

Population Structure and Life Cycle of *Borassus aethiopum* Mart.: Evidence of Early Senescence in a Palm Tree¹

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ABSTRACT

As with other plants having a relatively simple morphology, solitary palms are useful biological models for studying the life histories of long-lived plants. In the first study to investigate the life history of *Borassus aethiopum*, a widespread dioecious palm growing in African savannas, we found that: (1) the number of leaves increased up to reproductive maturity and then decreased during the reproductive period, while height increased throughout life; (2) female fecundity, measured as the number of seedlings within a few meters under the female canopies, decreased markedly in old individuals with few leaves; and (3) height distribution was strongly bimodal. This bimodality was due to variations in the stem elongation rate during the life of the palm and the accumulation of adults with low mortality rates in the taller height classes. The observed pattern of fecundity and number of leaves in relation to height clearly suggests a senescence period that began just after sexual maturity and appeared to be protracted. Comparisons between the life history of *B. aethiopum* and the life histories of some forest palms showed that environmental conditions cannot in themselves explain the various palm life histories.

RÉSUMÉ

Comme toutes les plantes avec une morphologie assez simple, les palmiers solitaires sont des modèles biologiques utiles pour l'étude des stratégies biodémographiques des plantes longévives. Par une première étude de *Borassus aethiopum*, un palmier dioïque des savanes africaines, nous avons montré que (1) le nombre de feuilles croît jusqu'à la maturité sexuelle, puis décroît au cours de la période de reproduction, pendant que la croissance en hauteur se poursuit; (2) la fécondité, estimée par le nombre de plantules trouvées au pied de chaque femelle, décroît pour les individus âgés qui ont peu de feuilles; (3) les distributions en classes de hauteur des populations étudiées sont nettement bimodales; cela peut être expliqué par des variations de la vitesse d'accroissement en hauteur et l'accumulation d'adultes, dont le taux de survie est relativement élevé, dans les classes de taille supérieures. Le patron observé pour la fécondité, et le nombre de feuilles définissent nettement une phase de sénescence qui commence juste après la maturité sexuelle, et semble longue. La comparaison entre *Borassus aethiopum* et des palmiers forestiers montre que les conditions du milieu ne peuvent expliquer à elles seules leurs différentes stratégies biodémographiques.

Key words: *Borassus aethiopum*; growth; humid savanna; Ivory Coast; life history; palm tree; population structure; reproduction; sex ratio.

FINDING PATTERNS AMONG LIFE HISTORIES is a challenge for modern ecology (Begon *et al.* 1990). It requires linking evolution and demography and has led to many theoretical models and field studies (Stearns 1992). Yet, few data are available about long-lived perennial plants (Van Valen 1975, Stearns 1992). In this context, solitary palms are good biological models: their architecture is simple, and it is usually easy to define, observe, and record stages based on morphological traits.

We investigated the evolution of stem height, the number of leaves, and female fecundity during the life cycle of *Borassus aethiopum* Mart., a widespread palm of African savannas. We defined the stages of morphological characters as a basis for a

future demographic study. Because *B. aethiopum* is dioecious, we also investigated a possible vegetative sexual dimorphism.

Studies on noncultivated palms usually concern forest species (Van Valen 1975, Piñero *et al.* 1982, de Steven 1989, Chazdon 1992, Enright & Watson 1992). Environmental constraints are not the same in forests and savannas; fire is frequent in savannas, whereas competition for light is much more intense in forests. Since environmental conditions are expected to be an important factor in life history evolution (Begon *et al.* 1990, Stearns 1992), the life histories of savanna palms could be different from those of the previously studied forest palm species. For example, we could expect that growth in height is earlier and quicker for forest palms that must face competition for light than for savanna palms. We tested if environmental conditions were deter-

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minant for palm life histories, and if the distinction between savanna and forest palms was relevant.

STUDY SPECIES

Borassus aethiopum is a common palm in west African humid savannas. It also can be found in drier areas but is then restricted to riversides (Vuattoux 1968). It is very useful to local human populations. The sap is used to make wine (Herzog *et al.* 1995); although sap extraction results in the palm's death in our study area. Stems and leaves are used to construct houses. Fruits and young germinated seeds are edible (Portères 1964).

