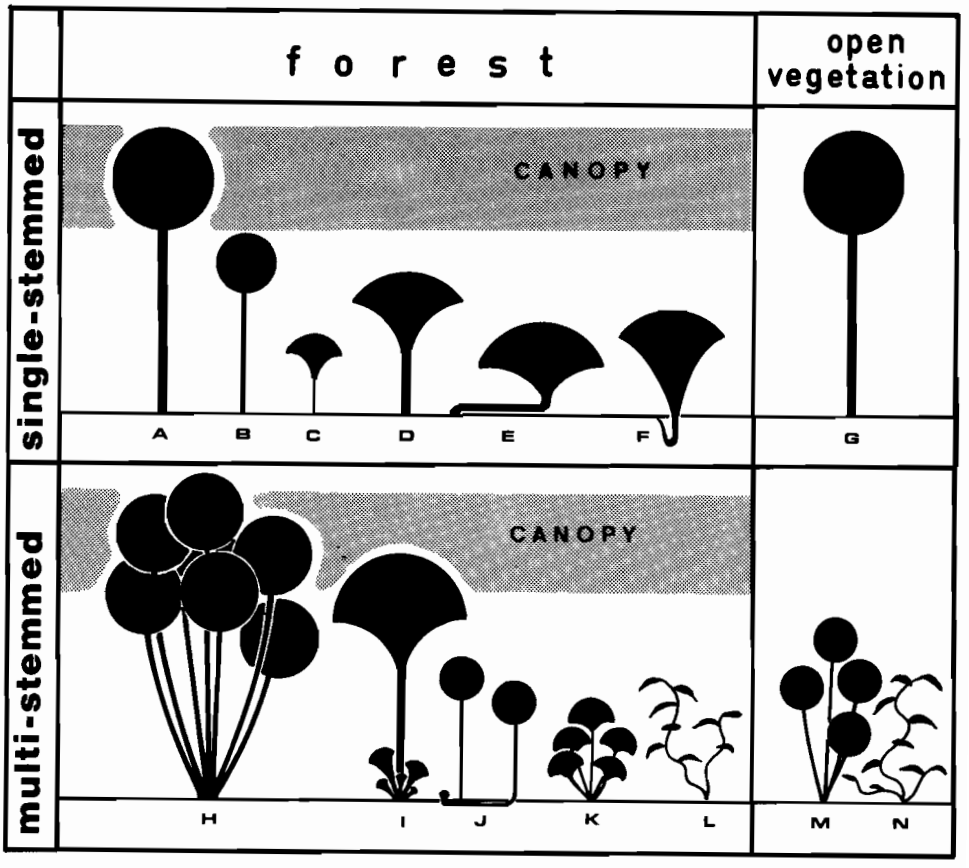

Fig. 1 - Life forms of palms. Single-stemmed palms: A-D. Forest palms with erect trunk: tall palms of the canopy (A), small, slender palms of the understory (B,C), short-stemmed palms with large leaves of the understory (D); E. Procumbent palms of the understory; F. Subterranean trunked palms of the understory; G. Savanna palms with erect trunk. Multi-stemmed palms: H. Caespitose palms of the canopy; I. "Sub-solitary" palms; J. Rhizomatous and stoloniferous palms; K. Caespitose palms of the understory; L. Climbing palms of the understory; M. Caespitose palms of open vegetations; N. Climbing palms of open vegetations.

- Small palms living in the shade of the understory possess more various growth habits than the canopy species. Species of *Asterogyne* and *Geonoma* are tiny palms under two to three meters with slender stems less than 3 cm in diameter (*Geonoma umbraculiformis*, Fig. 1C) or they are rarely stemless (*Geonoma poiteauana*). The genus *Syagrus* is represented by solitary, medium-sized palms up to 12 meters tall (Fig. 1B). A third habit corresponds to short-stemmed palms with large leaves (Fig. 1D) like *Manicaria saccifera* and *Astrocaryum sciophilum* (Fig. 2C).

Procumbent palms (Fig. 1E). *Elaeis oleifera*, which grows in the swamp forest understory, is the only Guianan palm with a procumbent life form.

Fig. 2A - *Mauritia flexuosa*, a single-stemmed palm with a stout erect trunk and costa-palmate leaves, mostly growing in open vegetation.

