Rev. Biol. Trop., 31(1): 103-112, 1983

Leaf morphology of the Pejibaye palm (*Bactris gasipaes* H.B.K.)

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(Received for publication December 7, 1982)

Abstract: This is a preliminary study of the Pejibaye (*Bactris gasipaes*) frond and begins with a general morphological description of the leaf, complementing those already in existence. The data obtained from Central American Pejibayes show that the rachis length of their fronds is considerably longer than those recorded from Surinam populations and it is assumed that at least part of this difference has a genotypic background. It was also found, contrary to expectations, that the older fronds have a longer rachis than younger mature ones from the same trunk. This difference could be due to seasonal environmental factors such as variations in rainfall. The association of leaflets in groups, each leaflet having a different angle of insertion on the rachis within the group, gives a many-planed leaflet arrangement that may increase light-use efficiency. The groups are formed by a variable number of leaflets and consequently are not a reliable character for use as a descriptor. The many-planed arrangement fades in old fronds when drooping of the leaflets increases, obscuring the effect of the different angles of insertion. It was also found that assymetry exists between opposite sides of the same frond in regard to leaflet number and length. An assymetrical frond outline is evident on both sides of the frond. A larger leaflet number was found in the younger fronds when compared with the older ones from the same plant in spite of the longer rachis of the latter ones. This may indicate that even 12 year-old palms have not reached the maximum development of their fronds since it is assumed that leaflet number is less affected by environmental variations than rachis length.

The frond of a palm is its principal photosynthetic organ and is ultimately responsible for bio-mass increment. For this reason a knowledge of the frond is essential for understanding many genetic and agronomic data of a given species.

In the oil palm (*Elaeis guineensis* Jacq.) these studies were initiated in 1925 (Broekmans, 1957) and have led to an extensive knowledge of the frond and its relation to growth and production. In Malaysia Hardon *et al.* (1969) found in the oil palm a positive correlation between leaf area and production, although this was less evident in other studies in West Africa (Hartley, 1977). The study of the frond has led to the calculation of various parameters such as the Leaf Area Index, Leaf Area Ratio, Relative Leaf Area Growth Rate, which permit a more detailed analysis of the growth of the palm (Hartley, 1977).

The frond of the date palm (*Phoenix dactylifera* L.) has also been intensively studied. In this species various morphological characteristics of the leaf are constant enough to be used in the description of varieties (Nixon, 1950). For the Pejibaye palm (*Bactris gasipaes* H.B.K.) very few bibliographic references on the fronds are found.

General morphology: Among the various articles by taxonomists who have described the Pejibaye palm, the one by Wessels-Boer (1965) is one of the most complete in terms of frond description: "...10-20 contemporaneous leaves in a plumose crown, leaves curling and drooping, up to 3 m long of which the rachis about 2 m long, more or less sparsely armed, with up to 120 pairs of pinnae clustered into groups of usually 4 inserted in various directions, 50-60 cm long, about 3 cm wide". The works of Humboldt, Bonpland and Knuth (1816), Martius (1824) and Barbosa-Rodrigues (1903) contain some information but give a less complete description of the fronds.

In general, the above descriptions serve well for the Pejibaye from Surinam and perhaps from the Amazon Basin as a whole. However, the plants studied in Costa Rica and reported here show generally larger dimensions. Some additions to this description that are worth mentioning come from Tomlinson (1961): "...leaflets narrowly lanceolate, reduplicate, each with a prominent adaxial midrib, often setose. Rachis and petiole densely spinous below". From MacBride (1960): "...midnerve prominent above, the 3 or 4 secondaries on both sides, margins, remotely setulose or minutely aculeate..." From Martius (1824) (translated by W. Rodriguez, pers. com.): "...petiole base convex vaginate lanceolate... rachis bifacial on dorsal part, on ventral side convex, spiny... pinnae... the more apical and basal crispate, linear-lanceolate acuminate...".