Borassus aethiopum is a dioecious, tall, solitary and pleonanthic palm of the Borasseae tribe (Uhl & Dransfield 1987). Leaves are fan-shaped, induplicate, and costapalmate. The stem is massive and covered with leaf bases abscising cleanly in older individuals.

Seed germination is remote-tubular (Uhl & Dransfield 1987, Tomlinson & Jeffrey 1990): the cotyledonary axis extends downward into the soil and carries the seedling to a depth of 40 cm, where the first roots and leaves develop (Monnier 1968). The youngest seedlings have one or two 0.5- to 1.0-m long elongated entire leaves (first eophyll); older seedlings have one or two 0.5- to 1.0-m long leaves that have a few slits (second eophyll). Older individuals may or may not have an emerging stem (Tomlinson & Jeffrey 1990), but all bear the same fan-shaped costapalmate leaves (Vuattoux 1968). In juvenile individuals, the petioles of dead leaves remain on the stem, until the stem is ca 9- to 10-m high. Then, roughly at the same time a swelling appears on the stem, all dead petioles fall off, and sexual maturity is reached (a possible causal link between these events is not clear). The stems of taller palms are self-cleaning; dead leaves fall off as a single unit (Tomlinson 1963, Tomlinson & Jeffrey 1990). Mature palms are usually > 10-m high from the ground to the terminal bud. They bear from 10 to 25 living leaves. The diameter at breast height (DBH) varies between 30 and 40 cm.

The age of palm trees usually is determined easily by counting the number of leaf scars (Tomlinson 1963, Tomlinson & Jeffrey 1990). This is not true for *B. aethiopum*; leaf scars are particularly inconspicuous due to annual fire and termite feeding activity along the stem. Yet, by crosschecking, it has been deduced that age at first reproduction is higher than 40 years and the oldest palms are more than 100 years old (Vuattoux, pers. comm.; Giffard 1967).

Borassus aethiopum is dioecious and no case of sex switching or clonal reproduction is known. Females bear 50–100, 1.0–1.5 kg fresh weight fleshy fruits, with 2 to 3 seeds per fruit (Vuattoux 1968). *B. aethiopum* has developed a particular root foraging strategy that enables it to exploit sparse nutrient-rich patches (Mordelet *et al.* 1996).

STUDY SITE

The study was conducted at the Station d'écologie tropicale de Lamto, Ivory Coast (6°13'N, 5°02'W; Fig. 1) at the edge of the rain forest domain (Menaut & César 1979). It lies in the Guinean bioclimatic zone, according to Monod's classification (Monod 1957) adapted by Menaut (1983). Rainfall is ca 1200 mm/yr, and the mean monthly temperature is 27°C (Pagny 1988). Two main soil types are present in Lamto: tropical ferruginous soils in most areas and hydromorphic pseudogley soils in thalwegs and flat areas (Riou 1974). Savanna vegetation is composed of grass and small dicotyledonous trees. Adult palms of *B. aethiopum* form a third stratum above the two others (henceforth, the term "palm" will refer to *B. aethiopum*). These three strata characterize the so-called "*Borassus aethiopum* savannas" common in west Africa. Two savanna types have been defined in Lamto, corresponding to the two different soil types, differences in the dominant grass species, and the spatial patterns and densities of trees (Menaut & César 1979): shrub savanna on the ferruginous soils and grass savanna on the hydromorphic soils. Each year the grass layer and all standing vegetation up to 2-m high is burned by fire in the middle of the dry season.

Palms have not been exploited for sap wine since 1961 in the Lamto Reserve (2500 ha) surrounding the research station; palm exploitation was already very low before the creation of the reserve because of the formerly low human population density in the area.

METHODS

We defined four stages based on palm morphology (Table 1): Entire-Leaved seedlings bearing only one or two first eophylls (EL-seedling), Slitted-Leaved seedlings bearing at least one second eophyll (SL-seedlings), juveniles with fan-shaped leaves (stemmed or not stemmed), and adults (reproductive, stemmed, and with the same fan-shaped leaves).

