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Demography of Astrocaryum sciophilum, an Understory Palm of French Guiana

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The relatively simple growth form of palms has prompted the interest of many population ecologists in recent years (Bannister 1970, Van valen 1975, Sarukhan 1978, Savage and Ashton 1983, de Steven 1986, Sist and Puig 1987, Sist 1989).

Although the systematics and ecology of palms in French Guiana are quite well known (Wessels Boer 1965, De Granville 1978, Kahn 1983), demographic studies have been slow to develop.

In 1985 I started research on the demography and population dynamics of five common palm species in French Guiana (Sist 1989). My purpose was to follow the process of natural regeneration of palms in a tropical rain forest and to point out population strategies of palms in relation to their ecology. The demographic structures of these populations have been analyzed by defining several developmental stages.

Palm fruits are an important food source for a wide range of mammals and birds. These animals play a fundamental role not only in the regulation of palm populations through seed predation, but also in seed dispersal which, in turn, will determine the distribution of seedlings. The rodents of South America have been the subject of studies (Morris 1962, Smythe 1978). Other important predator-dispersal agents, at my study site in French Guiana, include the white lipped peccary and several arboreal mammals of French Guiana (Charles-Dominique et al. 1981).

This paper summarizes the first results of a study of the demography and seed dispersal of the palm *Astrocaryum sciophilum* (Miquel) Pulle. The establishment growth occurring in seedling and juvenile stages is described and correlated with their mortality rate.

The relatively high density of this species in the understory of Guianan forests allows analysis of population dynamics in a relatively small area.