With these additions and the observations gathered for this article, a more detailed description may be presented: 10 to 25 (rarely reduced to 4 or 5, or up to 36) contemporaneous fronds in a plumose crown, fronds curving, when old even curling, and drooping; 300 to 450 cm in length of which the rachis is 200 to 330 cm long; petiole sheath involves one half to two thirds trunk circumference, margins broken somewhat fibrous, concave above, convex below (Fig. 1); rachis concave becoming bifacial above, convex beneath; spinyness absent to extremely dense on trunk and frond, usually more or less aligned on petiole, less so on rachis, occasionally stattered; leaflets in groups of 2 to 9 with lower leaflet of group more perpendicular to the rachis dorsel surface, following leaflets less perpendicular, giving a many-planed arrangement; 110 to 140 leaflets per side, arranged in sup-opposite pairs or alternately on rachis with more on one side than on the other, basal and apical leaflets frequently fused with grouping less pronounced or absent; leaflets linear-lanceolate bi-acuminate, length 20 to 80 cm, width 3 to 5.8 cm; midnerve prominent above, with 3 or 4 secondaries on both sides; midvein, secondaries and/or margin of leaflets may present small spines; leaflet base convex vaginate-lanceolate at insertion on rachis; leaflets glossy dark green above, opaque green below with more trichomes and stomata below; frond outline irregular to occasionally ovoid or obovoid.

Although this description is more detailed than the others given here, it is still general. Thus to distinguish between genotypes, a qualitative and quantitative analysis of the different characters is required. Preliminary information on some characters is here presented, based on six different plants (B/3, 4/1, 9/1, 16/1, 1/8 and 1/10). One –B/3– from Panamá, planted in 1973 (Morera Monge, 1981), and the other five from Costa Rica planted in 1968; both collections at CATIE, Turrialba. The older frond was chosen between positions 12 and 16 and the newer between 8 and 12, thus both were probably mature.

Rachis length: The rachis lengths observed are presented in Table 1. One notes immediately that these fronds are indeed much larger than those described from Surinam (Wessels-Boer, 1965), the smallest being more than 50 cm longer and the largest 130 cm longer. As mentioned above this may be due to the genetic variation between the populations of Pejibaye from Costa Rica and those of Surinam, or to the richer soils of Costa Rica, or to a combination of both. Further study is necessary to determine the cause of these differences. One also notes that the younger group of fronds is smaller. This result was not expected to be so constant as is shown here. In the oil palm, the size of the leaf increases during the juvenile stage, until it reaches full maturity, after which it stabilizes for a while and then starts to diminish slightly (Hardon, *et al.*, 1969; Corley and Gray, 1976), although the age factor alone cannot explain these results in Pejibaye. The difference in size is too large between fronds close in age. In addition, one of the palms –B/3 from Panamá– also presents a rachis length reduction which is not expected to occur in an immature plant. Because all the palms show the same size reduction one must assume that there is an environmental factor, such as rainfall, that influences rachis length and frond size. Such changes must consequently be seasonal and superimposed on the change which occurs with age. This subject obviously requires more study.

Leaflet number: The number of leaflets per frond and per frond sides are presented in Table 2. In all the fronds studied there was a notable spacial difference in the point of insertion of the first basal leaflets between the two sides of the frond. It will be noted that plants 9/1 and 16/1 have more leaflets on the right side, while B/3, 4/1, 1/8 and 1/10 have more on the left