All individuals were censused in April 1996

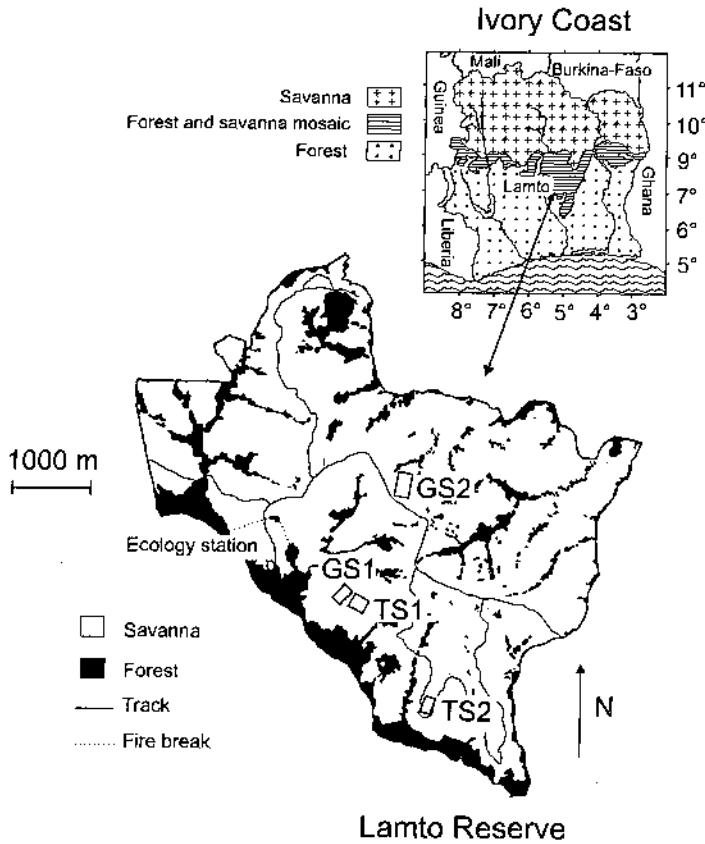


FIGURE 1. Location of Lamto Reserve in the Ivory Coast, and locations of the study plots. Adapted from Gauthier (1990).

(Table 2) on two plots of shrub savanna (TS1: 4.00 ha and TS2: 3.75 ha), and two plots of grass savanna (GS1: 3.75 ha and GS2: 6.00 ha; Fig. 1). The size and location of the plots were chosen so that plots could be considered representative of their facies with respect to soil characteristics and tree and palm densities.

Adult palm girth was measured at breast height. Palm height (from the ground to the base of terminal the bud) was measured with a dendrometer (April 1996 and April 1997). Green leaves were counted. In the field, female palms were

usually far from each other (>10 m), so that EL-seedlings around females were easily attributed to a single female; the very few seedlings growing away from females were also easy to associate with a single female. Thus, EL-seedlings with one or two leaves were numbered around each female. Adults were classified into four reproductive classes: (1) male adults bearing flowers during the year of the census (M); (2) females bearing fruits or flowers in the year of the census (F); (3) female adults bearing neither fruit nor flower but distinguishable by a high number of EL-seedlings within a few meters

TABLE 1. Description of the four stages used in the study

	Leaves	Stem	Reproduction
Entire-Leaved Seedlings	Entire elongated	No	No
Slitted-Leaved Seedlings	Slitted a few times	No	No
Juveniles	Fan-shaped costapalmate	Only for the older juveniles	No
Adults	Fan-shaped costapalmate	Massive	Yes

TABLE 2. Number of individuals censused by plot and by stage. Mean number of leaves and mean stem height are given for each stage with the standard deviation in parentheses.

	TS1	TS2	GS1	GS2	Nb leaves	Stem height (m)
EL-seedlings	1441	1773	1362	2210	1.3 (0.5)	0 (0)
SL-seedlings	127	169	249	200	1.9 (0.6)	0 (0)
Juveniles	153	269	228	154	4.5 (3.3)	0.7 (1.6)
Adults	110	111	66	93	11.9 (4.2)	14.8 (2.2)

of their stem base (f); and (4) adult individuals with no mark of reproduction during the year of the census (*i.e.*, no flower, fruit or seedling; 0). These individuals were not reproductive during the census year, and their sex could not be determined because it was not possible to attribute any seedling to them.

All variance and covariance analyses (for height and the number of palm leaves) were performed with SAS software (SAS 1989). We used the PROC GLM procedure with type III sum of squares to perform unbalanced analyses of variance and covariance. Variables were square root or log transformed so that residuals could be considered to have a normal distribution, and have equal variances among the different levels of explanatory class variables. The LSMEANS method was used to compare the least square means (LSmeans) across levels of class variables. In tables, LSmeans values have been transformed back into their original units (meters, no. of leaves, no. of seedlings). All tests were performed at the 5 percent significance level.

