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Demography of a savanna palm tree in Ivory Coast (Lamto): population persistence and life-history

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ABSTRACT. *Borassus aethiopum* is a dioecious palm tree. of African savannas. A stage-classified matrix population model has been parametrized with field data (Lamto reserve, Ivory Coast). It enabled the study of the persistence of the population, and analysis of its sensitivity to different vital rates. Age of palms in each stage were estimated to complete the description of the palm life-history. The main results are: (1) The studied populations are very close to the equilibrium but the stable stage distribution (predicted by the model) and the observed distribution are significantly different indicating a former change in the vital rates. (2) Reproduction seems to be highly delayed (first reproduction on average at 114 y), while the estimated duration of the reproductive part of the life-cycle is relatively short (22 y).

KEY WORDS: age estimation, demography, humid savanna, matrix population model, palm tree, senescence, stage classified matrix model

INTRODUCTION

Matrix population models have been widely used to analyse the demography of plant populations (Silvertown *et* al. 1993). They constitute very good tools to analyse the persistence of populations, to describe the life-histories of the species concerned, and to compare different populations (Caswell 1989). For animals such as birds or mammals, survival and fecundity are usually said to depend mostly on age, whereas size is more relevant in the study of plant dynamics (Caswell 1986). Indeed, plants are modular organisms, and are generally much more plastic in their growth than animals (Begon et *al. 1990*, Trewavas &Jennings 1986, Watkinson & White 1985). Consequently, the relation

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between age and size (or stage) is obscure in plants. Thus, matrix models are usually age-classified for animal populations, while they are usually stage-classified for plant populations, and particularly for long-lived plant populations. In this context palm trees are good biological models since their architecture is relatively simple (Tomlinson &Jeffrey 1990): they are easy to identify at all stages, and stages are easily determined.

Several matrix population models have already been published for palm trees growing in forest (as canopy or understorey trees) (Bullock 1980, Enright & Watson 1992, Olmst ed & Alvarez-Buylla 1995, Pinard 1993, Piñero *et* al. 1984). We present here, as far as we know, the first matrix model for a savanna palm tree, *Borassus aethiopum.* A first description of its life-cycle was obtained using static data (Barot & Gignoux 1999). Other studies have analysed the respective roles of different processes in palm demography in Lamto savanna (Ivory Coast): intraspecific competition, seed dispersal, formation of spatial patterns of individuals in each stage (Barot *et al.* 1999a, b). Yet, no study has been published that could enable a global analysis of the palm's demography, and particularly to assess persistence of the studied populations. Consequently, we had two aims: (1) To build a matrix model and use it to determine the demographic status of the studied palm populations (are the populations growing, remaining stable or declining?), and determine sensitivities to the demographic parameters (fecundity, survival and recruitment rates in each stage), (2) To use the model to complete the former description of the palm's life-cycle and particularly to test for the senescence pattern that has already been pointed out by Barot & Gignoux (1999). For the first time, age estimates were derived for *B. aethiopum* by the rarely used method of Cochran & Ellner (1992).

STUDY SPECIES

Borassus aethiopum is a common palm in West Africa humid savannas. It is a tall, solitary and pleonanthic palm of the Borasseae tribe (Uhl & Dransfield 1987). Seed germination is remote-tubular (Tomlinson &Jeffrey 1990, Uhl & Dransfield 1987): the cotyledonary axis extends downwards in the soil and carries the seedling down to 40 cm deep (Monnier 1968). The youngest seedlings have one or two 0.5 - 1.0 m long elongated entire leaves, older seedlings have one or two 0.5 - 1.0 m long leaves which are slit a few times, Older individuals all bear the same fan-shaped leaves (Vuattoux 1968). In the youngerjuveniles, the terminal bud is below ground, which defines the establishment phase (Tomlinson &Jeffrey 1990). The number of leaves increases during the juvenile stage (up to about 20) and decreases during the adult stage (Barot & Gignoux *1999). B. aethiopum* is dioecious and no case of sex switching or clonal reproduction is known. Females bear 50-100, l-l.5 kg fresh weight fleshy fruits, with 2-3 seeds per fruit (Vuattoux 1968).