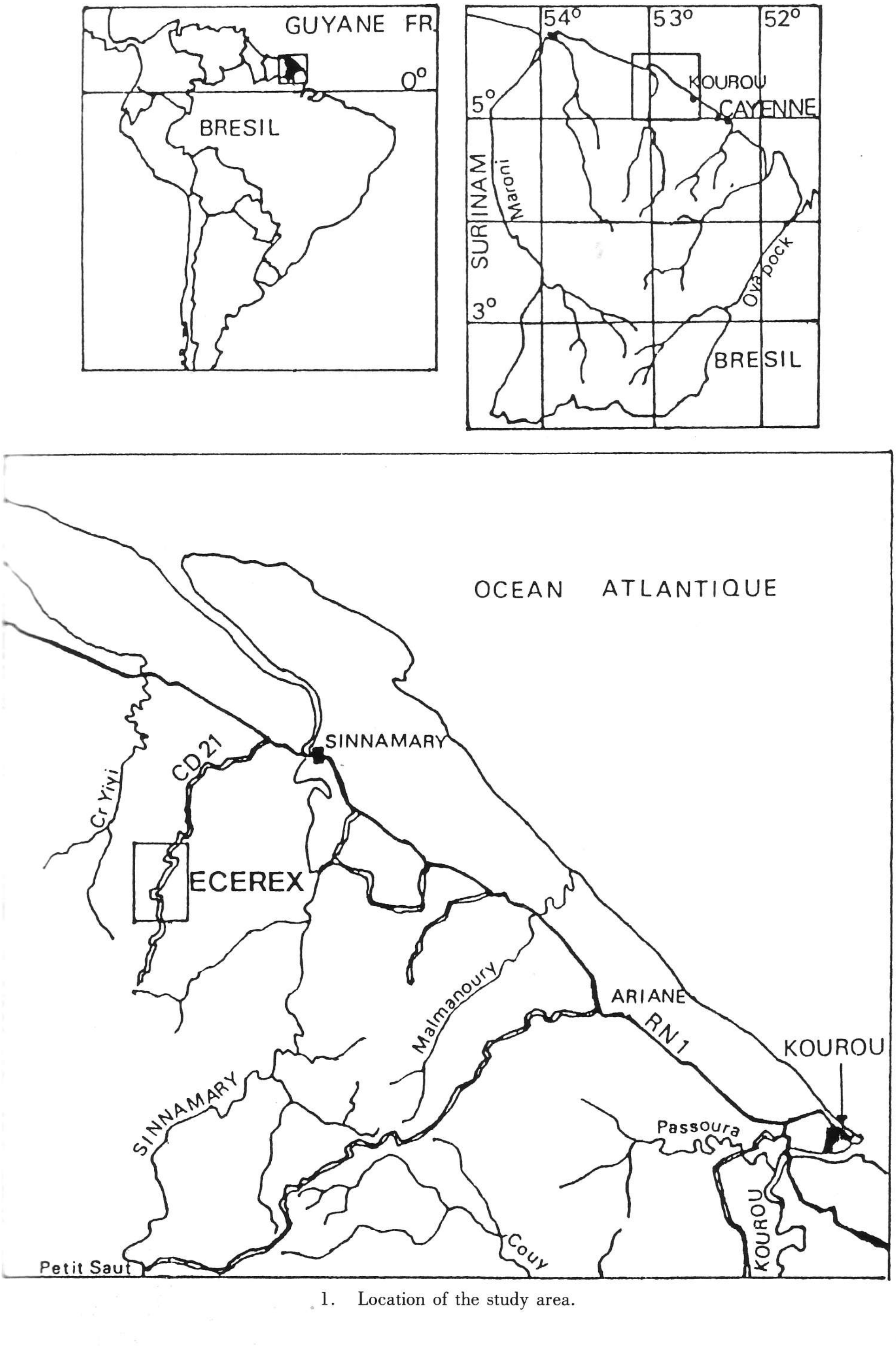
Study Area

The study was conducted at the field station of "Piste de Saint Elie" (Fig. 1) which was created in 1977 for experimental studies of forest ecology, regeneration, and soil erosion ("ECEREX" programme, Sarrailh 1980). This area is covered by tropical rain forest and most of the canopy trees (DBH (diameter breast height) > 20 cm) belong to three families in the following proportions: Lecythidaceae (26%), Caesalpiniaceae (22%), Chrysobalanaceae (12%) (Puig et Lescure 1981).

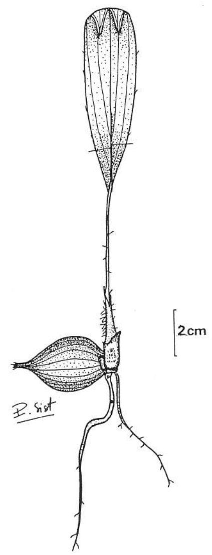
There is a dry season of three to four months, from August to November, and a long rainy season for the rest of the year. However, the rainy season is often interrupted in February or March by a short but variable dry season. Annual rainfall at the station in 1986 was 3,010 mm, and the number of rain days was 268.

Methods

Three populations of *A. sciophilum* were studied in three different plots (B, D1, D2) of 2,500 m^2 each. Plots B and D1 differ



1. Location of the study area.



2. Young seedling of *Astrocaryum sciophilum.*

from each other in the type of drainage. Plot B is characterized by impeded vertical drainage whereas D1 and D2 are on well drained soil with free vertical drainage (Boulet 1978). Plot D2 is actually a continuation of D1 and was marked out in February 1986, to test whether doubling the surface area would result in a proportional change in the number of palms present.

Study of the demography and population dynamics of this species was simplified by defining several developmental stages of the palm. The criteria used were the degree of leaf division, leaf number, and leaf size.

Since plants exhibit great plasticity in growth rates, plant age is not always useful (Harper 1977) nor can age be assumed from size. In order to estimate the age of palms it was necessary to know the growth rate, including the time passed in the acaulescent, establishment growth, phase. Growth rate of *A. sciophilum* varied greatly and depended on external conditions but also on the developmental stage of the palm. For this reason, analysis of the demographic structure of palm populations was approached on the basis of stages of development rather than age per se.

The population in each plot has been mapped to follow the spatial distribution of palms and knowing the behavior of seed dispersal agents to explain this distribution. Rodents such as squirrels, agoutis or acouchis are known to scatterhoard fruits, particularly endocarps of palms, near objects such as tree bases, logs, roots, and beneath lianas (Morris 1962, Smythe 1978). In addition to the white lipped peccary they are the only mammals able to masticate very hard endocarps such as those of palms. In order to find the consequences of the feeding behavior of these rodents on the spatial distribution of seedlings, I measured the distance from each seedling to the nearest object following the method of Kiltie (1981). The process of seed dispersal was also assessed by searching for endocarps or fruits in a plot of 280 m^2 (called E) where there were only two fertile *A. sciophilum.* The soil was racked to a depth of 5 cm, all intact, decaying or masticated endocarps were counted, and the distance from them to the nearest object measured.