RESULTS

ALLOMETRY.—Table 2 displays the mean number of leaves and the mean stem height for each stage. For juveniles, average heights are low because of skewed size distributions (see population structure below).

TABLE 3. Covariance analysis of palm height (dependent variable) for juveniles as a function of plot (class variable) and number of leaves (covariable); logarithm of height and number of leaves was used; $R^2 = 0.61$, model $df = 8$, error $df = 789$, model $F = 461.77$, $P = 0.0001$; bold numbers indicate significant effects.

Source	df	F	P
Intercept	1	2231.86	0.0001
Nb leaves	3	0.47	0.0222
Plot	1	5.94	0.0001
Plot *Nb leaves	3	4.14	0.0029

The relation between stem height and the number of leaves was first assessed graphically (Fig. 2). For each plot, a log-log regression curve was fitted for juveniles and another was fitted for adults. The relation between height and the number of leaves changed radically during the life of a palm: there was a positive relationship between height and the number of leaves for juveniles and a negative relationship was found for adults.

Because height can only increase with age, this shows that for young palms, the number of leaves only increased until sexual maturity and then decreased. On Figure 2, a few juveniles and adults had fewer leaves than other individuals of the same height (they are far to the left on the fitted curves). We observed in the field that most of these palms were in poor health (having a constriction of the trunk at some level, and/or small leaves), probably due to accident or stress.

The positive relationship between height and number of leaves for juveniles (Fig. 2) was significant and varied slightly among plots (Table 3). A significant effect of plot on the intercept and slope was detected. Comparisons of LSmeans showed that juveniles were slightly taller in the GS2 and TS2 plots than in the other two (Table 7). LSmeans were very low (a few centimeters) because a large proportion of juveniles had two or three leaves and no stem (height = 0).

The relationship between height and the number of leaves for different classes of adults was determined using two covariance analyses. We first expressed height as a function of the number of leaves and then express the number of leaves as a function of height.

The relationship between height of adults and their number of leaves (independent variable) varied with plot and reproductive class. We found significant effects of reproductive class and plot on the intercept, and a significant effect of plot on the slope (Table 4). Comparisons of LSmeans (Table 7) showed that adults with no sign of reproduction (0) were smaller than others, and that there was no

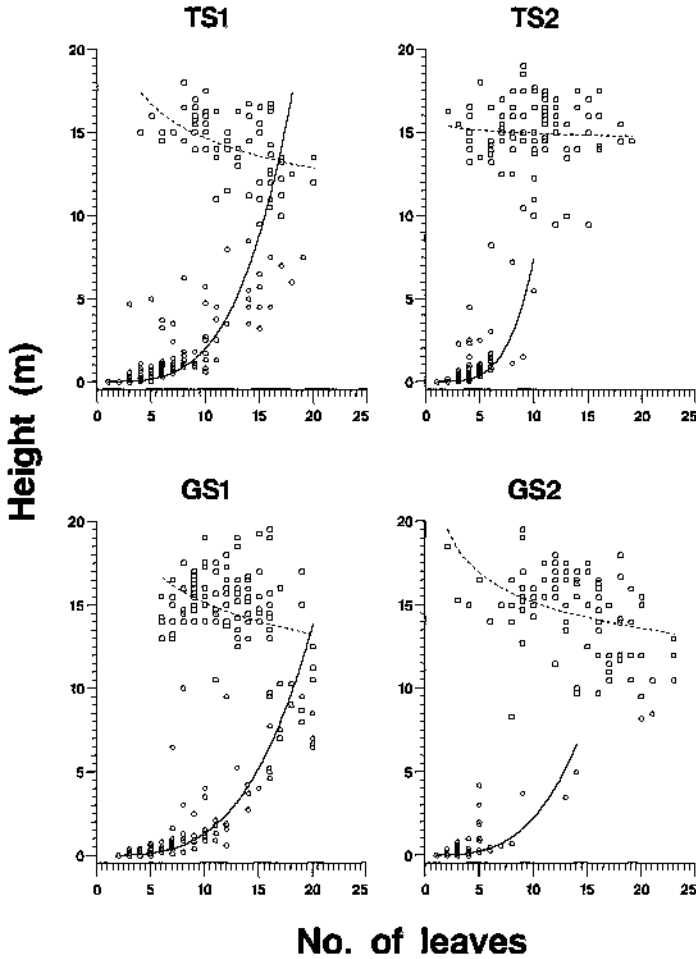


FIGURE 2: Plot of height for all measured palms against their number of leaves. Square: adults; circle: juveniles; dotted line: log-log regression curve for adults; solid line: log-log regression curve for juveniles.