Subterranean trunked palms (Fig. 1F). Formerly incorrectly called "stemless" or "acaulescent" (Holttum, 1955) these palms have geotropic, saxophone-shaped stems which penetrate deep in the soil (up to 1 meter) and give rise to funnel-shaped crowns of large leaves which act as a litter collector (Granville, 1978b): dead leaves falling from trees are collected at the base of the palm where they form a mound rich in organic substances which may be exploited by the roots of the palm (Fig. 2C). They are exclusively found in the forest understory. *Astrocaryum paramaca*, *Scheelea* spp. and *Orbignya polysticha* (Fig. 2B) are examples of this growth form.

Fig. 2B - *Orbignya polysticha*, a single-stemmed palm with a subterranean trunk and regularly pinnate leaves, growing in forest understory.

Fig. 2C - *Astrocaryum sciophilum*, a single-stemmed palm with a short, erect trunk and regularly pinnate leaves, growing in forest understory.

2. Multi-stemmed palms (Fig. 1H-N)

Palms able to branch at the base belong to Tomlinson's model. They are much more frequent than single-stemmed species and represent 66% of the palm flora of the Guianas (54 species). Eighty three percent of them live in forest (44 species, only two of which reach the canopy) whereas 17% (9 species) are found in open vegetation types. Branching palms are usually much smaller than are solitary single-stemmed palms.

All multi-stemmed palms have erect, rarely creeping (stolons) or subterranean (rhizomes) axes. The subterranean form occurring in single-stemmed palms with a leaf crown emerging directly from the ground is never found among multi-stemmed species. The leaf crown of multi-stemmed species always ends an erect axis which may be very short. Basal branching results in the following patterns which depend on the number and the relative position of the contemporaneous axes.

Either a clump of several contemporaneous erect axes is produced (caespitose palms; Fig 1H, K, M), or only one trunk is elaborated while branching is restricted to a few basal shoots so that the palm has a single-stemmed habit (Fig. 1I). It is impossible to give the proportion of each growth habit because all intermediates are found depending on the number of contemporaneous stems. For example, *Euterpe*

oleracea and *Syagrus stratincola*, which are respectively tall and medium-sized palms of the canopy, generally develop a large clump of many erect stems (up to 10 in the former, 20 in the latter). *Astrocaryum vulgare*, *Bactris campestris* (Fig. 2F) and *Mauritiella martiana* in savannas, *Astrocaryum munbaca*, *Bactris acanthocarpoides*, *B. maraja* in forest understory as well as many other species, produce a fewer number of stems (two to five). Most small palms of the understory, especially in *Geonoma* (Fig. 2E), *Bactris* and *Hyospathe* (Fig. 2D), develop one or two very slender axes at a time, with basal branching giving rise to new erect stems as soon as the former degenerate. Climbing palms (*Desmoncus* spp.) generally branch at the base (Fig. 1L, N). Lastly, a few species, like *Astrocaryum murumuru*, which usually grows in coastal swamp forests, have a solitary trunk with small basal shoots.

When the axes produced by basal branching first have a subterranean, horizontal, leafless growth phase, the aerial erect stems are more or less distant instead of forming a clump (Fig. 1J). A good example is found in the colonial palm *Bactris major* which forms almost pure stands along estuaries and coastal mangrove. The aerial stems are connected by a dense network of rhizomes creeping in the mud. All intermediates between caespitose and rhizomatous forms have been observed, depending on the length of the rhizomes.

Fig. 2D -*Hyospathe elegans*, a small, multi-stemmed palm with a slender, erect trunk and tri-jugate leaves, growing in forest understory.

Fig. 2E - *Geonoma stricta*, a small, multi-stemmed palm (only one stem developed) with a minute erect, erect trunk and entire leaves growing in forest understory.

Fig. 2F - *Bactris campestris*, a medium sized, multi-stemmed palm with several erect trunks developed and irregularly pinnate leaves (pinnae arranged in groups), growing in open vegetation.

Lastly, some palms produce stolons with functional leaves, running on the ground before giving rise to erect trunks. In the Guianas, only two iriarteoid palms are known to have such a growth habit : *Dictyocaryum ptariense* (Kahn & Granville, in press) and *Iriartella setigera* (Kahn, 1983; Henderson, 1990).

3. Types of leaves and habitat

Leaf morphology of Guianan palms is related to their habitat.