Study Species

Description. Astrocaryum sciophilum (Arecoideae: Cocoeae: Bactridinae, Uhl and Dransfield 1987) (Fig. 6) is the commonest understory palm in the lowland forests in the interior of French Guiana. This solitary palm develops an unarmed stem usually 2 to 5 m tall but reaching a height of 12 m in well developed specimens. The crown is composed of 10 to 14 leaves, 6–7 m long with 75–85 pairs of pinnae, whitish abax-

Table 1. Morphological characteristics of developmental stages in plots B, D1, and D2. S, Seedlings; N = Number of individual (D1 + D2 + B); L cm = Mean leaf length; NL = Mean Leaf Number; NPi = Mean Pinna Number per leaf.

Stages	S	J1	J2	J3	A
N	231	88	25	20	24
L cm	59 ± 4	155 ± 7	295 ± 20	560 ± 34	630 ± 35
NL	4 ± 0.22	6 ± 0.34	8 ± 0.68	8 ± 0.64	9 ± 0.91
NPi	0	4 ± 0.51	18 ± 0.83	106 ± 15	145 ± 9

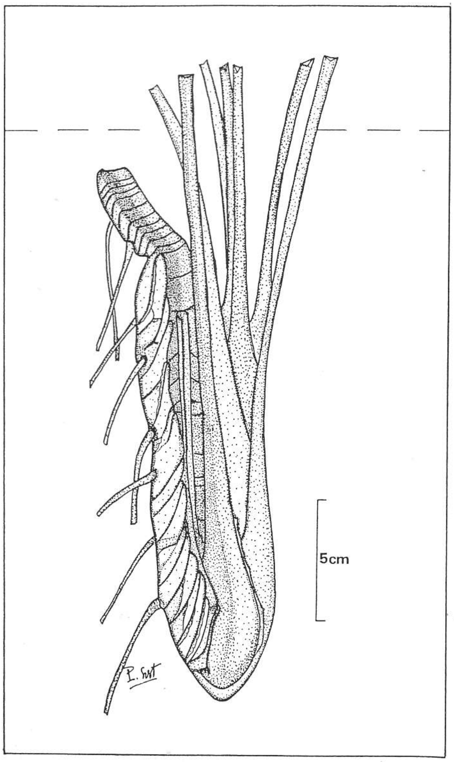
ially and inserted at regular intervals on the rachis. The lower faces of the rachis and the petioles are armed with flat spines, 1–25 cm long, arranged in oblique rows. The single seeded fruits are covered by prickles 0.5 cm long and are obovoid in shape, about 6 cm long, 3–4 cm in diameter. The mesocarp is fibrous, and the very hard endocarp protects the single seed which contains a white endosperm with a central cavity.

In the study area *A. sciophilum* grows mainly on the crests or slopes of hills but rarely on flooded sites (Sist 1989).

Developmental stages. Five developmental stages have been defined (Table 1):

1. Seedlings: the first leaf or eophyll (Tomlinson 1961) is entire, 18–20 cm long and 3–4 cm wide, slightly indented at apex. The petioles of their leaves bear some black filiform spines (Fig. 2). I define as seedlings the palms with only entire leaves. The seedlings in plots B, D1, D2 (Table 1), have 4 entire leaves 18–120 cm long. This developmental stage includes individuals of different size with two common characters: the absence of division of leaves and the low number of leaves.
2. Stage 1 juveniles (Fig. 7) possess 6 leaves 120–250 cm long which are poorly divided into 1 to 8 pinnae (Table 1).
3. Stage 2 juveniles (Fig. 8) are palms with 8 well divided leaves (4–23 pairs of pinnae), 250–450 cm long.
4. Stage 3 juveniles (Fig. 9) have 8–11 leaves longer than 450 cm and composed of 30–70 pairs of pinnae.
5. The adult stage is defined as palms able to flower.