TABLE 4. Covariance analysis of palm height (dependent variable) for adults as a function of reproductive class (RC), plot (class variables), and number of leaves (covariable); logarithm of height and number of leaves were used; $R^2 = 0.20$, model $df = 11$, error $df = 379$, model $F = 12251.09$, $P = 0.0001$; bold numbers indicate significant effects.

Source	df	F	P
Intercept	1	3105.27	0.0001
Plot	3	6.45	0.0003
RC	3	12.31	0.0001
Nb leaves	1	72.27	0.0001
Plot *Nb leaves	3	6.29	0.0004

significant height difference between reproductive males (M) and females (F). These comparisons also showed that there was on average no height difference among plots for adults (although the slope was slightly different among plots).

The relationship between the number of leaves and height (independent variable) varied significantly with reproductive class (Table 5; significant effect of reproductive class on the slope). Comparison of LSmeans (Table 7) showed that: (1) non-reproductive adults during the year of the census (f and 0) had less leaves than the others; (2) there was no significant difference in the number of leaves between reproductive females (F) and reproductive males (M); and (3) adult palms had fewer leaves in the TS2 plot than in the others.

A covariance analysis of adult girth at breast

TABLE 5. Covariance analysis of palm leaf numbers (dependent variable) for adults as a function of reproductive class (RC), plot (class variables), and height (covariable); logarithm of height and number of leaves were used; $R^2 = 0.45$, model $df = 23$, error $df = 356$, model $F = 1022.63$, $P = 0.0001$; bold numbers indicate significant effects.

Source	df	F	P
Intercept	1	134.98	0.0001
Plot	3	1.90	0.1300
RC	3	1.71	0.1636
Height	1	31.47	0.0001
RC*Plot	9	0.84	0.5810
Height*Plot	3	1.46	0.2242
Height*RC	3	2.79	0.0403

height as a function of height, the number of leaves, plot, and reproductive class, was also performed, but no significant effect was found ($R^2 = 0.16$, model $df = 47$, error $df = 321$; model $F = 1.33$, $P = 0.0822$).

GROWTH PATTERN.—Figure 3 displays juvenile height increment (between April 1996 and April 1997) as a function of height (in 1996) and number of leaves. Only juveniles < 6 m were considered (height increment measurement error with a dendrometer was too large for taller juveniles and adults). All plots were pooled together because no clear difference was found among them. Figure 3 shows a positive correlation between height increment and both height and the number of leaves.

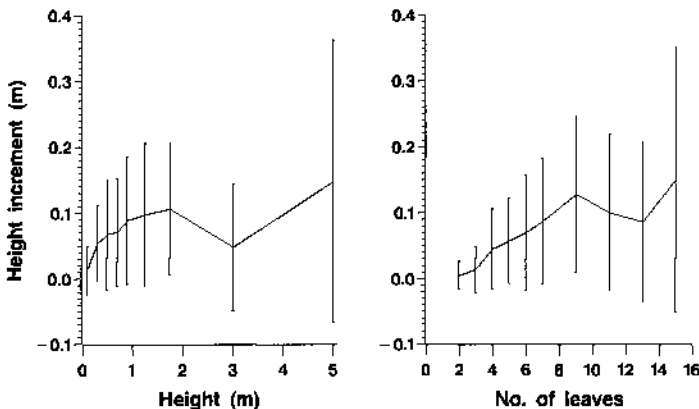


FIGURE 3: Yearly stem increment against number of leaves and height for juveniles in the four plots. Juveniles were pooled in classes according to their height and number of leaves to attain more than ten individuals in each class. Standard deviations are displayed for each class.

TABLE 6. Covariance analysis of the number of EL-seedlings per adults female (dependent variable) as a function of reproductive class (RC), plot (class variables), and number of leaves (covariable); square root of the number of EL-seedlings was used; $R^2 = 0.33$, model $df = 6$, error $df = 150$, model $F = 15.09$, $P = 0.0001$; bold numbers indicate significant effects.