As a general rule, palm crowns exposed to full sun (canopy, forest margins, riverbanks, savannas, herbaceous swamps) have narrow leaflets which are often more or less coriaceous, generally hanging (*Euterpe* spp.), erect (*Bactris major*) or oriented in all directions (*Mauritia flexuosa* -Fig. 2A-, *Maximiliana maripa, Astrocaryum vulgare*). This leaf morphology seems fairly well adapted to such habitats because available light exceeds the level of light energy required by the palm. Therefore, entire blades or wide leaflets able to capture the maximum of energy would be useless or even harmful to the plant by causing excessive evapotranspiration. Moreover, narrow hanging or erect leaflets are more efficient for capturing light energy from all directions as it is distributed in open places.

On the contrary, palms growing in the understory have leaf types adapted to much lower light intensity. The blade is membranaceous and often entire or divided into a few broad segments, e.g. in *Asterogyne guianensis*, almost all species of *Geonoma* (Fig. 2E), *Bactris oligocarpa, B. trailiana, Hyospathe elegans* (Fig. 2D) and *Manicaria saccifera*. When the leaves are pinnate, the pinnae are generally broad and sigmoid and clustered in groups of two to five pairs with each group forming a flat horizontal surface (e.g. *Bactris constanciae, B. gastoniana, B. humilis, B. maraja*). If the pinnae are narrow and regularly spaced along the rachis, they are more or less horizontally arranged like in *Astrocaryum paramaca, Bactris rhaphidacantha, Orbignya* and *Scheelea* sp. pl. (Fig. 2B) and *Geonoma maxima*.

GROWTH STRATEGIES

Growth phases (Fig. 3)

Tall single-stemmed palms of forests have a very low leaf productivity in the understory (Kahn & Granville, in press). Consequently, they grow very slowly as long as they have not reached the canopy. As pointed out by Sist & Puig(1987) in their study on regeneration and population dynamics of *Jessenia bataua* in French Guianan forests, light intensity is the deciding factor for growth (waiting stages) and population structure. In most palm species, three growth phases can be roughly characterized (Granville, 1978a) -Fig. 3A-:

(1) "Establishment growth" (Tomlinson & Zimmerman 1966) in which "successive internodes are progressively wider as the primary thickening meristem becomes progressively more massive" (Tomlinson, 1979). Concomitantly, the size of the crown progressively increases. This phase requires a gradual increasing of light intensity.

(2) Homeostatic phase which starts as soon as the meristem and the crown have reached their final size. At this time, the leaf surface remains probably approximately constant. Except in a few species like *Socratea exorrhiza*, this phase lasts as long as light intensity level is too low to enable the elaboration of a stem.