Seedlings and juveniles appear acaulescent but develop, in fact, an underground, positively geotropic stem. This results in the stem growing down in the soil (about 40–50 cm in depth for stage 2 juveniles, Fig. 3). The largest of stage 2 juveniles build the basal upward-growing part of the

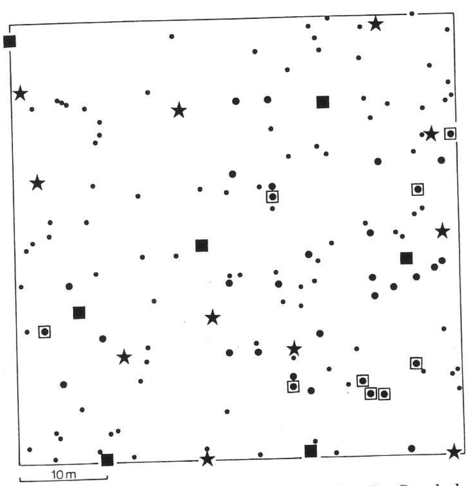


3. Underground stem of *A. sciophilum*, juvenile stage 2.

Table 2. Demographic structure of the three populations in plots B, D1, D2, and D. N, Number of individuals.

Stages	S	J1	J2	J3	A
NB	84	29	9	7	11
%B	60	20.71	6.43	5	7.86
		Total NB = 140			
ND1	71	36	6	5	4
%D1	58.20	29.51	4.91	4.10	3.27
		Total ND1 = 122			
ND2	76	23	10	8	9
%D2	60.32	18.25	7.94	6.35	7.14
		Total ND2 = 126			
ND	147	59	16	13	13
%D	59.27	23.80	6.45	5.24	5.24
		Total ND = 248			

stem which corresponds with the end of the establishment growth phase (Tomlinson and Zimmermann 1966). Stage 3 juveniles present an underground stem with a negative geotropism and the same morphology as that of adults. This pattern of growth has already been described for other Amazonian palms including *Jessenia bataua* (Mart) Burr. and *Syagrus* sp. (Castro dos Santos 1981) but I did not find any published descriptions of this growth form in *A. sciophilum*.



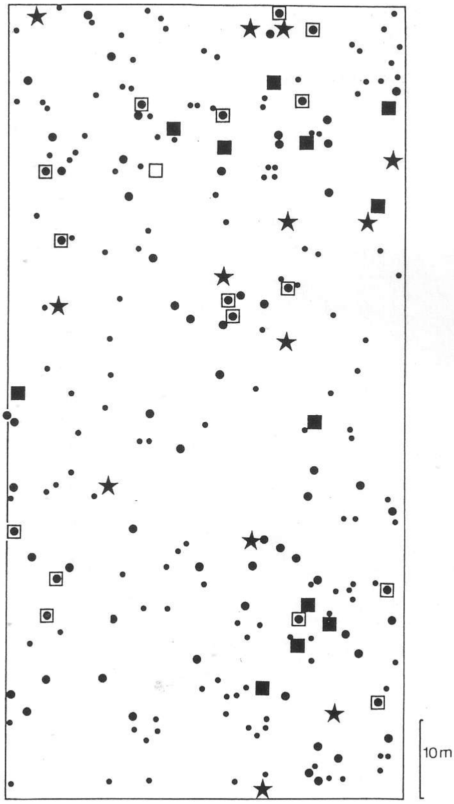
4. *A. sciophilum*, population in plot B. Symbols for Figs. 4 and 5: ● Seedlings, ● Juveniles 1, □ Juveniles 2, ■ Juveniles 3, ★ Adults.

A strong correlation has been found between leaf length and the number of pinnae (r = 0.995; N = 258, p = 1%; Y = 0.23X − 38.58; X = length leaves, Y = number of pinnae). The length of leaves and the number of pinnae are thus the main indicators which express the ontogenic stage of the species. Because of its relatively high density and the definition of easily identified developmental stages, *A. sciophilum* is a suitable species for population ecology studies.