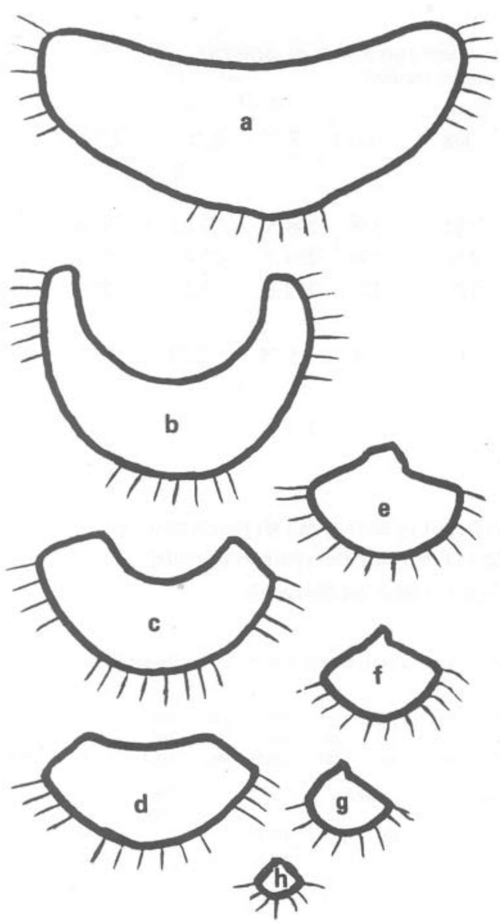

Fig. 1. Petiole and rachis cross-sections in *Bactris gasipaes* H.B.K.: a. 50 cm below the first leaflet; b. at the first leaflet; c. 50 cm above the first leaflet; d. 100 cm above the first leaflet; e. 150 cm above the first leaflet; f. 200 cm above the first leaflet; g. 250 cm above the first leaflet; h. 300 cm above the first leaflet and 35 cm below end of rachis. Actual sizes are shown.

side. This bilateral assymetry is common in palms and especially evident in pinnate palms. This assymetric character seems to be related to the direction of the helix in which the fronds are inserted on the trunk (Davis, 1968). Thus one may assume that plants 9/1 and 16/1 have a right-handed orientation to their helix while the others have left-handed phylotaxis. This assymetry is also observed in several of the other characters that will be presented below.

There is a small difference between the fronds on the same plant with respect to the number of leaflets. Except for plant 1/10, there is a greater number of leaflets in the younger fronds. This is to be expected on immature plants where leaflet number is assumed to increase with age until maturity and then remain relatively constant. The difference is only 1.67% and so statistically not significant; and consequently, it may be attributed to environmental influence. However, comparing Tables 1 and 2, the younger fronds are shorter and have more leaflets than the older, so that one finds more leaflets per meter on the younger fronds. Thus the older fronds have an average of 86.8 leaflets per meter while the younger have 96.6 (11.3% more per meter). These two results, rachis length and leaflet number, seem somewhat contradictory. It may be assumed that leaflet number may have a stronger genetic determination than rachis length but this may be affected by age difference while the palm has not fully matured. If such is the case, then it must be concluded that even the 12-year-old plants, such as those from Costa Rica, have not reached complete maturity since the number of leaflets is still on the increase.

Grouping of leaflets: The architecture of the Pejibaye frond is intimately related to the grouping of the leaflets. The main portion of the lamina has the leaflets arranged in groups that are easily distinguished by their angles of insertion on the rachis. Thus the first leaflet of each group is always the one that is inserted most perpendicularly to the rachis. Each succeeding leaflet in the group is less perpendicular, with the last being most parallel to the rachis or even falling below the rachis plane. Figure 2 (a, b) presents groups of leaflets, cut to allow them to remain as erect as possible to make more obvious their angles of insertion. These different planes of leaflet arrangement on the fronds are lost somewhat with age when they tend to flatten out, losing some of the architectural efficiency to capture light.

The groups of leaflets observed on the older fronds of each plant studied are presented in Table 3. It is evident that the number of groups on each frond show a relation with the number of leaflets but not a very direct one. This is probably due partially to the fact that the first basal and last apical groups are masked by fusion of the leaflets, causing a relative lack of well-defined differences in insertion angle in those fused leaflets. Table 4 presents the number of leaflets fused, or not organized in

TABLE 1

Rachis length measurements. Comparison between two fronds of different age from each of the six plants studied

Plant / Frond	B/3	4/1	9/1	16/1	1/8	1/10	$\bar{x}$	S.D.	C.V.
older	275	277	330	293	282	316	295.5	22.63	7.66
younger	252	261	302	258	251	294	269.7	22.40	8.31
$\bar{x}$	263.5	269	316	275.5	266.5	305	282.6	22.27	7.88
dif. (%)	8.36	5.78	8.48	11.94	10.99	6.96	8.75	2.34	26.77

TABLE 2

Number of leaflets per frond. Data taken from two fronds of each of the six plants studied. Each frond is separated for comparison into right vs left side and (bottom of table) into the sides where leaflets start lower vs higher on the rachis