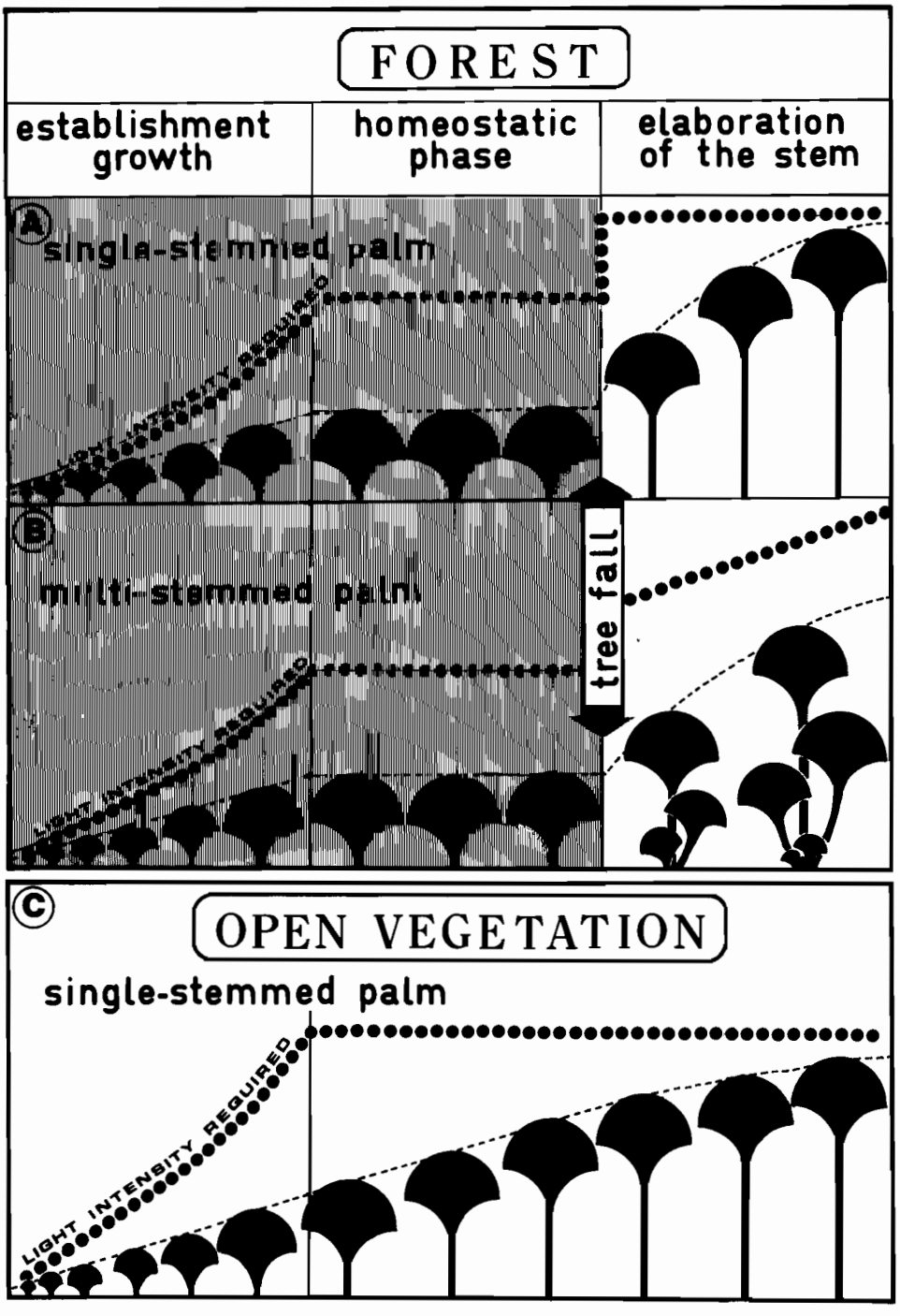

Fig. 3 - Growth phases of palms: A. Forest single-stemmed palms; B. Forest multi-stemmed palms; C. Savanna single-stemmed palms.

(3) The third phase corresponds to the elaboration of the stem and requires higher light intensity. It starts as soon as a tree fall occurs and produces a gap in the canopy. According to F. Kahn (1986) in his comparative study of Central Amazonian and Eastern Amazonian forests, subterranean-trunked palms "must be regarded as an adaptation to forests 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".

In consequence, subterranean trunked palms are more abundant in low forests with closed canopy than in high forests where tree fall cause large complex clearings.

In open vegetation types, the light intensity available is always much higher than the level required by palms, therefore the homeostatic phase does not occur. Under these conditions, the elaboration of the stem immediately follows establishment growth (Fig. 3C).

Palms with multiple stems have the same growth phases as single-stemmed palms. However, as soon new stems are produced, the light intensity required by the palm progressively increases (Fig. 3B).

Vertical and horizontal growth strategies

Because of the constant size of the crown during the elaboration of the stem, the volume of the ecotope (Whittaker *et al.*, 1973; Oldeman, 1974) during vertical growth of single-stemmed palms fits into a cylinder (Fig. 4A). On the contrary, the growth of a tree which constantly increases in diameter has a volume which is more or less a reversed cone (Fig. 4B). In consequence, tall, single-stemmed palms are much better adapted to fill narrow gaps in the canopy than are dicotyledons. This is important for understanding the role of palms in sylvigenesis and could be one of the reasons why palms are often so abundant in disturbed forests.

Palms with multiple stems have both a vertical and a horizontal growth strategy (Fig. 4C). Each individual stem is similar to a single-stemmed palm. However, the production of new stems on the same clump provides the palm with the possibility to spread horizontally especially in rhizomatous and stoloniferous species. The most efficient are palms with rhizomes which allow the palm to spread and colonize new places (Fig. 5). An unusual type of suckering regularly occurs in *Geonoma baculifera*. In this species, the tallest stems of a clump bend to the ground and new clumps are produced from suckers which develop and root from axillary buds (Granville, 1978b).