Palm age is often assessed using the number of leaf scars (Tomlinson 1963, Tomlinson & Jeffrey 1990). This is not possible for *B. aethiopum* because leaf scars are particularly inconspicuous due to the annual fire and to termite feeding activity along the stem. Moreover, age assessments based on leaf scars are probably biased, because comprehensive data on the leaf dynamics are hardly available, and because during the establishment part of palm life-cycles the terminal bud is often underground (Tomlinson & Jeffrey 1990). The corresponding leaf scars cannot be counted to assess the duration of this part of the life cycle,

STUDY SITE

The study was conducted at the Lamto station, Ivory Coast (6°13′ N, 5°02′ W) at the edge of the rain forest domain (Menaut & César 1979). This 'site has been described thoroughly elsewhere (Menaut & César 1982). Savanna vegetation is composed of grass and small dicotyledonous trees. Adult palms – *B. aethiopum* – form a third stratum above the two others (from now on the term 'palm' will be used for B. *aethiopum*).

The demographic study was implemented in two different savanna types, corresponding to two different soil types (Menaut & César 1979): tree savanna on the ferruginous soils and grass savanna on the hydromorphic soils in poorly drained areas. Palms have been proved to have different spatial patterns in these two savanna types: *adults* are clumped' in grass savanna, whereas they have a random pattern in tree savanna (Barot et al. 1999a). Each year the grass layer and all standing vegetation up to 2 m high is burnt by a fire in the middle of the dry season.

Lamto station lies in the middle of a 2500-ha reserve founded in 1961 so that palms have not been exploited 'since 38 y. Palm exploitation was already very low before the creation of the reserve because of the former low human population density in the area at this date. Around the reserve, the palm population is nowadays exploited intensively: wine is made out of the sap ((Herzog et *al.* 1995), which in this area is extracted from adults until their death), fruits are eaten, trunks and leaves are used for construction.

METHODS

Field data

We defined five stages based on the palm morphology: seeds, entire-leafed seedlings bearing only one or two entire leaves (EL-seedling), slit-leafed seedlings bearing at least one slit leaf (SL-seedlings), juveniles with fan-shaped leaves (stemmed or not stemmed), and adults (reproductive, stemmed and with the same fan-shaped leaves as juveniles).

Palm individuals were censused in April of 1996, 1997 and 1998 on two plots of tree 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). Size and location of the plots were chosen so that plots could be considered as representative of their facies regarding soil characteristics, tree and palm densities. Basic data on Lamto palm population have already been gathered in these plots (Barot & Gignoux 1999). All SL-seedlings, juveniles and adults were censused in the four plots (Table 1). EL-seedlings of three females were censused in both the GS2 and TS2 plots and their survival and recruitment rates as a function of the distance to their mother palm have been analysed (the detailed results of this study have been already published elsewhere) (Barot *et* al. 1999b). Overall, 3200 palms were labelled, and censused annually. At each census, number of leaves (LN) and height (H) of the palm tree (juveniles and adults) were also recorded.

Fecundity (number of seeds) was estimated in 1997 and 1998 by numbering along the year all the falling fruits of 31 females (16 in the TS1 plot and 15 in the GS2 plot) and the seeds they contained. The germination rate (probability for a seed to germinate × probability for the young seedling to survive 1 y below ground and to set its first leaves during the next wet season) was estimated by distributing, in 1996, 145 fruits (435 seeds) between the two savanna types.