Source	df	F	P
Intercept	1	13.84	0.0003
Plot	3	6.02	0.0001
RC	1	11.51	0.0001
Nb leaves	3	14.00	0.0003

Since the usual assumptions of regression could not be met (mostly because of a high number of individuals with a null height increment), we used the performed nonparametric Kendall's coefficient of rank correlation (τ) test to test the significance of these correlations. They were both significant (for the effect of height: $N = 384$, $\tau = 0.414$, $P = 0.028$; for the effect of number of leaves: $N = 112$, $\tau = 0.373$, $P = 0.028$).

REPRODUCTION.—The number of EL-seedlings around females was affected by plot, reproductive status of females, the year of the census (F or f), and the number of leaves (Table 6). The more leaves there were on a female, the more seedlings there were around it (no. seedlings) $^{1/2} = 3.35 + 0.24 \times \text{no. leaves} + \text{plot effect} + \text{reproductive class effect}$). LSmeans comparisons showed that repro-

TABLE 7. Comparisons of the LSmeans for the covariance analyses of juvenile height (Table 3), adult height (Table 4), adult number of leaves (Table 5), and number of EL-seedlings per female (Table 6). LSmeans with the same letter are not significantly different (t-test).

Plot	Height (m) (juveniles)	Height (m) (adults)	Number of leaves (adults)	Number of seedlings (female adults)
0	—	13.37 ^a	7.97 ^a	—
f	—	14.54 ^b	8.46 ^a	26.2 ^a
F	—	15.25 ^b	12.47 ^b	46.2 ^b
M	—	15.20 ^b	12.56 ^b	—
GS1	0.014 ^b	14.35 ^a	10.53 ^b	17.5 ^b
GS2	0.035 ^a	14.75 ^a	11.17 ^b	58.6 ^a
TS1	0.016 ^b	14.54 ^a	10.49 ^b	31.5 ^b
TS2	0.062 ^a	14.63 ^a	8.49 ^a	31.7 ^b

ductive females (F) had almost twice as many seedlings as nonreproductive ones (f), and that females of the GS2 plot had more seedlings than others (Table 7).

For all plots, ca 25 percent (reproductive classes 0 and f) of individuals did not reproduce during the year of the census. Chi-square tests indicated that the sex ratio was significantly male-biased for the GS2 plot, regardless of the sex of individuals in the (0) reproductive class (Table 8).

POPULATION STRUCTURE.—There was a general strong decrease in density of individuals between successive stages (Fig. 4). A bimodal distribution of stem height was found (Fig. 5). There was a very low number of palms in the intermediate height classes, many more in the two smallest height classes ($0 \leq h \leq 2$) and in the higher classes ($h > 12$ m). There were few tall juveniles and small adults.

TABLE 8. Sex ratios in the different plots according to three models: model 1: M/F = sex ratio of reproductive individuals; model 2: $(M + 0)/(F + f)$ = sex ratio of all individuals regarding individuals with no reproduction sign to be males; model 3: $(M + 0/2)/(F + f + 0/2)$ = sex ratio considering half of the individuals with no reproduction sign to be males. The four reproductive classes (M, 0, f, F) are defined in the text. Sex ratios in bold numbers are significantly different from 1 (χ^2 test).

	Model 1	Model 2	Model 3
SS1	0.731	1.200	0.714
SS2	1.233	1.176	0.776
GS1	1.154	1.292	0.947
GS2	2.450	2.207	1.548

DISCUSSION

SENESCENCE.—The number of leaves increased during the juvenile stage, and started to decrease just after sexual maturity (Fig. 2). The number of leaves usually increased during the palm juvenile stage but remained quite constant during the adult stage (Van Valen 1975, Piñero *et al.* 1982, Enright 1985, Ash 1986, de Steven 1989). *B. aethiopicum* adults died when they had on average less than half the number of leaves they had when they were recruited as adults (Fig. 2). This is a clear and strong mark of senescence.