Plant / Frond	B/3(1)	B/3(2)	4/1(1)	4/1(2)	9/1(1)	9/1(2)	16/1(1)	16/1(2)	1/8(1)	1/8(2)	1/10(1)	1/10 (2)	$\bar{x}$(1)	$\bar{x}$(2)	$\bar{x}$(total)	S.D.(tot)	C.V.(tot)
right side	116	117	127	132	134	135	137	140	122	123	130	127	127.7	129	128.3	7.73	6.02
left side	117	118	132	136	131	132	135	137	123	135	133	131	128.5	131.5	130	6.85	5.27
total	233	235	259	268	265	267	272	277	245	258	263	258	256.2	260.5	258.3	13.93	5.39
$\bar{x}$/plant	234		263.5		266		274.5		251.5		260.5				258.3	14.07	5.45
lower	117		132		134		137		123		133		129.3			7.66	5.92
higher	116		127		131		135		122		130		126.8			6.85	5.40

(1) older fronds
(2) younger fronds
S.D. and C.V. from the older (1) fronds only

groups, found on the basal and apical extentions of the rachis. In these cases the leaflets are frequently identified as mid-ribs with their concomitant insertion swellings rather than as distinct leaflets. The average number of leaflets on the right and left sides of the lamina are almost equal, but the coefficient of variation shows how widely this number differs among plants.

The lack of a clear correlation between groupings of leaflets and other characters discussed in this paper suggests that this character and the one of fusion of basal and apical leaflets would be of little use as descriptors in these populations, although there are very few examples presented here to justify this conclusion. However, the grouping of leaflets appears to serve very well as a systematic randomizing factor for use in leaf area calculations.

Length and width of the leaflets: Again the results presented in Tables 5 and 6 show that the fronds of the Pejibaye in Costa Rica are generally larger than those of the plants described from Surinam (Wessels-Boer, 1965).

One architectural feature of importance is that the total width of the leaflets per side is greater than the rachis length, accounting for the way that the leaflets are intricately folded upon themselves before the opening of the frond.

The length and width of the leaflets are of importance because of their direct relation to area, an important component of the potential photosynthetic efficiency of the frond. Along the rachis the length and width of the leaflets vary considerably, with the first basal and last apical leaflets being the shortest and narrowest, while some of the mid-rachis leaflets are the

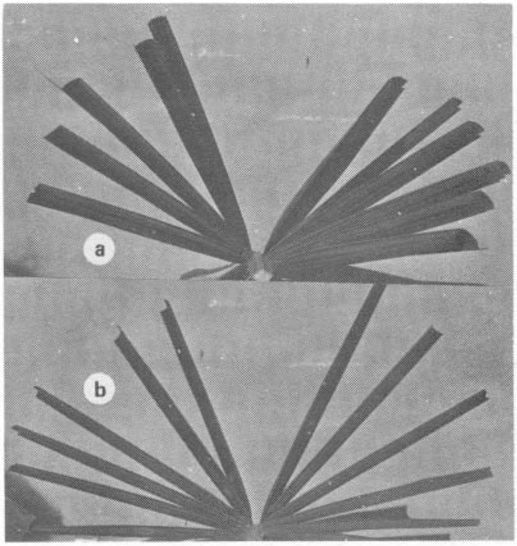

Fig. 2. Groups of leaflets –with far ends cut– showing the different angles of insertion to the frond rachis.

longest and widest. Minimum lengths approach 20 cm, rapidly increase along the rachis toward the center. Minimum widths approach 5 mm and are related to the breaking line between leaflets. It is not unusual to find some leaflets with the mid-rib on the margin because of the way that the leaflets split apart. Because of the irregularity of splitting, the minimum and maximum widths have more of an element of chance in their determination than do the minimum and maximum lengths. This may be seen by comparing Tables 5 and 6 with the observations about assymetry of the leaves of the palm. While the leaflets of maximum length are always found on the side of the rachis with the largest average length and the greatest number of leaflets, the leaflets of maximum width are not always so related, as may be seen on most of the plants observed in this study. The maximum lengths and widths found on the six plants studied are presented here for comparison with the averages and for some possible use in future calculations. However, because of the somewhat irregular splitting of the leaflets, the individual maximum width figure is of little use when calculating leaf area. It is of special interest to observe that the maximum width appears to be unrelated to the maximum length.