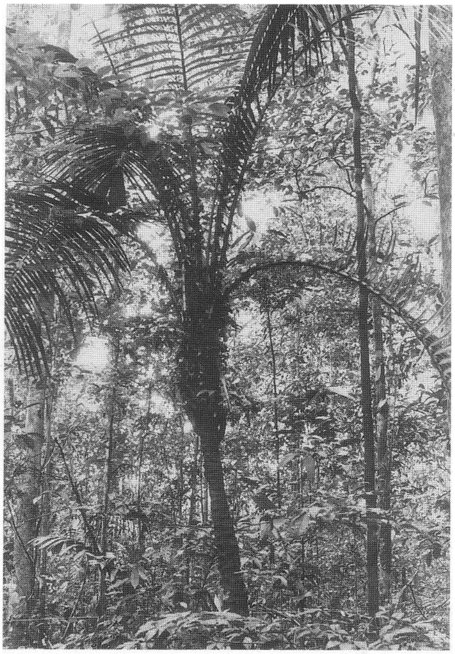
Demography

The proportions of individuals in the 5 developmental stages (Table 2) do not differ in the three populations (G = 8.07, df = 8, p = 1%). The absence of differences between the two populations in plots D1 and D2 (G = 3.33, df = 4, p = 1%), and the fact that D2 is the continuity of D1 allows grouping of these two into one population; 2,500 m^2 seems to be an adequate area for studying the population of *A. sciophilum*. The plots D1 and D2 are henceforth considered as one plot of 5,000 m^2 and called D.

Seedlings are the main component of the population, comprising 60% of the total population in B (Fig. 4) and 59% in D (Fig. 5). Immature plants (i.e., seedlings



5. *A. sciophilum* population in plot D. Symbols: see Fig. 4.



6. Mature *A. sciophilum.*

and juveniles) represent 92.74% of the total number of individuals in B and 94.74% in D, whereas adults with 7.86% in B and 5.42% in D are the minority (Table 2).

Seedlings and juveniles 1 apparently suffer high mortality rates (Table 3) which could be correlated with the increase in the number of leaves and of pinnae, occurring in the transition from seedlings to juveniles 1 and from juveniles 1 to juveniles 2. On the other hand, juveniles 2 suffer lower mortality (78% and 81% respectively in B and D reach the stage 3 juvenile). In this transition, even if the number of pinnae increases (Table 3), it does not involve a high mortality. However, in contrast to the first two transitions, the mean number of leaves is constant. So leaf number may be correlated with mortality for the smallest individuals (i.e., seedlings and juveniles 1). Large juveniles 3 did not suffer any mortality in the two plots.

One of the causes of mortality is debris fall. The development of a subterranean stem with a positive geotropism (Fig. 3) protects the meristem of old seedlings and juveniles from falling branches or trunks. Youngest seedlings which still possess a superficial stem, at about 5 cm in depth, are more likely to be damaged by fallen branches but it is not unusual to see older juveniles that have survived after a trunk or a big branch has fallen in the middle of the crown. The development of an underground stem with positive geotropism undoubtedly is of high adaptive significance to such events.

Spatial Distribution

The relatively high abundance of *A. sciophilum* in plots B and D (Table 2)

7. Individual at juvenile stage 1.

allows for quantitative analysis of the spatial distribution of populations. In plots B and D, seedling distributions, in terms of the entire plots, are random (S2/X = 1.10 for B, N = 60 subplots each of 25 m^2; S2/X = 0.97 for D, N = 120 subplots each of 25 m^2; no significant difference with a Poisson distribution for p = 1%). The total population has the same distribution as that of seedlings (S2/X = 0.97 for B and S2/X = 0.96 for D; no significant difference with a Poisson distribution for p = 1%).

Seedlings are, in reality, preferentially localized near objects (Table 4) and this particular distribution must be correlated with the feeding behavior of acouchis and agoutis. These rodents are known to make caches containing generally one seed (Morris 1962, Smythe 1978). This could explain both the absence of seedling aggregates near objects—the greatest number of young seedlings closed together and around the same object is 3 individuals in plots B and D—and the random distribution of seedlings in regard to the entire plots.

Predation and Seed Dispersal

In plot E, I found 72 endocarps of *A. sciophilum* but only 5 of them were intact. The inspection of the other 67 endocarps by G. Dubost (pers. comm.) indicates that 90% of them had been masticated by the squirrel *Sciurus aestuans.* The eaten endocarps represent 93% of those that show seed predation. The squirrel is the only mammal able to reach the infructescence in the middle of the leaf crown by moving on the upper and spine free part of the rachis. Other rodents and peccaries consume the fruits which have fallen on the soil.

Eaten endocarps are more often found near objects than are the seedlings (Table 4). The fact that 32% and 41% of the

8. Individual at juvenile stage 2. 9. Individual at juvenile stage 3.

seedlings in plots B and D are more than 50 cm from an object while few of the endocarps in plot E were that far away (20%), suggests that the rodents both scatterhoard and recover more seeds near large objects than in the open forest floor.