Model

We designed a one-sex female-based matrix population model (Caswell 1989) with five stages: seed, EL-seedlings, SL-seedlings, juveniles and adults (Figure 1). Since the population is stage classified, a Levkovitch matrix was used (Caswell 1986, 1989): for each stage (i) a probability of survival (P), and a probability of recruitment (G_i) have to be defined. It was not possible to determine the sex of non-reproductive individuals, and the male role in the fecundity has not been assessed so that the model was female-based. The seed stage has been introduced since (1) seeds have no dormancy and germinate immediately after fruits have fallen, (2) their first leaves only appear above ground 1 y after germination. The reserves contained in the seed enable the building of a cotyleclonary axis that extends downward into the soil and carries the seedling to a depth of 40 cm, where the first roots and leaves develop (Monnier 1968). Most fruits fall at the beginning of the rainy season (S. Barot, *pers. obs.*), after the annual fire that burns, in Lamto savanna, all above-ground non-ligneous vegetative material ($\leq$ 2 m in height). Thus, this germination strategy enables palm seedling terminal buds to be protected from the fire, and enables seedlings to set their first leaf just after the fire, when they will be able to develop during c. 1 y before being burnt by the next annual fire.

Table 1. Number of individuals of the savanna palm, *Borassus aethiopum*, censused by plot and by stage. All SL-seedlings, juveniles and adults were censused in each plot. The EL-seedlings of three females were censused only in the GS2 and TS2 plots.

	TS1	TS2	GS1	GS2	Total
EL-seedlings	–	756	–	535	1291
SL-seedlings	275	162	158	233	831
Juveniles	22H	297	152	124	HO 1
Adults	110	111	66	93	380

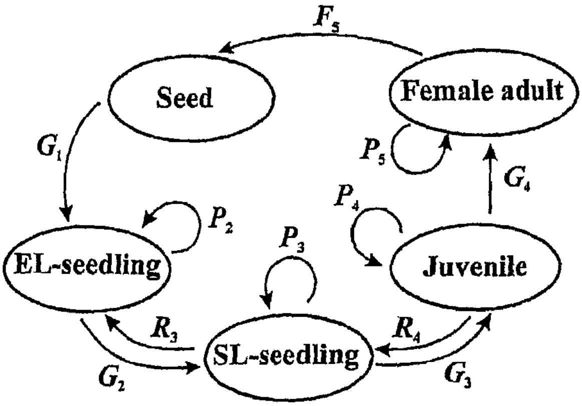

Figure 1. Life cycle diagram corresponding to the five-stage female-based matrix model used for *Borassus aethiopum* population. F_i, fecundity in stage *i*; G_i, probability in stage *i* of survival and recruitment to the next stage; P_i, probability in stage *i* of survival in the same stage; R_i, probability in stage i of survival and retrogression to the precedent stage.

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}(t+1) = \begin{bmatrix} 0 & 0 & 0 & 0 & F_5 \\ G_1 & P_2 & R_3 & 0 & 0 \\ 0 & G_2 & P_3 & R_4 & 0 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{bmatrix} \times \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}(t) \qquad (1)$$

This equation corresponds to a general matrix representation of the equation $n(t+1)$ =A x $n(t)$, where n is the vector describing numbers of individuals in each stage, and A the transition matrix, containing the fecundity (F), proportions of individuals that survive and remain in a stage (P), proportions of individuals that survive and recruit to the next stage (G), and proportions of individuals that survive but regress to the precedent stage (R). In our model (1) $P_1 = 0$ since seeds, the first stage, have no dormancy, (2) G_4 was calculated as the product of the global recruitment rate (g) from the juvenile stage (computed for all juveniles, whether they were males or females) to the adult stage by the percentage of females among all adult palms (sex ratio, sr). Fecundity was defined, as the number of seeds produced annually by a female adult (F_5). Since the model was female-based, recruitment rates of juveniles to the adult stage were defined as the recruitment probability multiplied by the proportion of females found in each plot ($G_4 = sr \times g$). We did not find any difference between adult male and female survival and growth rates.