Frond Shape: The shape of the Pejibaye fronds appears, at first glance, to be quite

Fig. 3. Mature frond.

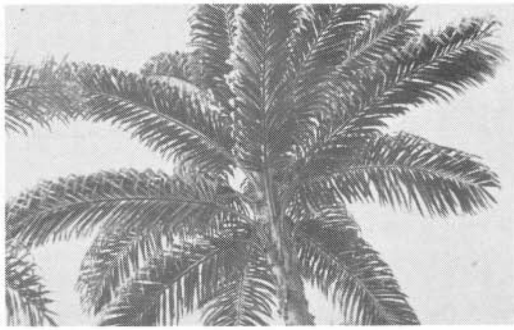

Fig. 4. Crown of fronds from an adult plant.

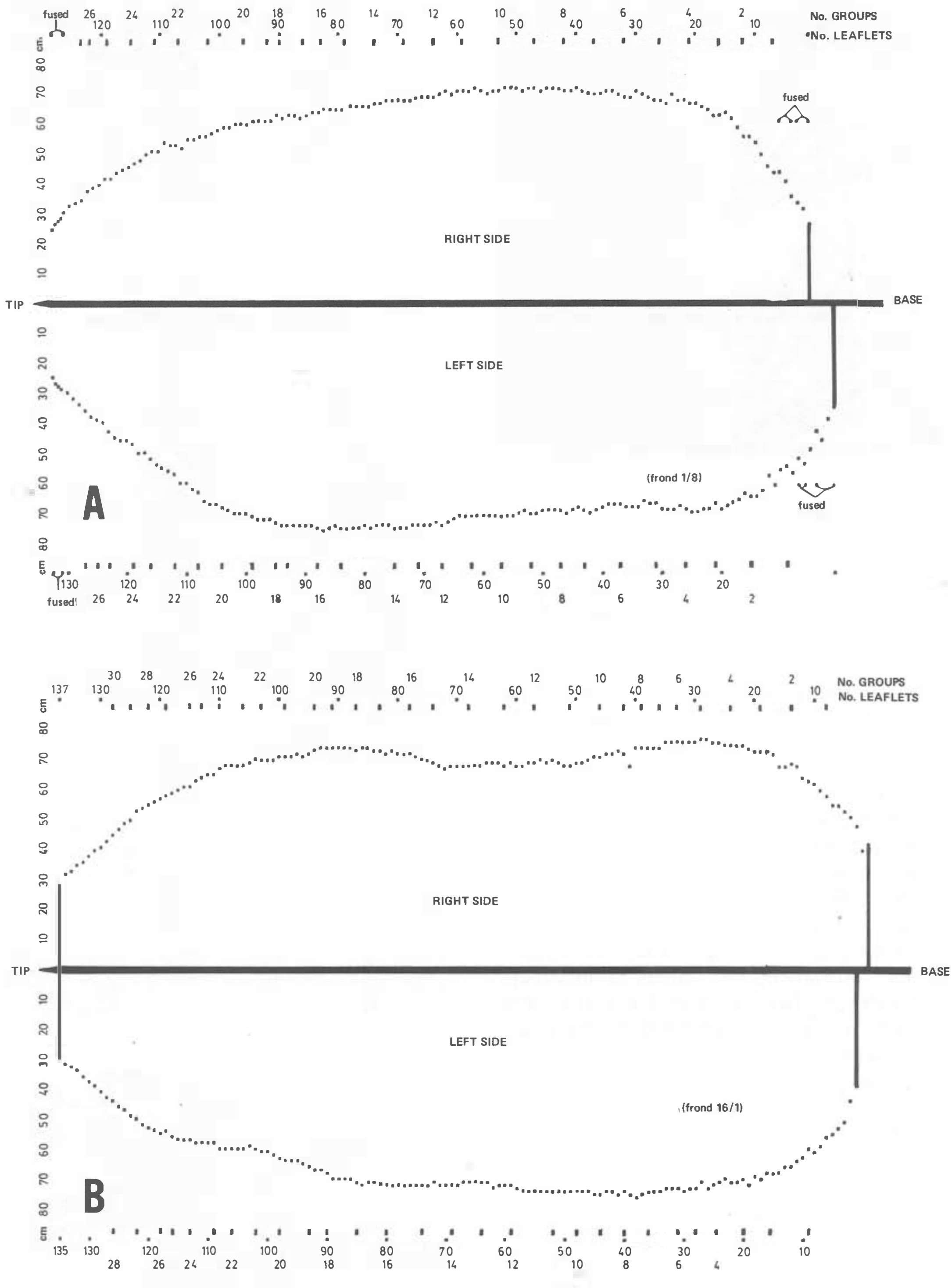

Fig. 5. Outlines of older fronds from two of the six different plants studied, showing number, length, distribution and grouping of leaflets: A, Frond 4/1; B. Frond B/3.