The number of seedlings cannot be a good estimate of annual fecundity, because it results from the accumulation of surviving seedlings produced over previous years. We can reasonably assume a high turnover of seedlings (S. Barot, pers. obs., high mortality and replacement by newly germi-

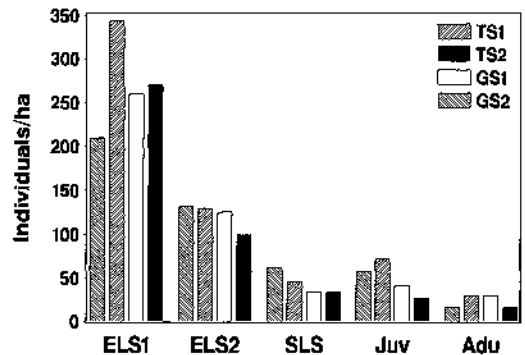


FIGURE 4. Palm density by stage (ELS1: one leaf, Entire-Leaved Seedling; ELS2: two leaves, Entire-Leaved Seedling; SLS: Slitted-Leaved Seedling; Juv: Juvenile; Adu: Adult) and by plot.

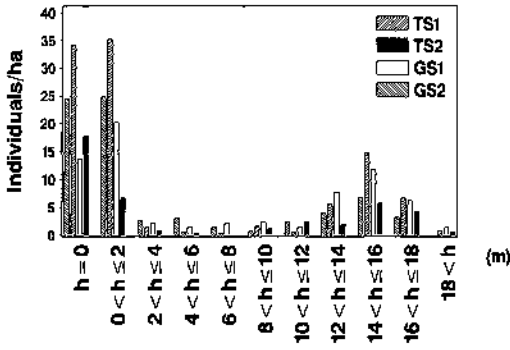


FIGURE 5: Adult and juvenile palm densities by height class and plot.

nating fruits), however, and under this assumption, the number of seedlings found under females yielded a rough estimate of the mean number of fruits they produced during the last few years. Thus, tall females with fewer leaves (considered old females in the previous section) had lower fecundities than younger females. Furthermore, nonreproductive individuals of either sex (f or 0; see the discussion on sex ratio below) had less leaves than the others (Table 7). Older individuals are less likely to reproduce. This reproduction pattern is further evidence of senescence and points to a positive relationship between the number of leaves and the amount of resources that can be invested into reproduction.

We know of only two other studies that report such a decrease in female fecundity among older individuals. In the case of *Rhopalostylis sapida* (Enright 1992, Enright & Watson 1992), the decrease in fecundity seemed to be slight and only occurred among the few oldest individuals. Evidence of senescence is also available for the clonal understory palm, *Geonoma congesta* (Chazdon 1992), in which a decrease was found in the reproductive potential of the older ramets.

Although it is hard to compare the life histories of clonal and non-clonal palms, it seems that *G. congesta* (Chazdon 1992), *R. sapida* (Enright 1985, 1992; Enright & Watson 1992), and *B. aethiopum* life histories display the same trend suggesting senescence: a simultaneous decrease in fecundity and investment to the stem or leaves among older adults. The pattern is nevertheless stronger for *B. aethiopum* than for the other two species, because both fecundity and the number of leaves began to decrease just after sexual maturity. A third of the adult individuals had < 10 leaves, and a fourth showed no sign of reproduction. For the other two

palm species, fecundity was globally correlated to adult size and age, and only decreased at the end of the adult stage for the oldest individuals: relatively short and rapid senescence. The senescence in *Bovassus Aethiopum* could be considered extremely gradual (Watkinson 1992). *Bovassus aethiopum*, in this way, displays an intermediate life history between semelparity and iteroparity: it can be considered an iteroparous palm with a very short period of high fecundity and then a period of decreasing fecundity, or an almost semelparous palm with reproduction associated to senescence, although senescence here is not as dramatic as in true monocarpic species.

We compared the senescence pattern observed in *B. aethiopum* to the theoretical predictions based on models of life history evolution. The pattern supports Caswell's (1986) prediction of increasing reproductive values for classes of individuals with increasing size, if we consider the number of leaves as a measure of size. It is also compatible with Charlesworth and Leon's (1976) prediction that reproductive effort increases with age when growth is continuous, if we consider the decrease in leaf number of adults as a rupture in the growth.