The transition matrix enables the computation of changes in the numbers of individuals from time t to time t+1 (y) simply by multiplying the transition matrix by the initial population vector (eqn 1), and to predict the asymptotic behaviour of the population: asymptotic growth rate (λ), and stable stage distribution. We computed the sensitivities (results not detailed) and the elasticities of λ to the matrix parameters (Caswell 1989, De Kroon *et al.* 1986). Sensitivities measure the absolute sensitivity of λ to absolute changes in vital rates, while elasticities assess the proportional effects of proportional changes in the vital rates (Caswell 1989, van Groenendael *et al.* 1988). We also computed the sensitivity of the predicted stable stage distribution to the matrix parameters as well **as** the elasticity of the asymptotic growth rate to the sex-ratio (lower level parameters elasticity) (Caswell 1989). Alvarez-Buylla & Slatkin's (1993) formula was used to estimate analytically the standard deviation of asymptotic growth rates due to the estimation of vital rates. It was further used to assign confidence limits to these rates and to test whether they are significantly different from 1.0, assuming a normal distribution.

A five-stage matrix was built with the average transition probabilities for the four plots and the two annual transitions-from now on, it will be called the average five-stage model. Four **five-stage** matrices were also constructed in a two-way design: savanna type (grass savanna + tree savanna) x two annual transitions (1996-97 + 1997-98). Variations in fecundities according to the year and the savanna type were analysed through an ANOVA model. The four matrices were compared through a two-way log-linear **analysis** of **variance** model (Caswell 1989) through the SAS CATMOD procedure (SAS 1989b).

We preliminarily analysed matrix models where adult and juvenile stages were divided in size classes. These models lead to the same conclusions as the five-stage model presented here, as far as asymptotic growth rates and stable stage distributions **are** concerned. Thus we only present here the five-stage model (the more simple one) **based on** stages defined objectively by morphological and reproductive features. These stages have already been shown to be relevant for demographic studies (Barot *et* al. 1999a, b).

Estimations of palm age in the different stages were computed using Cochran's method (Cochran & Ellner 1992). The basic idea underlying these estimations of age is that even **if** a stage-classified matrix model does not take age explicitly into account, age is implicitly present in the model since the matrix parameters (survival and recruitment rates, as well as fecundity) are estimated on an annual **base.** For each stage, we calculated (using the notation of Cochran & Ellner, 1992): the average age in the i^th^ stage (y_i), the mean age of residence in the i^th^ stage (S_i), the conditional remaining life-span of individuals in the i^th^ stage (Ω_i), the mean time to reach the i^th^ stage from the seed (first stage) ($\tau_{\text{seed},\ i}$), the total conditional life-span (Λ_i).

Ω_i. is the mean remaining life span of individuals that have reached the i^th^ stage, while Λ_i is the mean total life-span of individuals that have reached the i^th^ stage, *so* that Λ_i is the sum of $\tau_{\text{seed},\ i}$ and Ω_i.. y_i and S_i seem to be closely related parameters but y_i is calculated under the assumption that the stable stage distribution has been reached, as opposed to S_i. For each of these mean age-based parameters it was possible to compute a standard deviation, These standard deviations do not denote the uncertainty in the age estimations: they are estimates of the real standard deviations of the age of the individuals in the different stages. We also computed the predicted fraction of age *a* individuals in each stage *i*, $p_{i,a}$, at the stable stage distribution, and the fraction of age *a* individuals in the whole population Ω_a, i.e. the stable age distribution.

Matrix analyses were realized using the ULM software (Legendre & Clobert 1995), and some specially-designed *authors* SAS/IML (SAS 1989a) routines, particularly for the age estimations. Statistics were also implemented in the SAS statistical package (SAS 1989b).

RESULTS

Average five-stage model

The average transition matrix calculated for the four plots, and the two annual transitions (Table 2) is characterised by very high survival rates, even for the two seedling stages, and low recruitment rates between stages. The global percentage of females in the whole population was not significantly different from 50% (although the sex ratio was biased in some plots) (Barot & Gignoux 1999). The mortality pattern is U-shaped: the mortality rate ($1-G_i-P_i-R_i$, cf. eqn 1) decreases during the first stages and increases from the juvenile stage to the adult stage (respectively for seeds, EL-seedlings, SL-seedlings, juveniles, and adults: 0,774, 0.124, 0.028, 0.008 and 0.044).