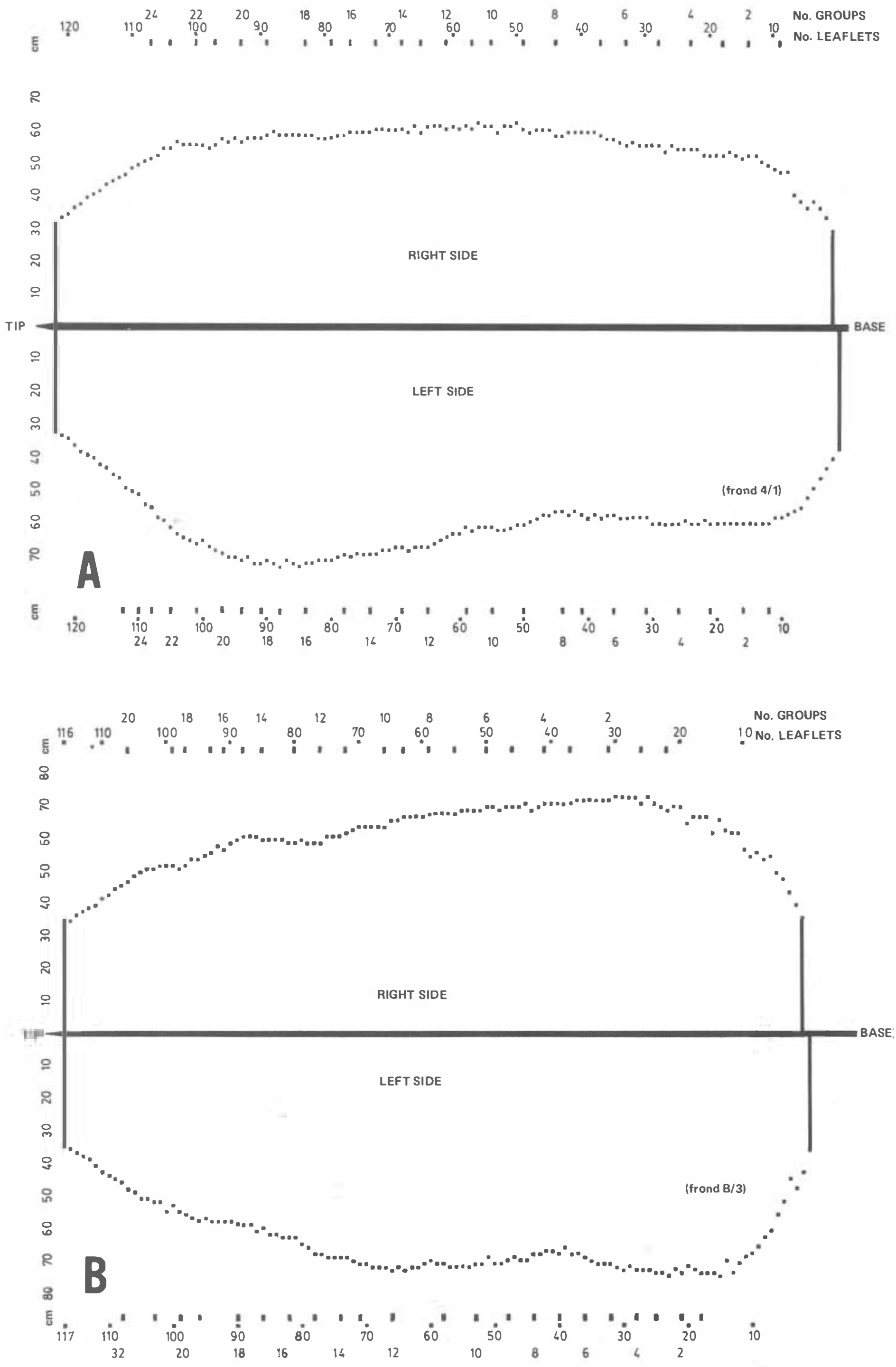

Fig. 6. Outlines of older fronds from two of the six different plants studied, showing number, length, distribution and grouping of leaflets: A. Frond 1/8; B. Frond 16/1.

TABLE 3

Number of groups of leaflets per frond. Data taken from one frond of each of the six plants studied. Each frond is separated for comparison into right vs left side and (bottom of table) into the sides where leaflets start lower vs higher on the rachis

Plant Frond	B/3(1)	4/1(1)	9/1(1)	16/1(1)	1/8(1)	1/10(1)	$\bar{x}$	S.D.	C.V.
right side	20	29	27	30	24	31	26.8	4.17	15.56
left side	22	29	27	28	25	29	26.7	2.73	10.22
total	42	58	54	58	49	60	53.5	6.86	12.82
lower	22	29	27	30	25	29	27.0	3.03	11.22
higher	20	29	27	28	24	31	26.5	3.94	14.87

(1) considers only the older frond of previous tables.

TABLE 4

Number of leaflets fused or not organized in groups. Data taken from one frond per plant from each of the six plants studied. Each frond is separated for comparison into right vs left side and (bottom of table) into the sides where leaflets start lower vs higher on the rachis

Plant	B/3(1)		4/1(1)		9/1(1)		16/1(1)		1/8(1)		1/10(1)		$\bar{x}$		S.D.		C.V.	
	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A
right	21	6	4	7	8	5	7	6	8	12	8	3	9.3	6.5	5.92	3.01	63.65	41.31
left side	17	5	7	6	6	5	8	7	11	8	6	6	9.2	6.2	4.26	1.17	46.30	18.87
total	38	11	11	13	14	10	15	13	19	20	14	9	18.5	12.7	9.89	3.93	53.46	30.94