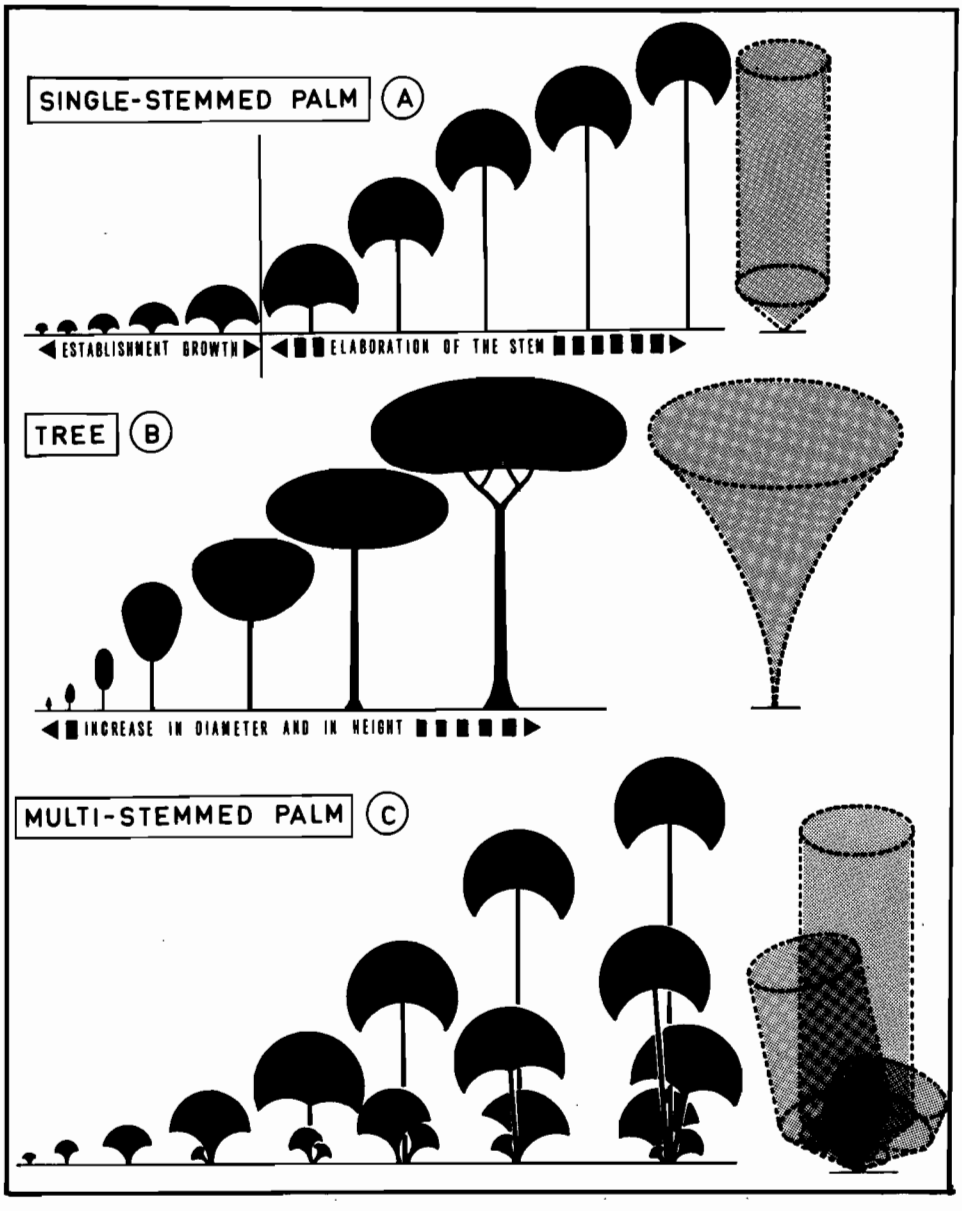

Fig. 4 - Growth strategies of arborescent monocotyledons and dicotyledons: A. Single-stemmed palm; B. Tree; C. Multi-stemmed palm.