Furthermore caches made by rodents can be visited by other animals such as peccaries, which preferentially seek seeds near objects (Kiltie 1981).

Discussion and Conclusion

The demographic structure of two populations of *A. sciophilum* is characterized by a high proportion of immature individuals and particularly of seedlings and young juveniles.

Seedlings and juveniles 1 apparently represent the two critical developmental stages as they suffer the highest level of mortality. This could be correlated with the increase in the number of leaves occurring at the transition from seedling to juvenile 1 and from juvenile 1 to juvenile 2.

It would be very interesting to know if the development of an underground stem is a general pattern of palms which spend a long part of their existence in the understory before developing a trunk.

The seeds suffer higher mortality due to predation by rodents and particularly by the squirrel *Sciurus aestuans* than the smallest individuals of *A. sciophilum*. Seed predation must be regarded as an important factor in the regulation of the popu-

Table 3. Rate of individuals reaching the next developmental stage.

Stage	S	J1	J2	J3
Plot B	35%	31%	78%	100%
Plot D	40%	27%	81%	100%

Table 4. Distribution of endocarps in plot E and of seedlings in plots B and D with respect to the nearest object. Classes: I, 0–10 cm; II, 11–20 cm; III, 21–30 cm; IV, 31–40 cm; V, 41–50 cm; VI, >50 cm. N.E.E., Number of Endocarps in plot E. N.S.B., Number of Seedlings in plot B. N.S.D., Number of Seedlings in plot D.

Classes	I	II	III	IV	V	VI	Total
N.E.E.	24	11	9	6	4	13	67
N.S.B.	37	6	5	7	2	27	84
N.S.D.	58	9	13	5	1	61	147

lation of *A. sciophilum.* The rodents, by hiding endocarps one by one near objects, create a random distribution of the seedlings and the whole population, in terms of the entire plots. The proximity of an object usually does not inhibit the development of the palm since it is common to see mature *A. sciophilum* growing directly at the base of large trees.

Summary

The present results deal with the demography and the seed dispersal of *Astrocaryum sciophilum,* the commonest understory palm in the French Guianan primary forest. The demography of two populations is analyzed by stages defined by the degree to which leaves are divided, the number of leaves, and leaf size.

The population structure is characterized by a high proportion of small immature palms. Seedlings and young juveniles represent the two critical developmental stages, as they suffer the highest level of mortality. Establishment growth occurring in seedling and juvenile phases is marked by the development of an underground stem with positive geotropism, which protects the meristem of large seedlings and juveniles.

Seeds are submitted to higher predation by the squirrel *Sciurus aestuans* than the smallest individuals of *A. sciophilum.* The rodents by storing endocarps one by one near objects create a random distribution of seedlings and the whole population, in terms of the total areas tested.

Acknowledgments

I thank G. Dubost who inspected the eaten endocarps I submitted to him and determined the squirrel *S. aestuans* as the main predator of them. I am grateful to Dr. J. B. Fisher for his help in the English manuscript and his valuable advice. Sincere thanks to M. F. Prevost and W. Hahn who kindly reviewed an earlier version of the manuscript.

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LETTERS

15 November 1988

Dear Dr. Uhl,

I thought you might be interested in knowing a bit more about the *Corypha umbraculifera* in this area. A German visitor was in the Garden yesterday. He told Don Evans that he saw several Talipot palms flowering in his travels through the Caribbean. He did not mention specifics.

Also yesterday, I received a letter from Mrs. Elizabeth Lee of Ft. Lauderdale telling me about two *C. umbraculifera* which are flowering in the town square on the island of St. Christopher (St. Kitts).

It might be interesting to ask readers of *Principes* if they know of any others in flower. The information might be valuable to someone's research one day.

CHUCK HUBBUCH
Fairchild Tropical Garden

Dear *Principes*,

While it is gratifying to see any palm depicted in a U.S. postage stamp; I was somewhat dismayed to see *Sabal palmetto* presented as a pinnate palm. The portrayal of the palmetto trunk however more correctly resembles the palm we in South Carolina know and love. I wonder what the chances might be of getting the U.S. Postal Service to issue a postage stamp honoring *Sabal palmetto* which actually has a picture of *Sabal palmetto* on the stamp?

GREGORY E. FLYNN, JR.
Travel Editor View Magazine

Eds. Note: Several other readers noticed this which is apparently due to the artist's depiction.