lower	17	5	7	6	8	5	7	6	11	8	6	6	9.3	6	4.13	1.09	44.41	18.16
higher	21	6	4	7	6	5	8	7	8	12	8	3	9.2	6.7	6.01	3.01	65.33	44.93

B basal leaflets
A apical leaflets
(1) older fronds

TABLE 5

Length of leaflets: summation, mean and maximum length. Data taken from one frond of each of the six plants studied. Each frond is separated for comparison into right vs left side and (bottom of table) into the sides where leaflets start lower vs higher on the rachis. Data given in cm

Plant	B/3(1)			4/1(1)			9/1(1)			16/1(1)			1/8(1)			1/10(1)					
	Σx	$\bar{x}$	max	Σx	$\bar{x}$	max	Σx	$\bar{x}$	max	Σx	$\bar{x}$	max	Σx	$\bar{x}$	max	Σx	$\bar{x}$	max	$\bar{x}$	S.D.	C.V.
right side	6939	59.8	72.4	4357	34.3	42.4	8445	63.0	74.5	8850	64.6	75.6	6537	53.6	61.8	8209	63.1	76.5	56.4	11.52	20.4
left side	7319	62.6	73.9	4682	35.5	44.9	7684	58.7	71.3	8573	63.5	74.6	7334	59.6	72.6	8873	69.3	79.2	58.2	11.73	20.2
total	14258	61.2		9040	34.9		16129	60.9		17423	64.1		13871	56.6		17082	66.2		57.3	11.45	20.2
lower		62.6			35.5			63.0			64.6		59.6			69.3			59.1	11.99	20.3
higher		59.8			34.3			58.7			63.5		53.6			63.1			55.5	10.99	19.8

(1) older fronds

TABLE 6

Leaflet width: summation for the frond, mean and maximum width. Data taken from one frond of each of the six plants studied. Each frond is separated for comparison into right vs left side and (bottom of table) into sides where leaflets start lower vs higher on the rachis. Data given in cm