Access to light is believed to be an important constraint for forest palms and may be an important factor in the evolution of their life histories (Oyama 1990, Enright 1992). In order to be recruited, a juvenile must grow as quickly as possible. Juveniles that do not grow fast enough die without reproducing, and adults display decreasing stem growth. The forest is an "offspring-size-beneficial habitat" (Begon *et al.* 1990); however, competition for light does not seem to explain all the differences among palm life histories. Some similarities can be found in the life histories of *B. aethiopum*, *G. congesta* (Chazdon 1992), and *R. sapida* (Enright 1985, 1992; Enright & Watson 1992), although the first one is a tropical savanna palm tree, the second one an understory tropical rain forest palm tree, and the third a canopy to subcanopy temperate forest palm tree. Also, *B. aethiopum* is the only palm (to our knowledge) that displays a strong senescence pattern starting early in the adult stage. Natural fire, frequent in all savannas may play the same role as competition for light; the taller a juvenile is, the less likely it is for its leaves to get burned. Therefore, a juvenile that grows fast will be able to maintain more leaves with the same resource investment than other juveniles and will be more likely to recruit.

POPULATION STRUCTURE.—The observed bimodal

size structure (Fig. 5) can be due to: (1) a temporal variation in survival and recruitment rates (a past disturbance could have prevented recruitment of adults during a certain period); (2) growth rate variations according to size (Huston & DeAngelis 1987); or (3) a combination of these processes. Since it has been shown that stem elongation is faster for taller juveniles (Fig. 2), size bimodality must be due to the accumulation of adults with relatively high survival rates in a few height classes. According to the parsimony principle, we do not need to invoke a possible past disturbance to explain the observed size bimodality.

Size bimodality previously has been reported for some other palm species (Ashton 1969, Savage & Ashton 1983, Enright 1985). Enright (1985) showed that the accumulation of slow-growing individuals in the larger size classes was the cause of size bimodality in *R. sapida*. The key point is that a bimodal population structure is evidence of a past disturbance only if the population is divided into age classes. For these two palm species (*B. aethiopicum* and *R. sapida*), populations were classified into size classes, the palms not remaining the same time in each class because the growth rates were not constant throughout the life cycle.

DIFFERENCES BETWEEN SEXES AND SEX RATIO.—A sexual dimorphism could have been predicted (Lloyd & Webb 1977) because reproduction costs seem higher for females (bearing many heavy fruits) than for males (bearing inflorescences with very small inconspicuous flowers); however, no difference between reproductive males and reproductive females was detected with regard to height, the number of leaves, and girth. This suggests that the resource allocation to stem elongation, leaf formation, and reproduction is not very different between males and females. The same pattern was found for another dioecious tropical palm tree (Oyama 1990).

It was not possible to establish *a priori* whether palms with no sign of reproduction (0) were males or females. They must be either nonreproductive males, or females with seedlings that have all died. Some living nonreproductive females (f) and some females that died a few years ago (S. Barot, pers. obs.) still have living seedlings a few meters around their stem. Therefore, it seems unlikely that all seedlings of a living female died and we hypothesized that more than half of the nonreproductive adults with no seedlings under their canopy (0)

were males. These males had fewer leaves than reproductive males (Table 7) and hence were older (Fig. 2). Consequently, old males reproduce less often than younger ones, and their average fecundity over several years was lower. The fecundity pattern of males appears similar to that of females, with a decrease in fecundity during the senescence period.

The sex ratio was male-biased in the GS2 plot. A male-biased sex ratio has been found in some dioecious plants (Waser 1984, Armstrong & Irvine 1989, Allen & Antos 1992), and is most likely linked to environmental conditions, with females being expected to be more numerous in favorable environments (Bierzychudek & Eckhart 1988). Savage and Ashton (1983) found a male-biased sex ratio for a palm in the same tribe as *B. aethiopicum* (*Lodoicea maldivica*). This pattern was attributed to a higher female death rate compared to that of the male. A long-term demographic study is needed to test this possibility on *B. Aethiopicum*, to understand the mechanism that determines the biased sex ratio found in the GS2 plot and to determine its ecological significance.

CONCLUSION.—Our main finding is the long senescence period in the life cycle of *B. aethiopicum* (a decrease in the number of leaves, and a decrease in female fecundity and probably in male fecundity). This senescence is extremely strong and seems to start just after reaching sexual maturity. The life expectancy of young adults is long (probably > 50 yr); therefore, a great proportion of adults (about a third) can be considered senescent, and the senescence period is very long. To our knowledge, such a severe senescence pattern has never been described in any other palm species. Because most studied palms are forest palms, it would be interesting to compare closely *B. aethiopicum* to other savanna palm species.

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