The asymptotic growth rate value, λ, was 1,009. The standard deviation of λ, due to the uncertainty on matrix parameter, was estimated as $\sigma(\lambda) = 0.010$. Assuming a normal distribution for λ, that means that the 95% confidence limit intervals were (0.989, 1.029): the asymptotic growth rate of the population was not significantly different from 1.0.

The observed stage distribution was different from the predicted stable stage distribution (Figure 2; χ^2-test, $df = 3$, $P < 0.001$). If the observed transition rates were constant in time, the proportion of EL-seedlings and adults in the whole population would have decreased, while the proportions of SL-seedlings and juveniles would have increased, Yet, the sensitivity of the right eigenvector (stable stage distribution) to the recruitment rate from the juvenile stage to the adult stage (G_4) was much higher than to all other parameters (the sensitivities to G_4 were respectively 37.1, 15.4, −9.2, -44.0, and 0.6 for seed, EL-seedling, SL-seedling, juvenile and adult frequencies, whereas sensitivities to all other demographic parameters were smaller than 2.0 in absolute value). This means that very small variations in G_4 could have produced the discrepancy between the observed and the predicted distributions.

Elasticities of λ to the recruitment rates are lower than to survival rates

Table 2. Average annual transition matrix for the palm tree *Borassus aethiopum* computed for the four plots and the 1996–98 period. EL-S, entire-leafed seedlings; SL-S, slit-leafed seedlings.

	Seed	EL-S	SL-S	Juvenile	Adult
Seed	0.000	0.000	0.000	0.000	68.0
EL-S	0.126	0.851	0.021	0.000	0.000
SL-S	0.000	0.025	0.918	0.012	0.000
Juvenile	0.000	0.000	0.043	0.978	0.000
Adult	0.000	0.000	0.000	0.002	0.956

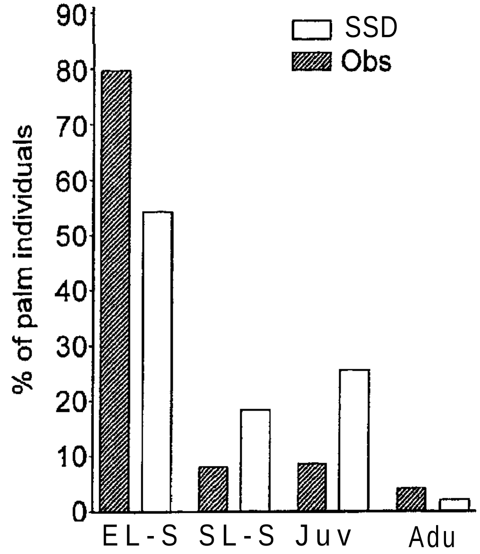

Figure 2. Observed stage distribution for the four plots pooled together (Obs), and predicted stable stage distribution (SSD) for the average (four plots and two annual transitions) five-stage *B. aethiopum* model. EL-S, entire-leafed seedling; SL-S, slit-leafed seedling; juv, juvenile; adu, adult.

(Table 3). The highest elasticity was obtained for juvenile survival. The elasticity for the fecundity is very low. As recruitment rates are much lower than survival rates, the pattern of sensitivities of λ to vital rates was partly different from the elasticity pattern (results not detailed): (1) sensitivity to the fecundity was also very low, but (2) sensitivities to recruitment rates were higher than to survival rates, (3) the highest sensitivity was for the juvenile recruitment rate to the adult stage (G_4).

G_4 was computed as the product of the global recruitment rate from the juvenile stage (g, both male and female individuals) to the adult stage by the proportion of adult females (sr) so that it was possible to compute the elasticity of λ to sr and g (elasticity to lower level parameters) (Caswell 1989). These elasticities were both small (0.0125, 0.0125) in comparison to the elasticities to survival rates.