Plant	B/3(1)			4/1(1)			9/1(1)			16/1(1)			1/8(1)			1/10(1)					
	Σx	$\bar{x}$	max	Σx	$\bar{x}$	max	Σx	$\bar{x}$	max	Σx	$\bar{x}$	max	Σx	$\bar{x}$	max	Σx	$\bar{x}$	max	$\bar{x}$	S.D.	C.V.
right side	333.5	2.88	3.8	523.2	4.12	5.8	413.5	3.09	4.0	561.6	4.10	4.7	359.8	2.95	3.7	575.1	4.42	5.6	3.59	0.69	19.22
left side	350.0	2.99	3.9	539.0	4.08	5.4	393.2	3.00	4.0	536.4	3.97	4.8	373.9	3.04	3.8	548.0	4.28	5.2	3.56	0.61	17.13
total	683.5	2.93		1062.2	4.10		806.7	3.04		1098.0	4.04		733.7	2.99		1123.1	4.35		3.58	0.65	18.16
lower		2.99			4.08			3.09			4.10			3.04			4.28		3.60	0.61	16.94
higher		2.88			4.12			3.00			3.97			2.95			4.42		3.56	0.64	19.38

(1) older fronds.

regular (Figs. 3, 4). However, the irregularity of the shape is apparent when the leaflets are cut off from the rachis and ranked in order. Figures 5 and 6 present the shapes observed on the older frond of each of four of the six Pejibaye plants studied. One notes immediately this irregularity since some fronds present their maximum width near to the petiole (B/3 and 1/10), others nearer to the rachis apex (4/1, 9/1), another showing two areas of maximum width (16/1) and still another (1/8) with different positions of the maximum width on both sides. One also notes that most of the fronds are more irregular on one side than on the other, and in four (B/3, 9/1, 16/1 and 1/8) the most irregular side is the one with the most leaflets. The other two leaves present frond shape irregularities on both sides. Because of the irregularities noted here the methodologies of frond area calculation developed by Hardon *et al.* (1969) and Mendham (1971) for the oil palm do not work quite as well in Pejibaye.

ACKNOWLEDGEMENTS

We thank, in Brazil, the BID/FINEP/CNPq (convenio No.531/CT) for financial assistance, Dr. William Rodrigues for translation and botanical orientation and Dr. Anthony Anderson for palm botanical orientation, and in Costa Rica, the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICIT) and the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) for economic and material assistance, respectively.

RESUMEN

Este estudio preliminar sobre la morfología de la fronda del pejibaye, *(Bactris gasipaes)* se inicia con una descripción morfológica de la hoja, que complementa aquellas existentes en la literatura. La información obtenida indica que los pejibayes de Centro América poseen un raquis foliar considerablemente más largo que aquel reportado para las poblaciones de Surinam y se supone que por lo menos parte de esa diferencia tiene un fundamento genotípico. Contrario a lo esperado, se encontró que las frondas de mayor edad poseen un raquis de mayor longitud que aquellas más jóvenes pero ya adultas del mismo estípite. Esta diferencia es posiblemente causada por factores ambientales que varían estacionalmente, tal como la lluvia. Se indica que los foliolos están asociados en grupos, en donde cada foliolo presenta un ángulo diferente de inserción en el raquis, dando muchos planos en su ordenamiento, lo cual aumenta la eficiencia en el aprovechamiento de la luz. Esta ventajosa disposición de los foliolos en múltiples planos desaparece paulatinamente en las frondas viejas al arquearse los foliolos cada vez más, anulando el efecto de los diferentes ángulos de inserción. También se encontró que existe asimetría entre los lados opuestos de la misma fronda con respecto a número de foliolos, longitud y área total. Asimismo, los foliolos de un mismo lado muestran una variación asimétrica. También se encontró un mayor número de foliolos en las frondas jóvenes cuando se compararon con otras más viejas de la misma corona, a pesar de presentar éstas últimas mayor longitud del raquis. Esto puede indicar que aún en palmares de 12 años de edad las frondas no han alcanzado su pleno desarrollo, puesto que se supone que el número de foliolos es menos afectado por variaciones ambientales que la longitud del raquis.

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