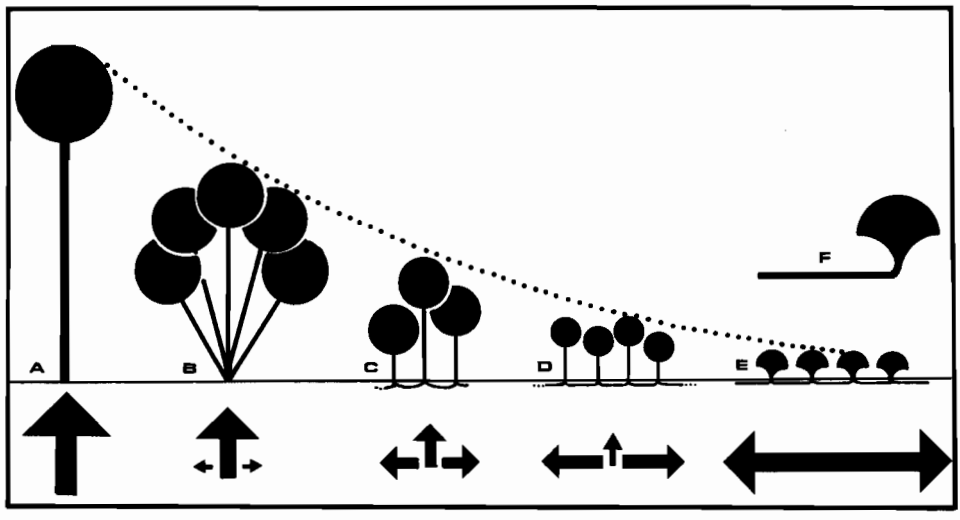

Fig. 5 - Growth strategies of palms from vertical growth (left) to horizontal growth (right): A. Single-stemmed palms with erect trunk (ex: *Jessenia bataua*); B. Caespitose multi-stemmed palms (ex: *Euterpe oleracea*); C. Medium sized rhizomatous palms (ex: *Astrocaryum munbaca*); D. Small rhizomatous palms (ex: *Bactris major*); E. Grasses and creeping rhizomatous palms (not in the Guianas; ex: *Syagrus vagans*); F. Procumbent single-stemmed palms (ex: *Elaeis oleifera*).

CONCLUSIONS

Life forms are generally more related to habitat than to specific genera. Nevertheless, some genera display a remarkable uniformity in life form. For example, almost all species of *Geonoma* are small, multi-stemmed palms with entire leaves or leaves divided into broad segments. All species of *Geonoma* grow in the same type of habitat, the forest understory. On the contrary, the genus *Astrocaryum* shows great diversity of life forms in spite of its limited number of species (tab. 3). *Astrocaryum rodriguesii* is a high, single-stemmed palm of the canopy, *A. sciophilum* is a single-stemmed palm with short trunk and large leaves of the understory, *A. paramaca* is a subterranean-stemmed palm, *A. murumuru* is a multi-stemmed palm with usually only one trunk developed and a few basal suckers growing in swamp forest, *A. munbaca* is a medium-sized, rhizomatous, multi-stemmed palm of the understory, *A. jauari* is a tall, rhizomatous, multi-stemmed palm found on inundated riverbanks and *A. vulgare* is a caespitose, multi-stemmed palm growing in savannas.

As pointed out by Hallé *et al.* (1978) for monocotyledons in general, palms which are able to branch at the base have a competitive advantage because :

- they can reproduce both vegetatively and sexually,
- their life is theoretically unlimited and
- they are able to grow both vertically and horizontally.

HABITAT LEAFLETS		FOREST regularly spaced and horizontally arranged	OPEN VEGETATION in groups, oriented in all directions
STEM :			
Solitary, erect	-tall	*A. rodriguesii* (canopy)	
	-short	*A. sciophilum* (understory)	
Solitary, subterranean		*A. paramaca*	
Several but only one developed + basal suckers		*A. murumuru*	
Several, in clump		*A. munbaca*	*A. vulgare* (savannas) *A. jauari* (riverbanks)

Table 3 - Diversity of life forms and habitats in the genus *Astrocaryum* in the Guianas.

In these characteristics, these palms are more or less similar to grasses in their growth strategy. These adaptations are also very important from the economic point of view. Clumps of multi-stemmed palms can be theoretically indefinitely exploited for palm heart and breeding of genetically pure lines is possible by vegetative reproduction.

Because of their growth strategy resulting from the lack of cambium and secondary growth, palms, as also most other monocotyledons, are well adapted to "marginal" habitats where there are ecologically limiting factors and/or quickly changing mediums (Granville, 1984). For example, there are tall single-stemmed palms in gaps of the canopy, small, caespitose palms in the shady understory, clonal populations of small and medium-sized palms in swamps, mangroves, and on riverbanks and tall palms are often abundant in disturbed vegetation. In contrast, woody dicotyledons are dominant in old sylvigenetic phases of stable rainforest on well drained soils where tall arborescent palms are scarce.

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