The recruitment to the adult stage (and thus sexual maturity) occurs relatively late in the palm's life-cycle: average age of adults, y_{adult} = 81.4 y, mean

Table 3. Elasticity matrices for the five-stage average *Borassus aethiopum* matrix model (Table 2). Existing transitions are indicated in bold. Stages as in Table 2.

	Seed	EL-S	SL-S	Juvenile	Adult
Seed	0.000	0.000	0.000	0.000	0.012
EL-S	0.012	0.069	0.000	0.000	0.000
SL-S	0.000	0.013	0.159	0.003	0.000
Juvenile	0.000	0.000	0.015	0.481	0.000
Adult	0.001~	0.000	0.000	0.012	0.222

Table 4. Age-based life-history parameters (Cochran & Ellner 1992) corresponding to the five-stage *Borassus aethiopum* average matrix model. Standard deviations are indicated in parenthesis. Average age in the i^{th} stage, y_i; mean age of residence in the i^{th} stage, S_i; conditional remaining life span of individuals in the i^{th} stage, Ω_i; mean time to reach the i^{th} stage from the seed stage, $\tau_{seed,i}$; total conditional life span of individuals that have reached the i^{th} stage, Λ_i.

	y_i	S_i	4	$\tau_{seed,i}$	Λ_i
Seed	1 (0)	1 (0)	3.1 (36.0)	1 (0)	4.1 (36.0)
EL-seedling	8.7 (10.7)	10.4 (18.6)	16.4 (97.9)	2.3 (6.1)	18.8 (104.0)
X-seedling	29.6 (31.9)	45.7 (56.7)	57.9 (208.9)	9.9 (11.9)	67.7 (220.7)
Juvenile	62.3 (45.3)	91.1 (72.3)	79.1 (248.0)	21.8 (14.2)	100.9 (262.2)
Adult	8.14 (48.9)	113.9 (75.7)	22.7 (103.7)	92.1 (72.3)	114.9 (176.0)

age of residence in the adult stage, S_{adult} = 113.9 y, mean time to reach the adult stage, $\tau_{seed,\ adult}$ = 92.1 y (Table 4). $\tau_{seed,\ adult}$ is consistent with S_{adult}, while the low y_{adult} value, is apparently not consistent with the two previous values. It is due to the fact that y_{adult} is computed for the stable stage distribution. That is linked to the asymptotic growth rate which is slightly higher than 1: many young individuals have been produced in the recent cohort. The population will rejuvenate if the matrix parameters do not change and when the stable age distribution is reached (Cochran & Ellner 1992).

The remaining life-span of individuals (Ω_i) increases until the-juvenile stage, emphasizing the relatively low duration of the reproductive (adult) part of the palm's life-cycle. The age distribution by stage displayed in Figure 3a has three characteristics: (1) frequencies of individuals strongly decreased from the seedling stage to the adult stage; (2) age distributions were increasingly symmetric with increasing stage order; (3) age distributions were increasingly even with increasing stage order, allowing for higher differences between ages of individuals that belong to the same stage. This last feature is clearly pointed out in Table 4 where all standard deviations increase from the seed stage to the adult stage, for the average age, the mean age of residence, and the mean time to reach the stage. This is due to the accumulation of uncertainty on the age at which recruitment between stages occurs. The standard deviations of both the conditional remaining life-span and the total conditional life-time decrease from the juvenile to the adult stage because adults do not recruit to another stage and because their mortality is higher than juvenile mortality. Figure 3b displays, as in most age classified population models (when the stable age distribution has been reached), an age distribution divided in two main parts: first a steep slope depending mainly on the high mortality rates in the first stages, second a milder slope depending on adult survival rate.

The four (two savanna types × two yearly transitions) five-stage models

There is no obvious difference between the four estimated matrices (Table 5), in spite of differences *in* estimated sex ratio between the two savanna types (45% of females in grass savanna, and 57% in tree savanna). Fecundity is not significantly different between the two savanna types and the two annual transitions (two-way analysis of variance df = 3, 6 1; r^2 = 0.02; savanna type, $P = 0.92$;

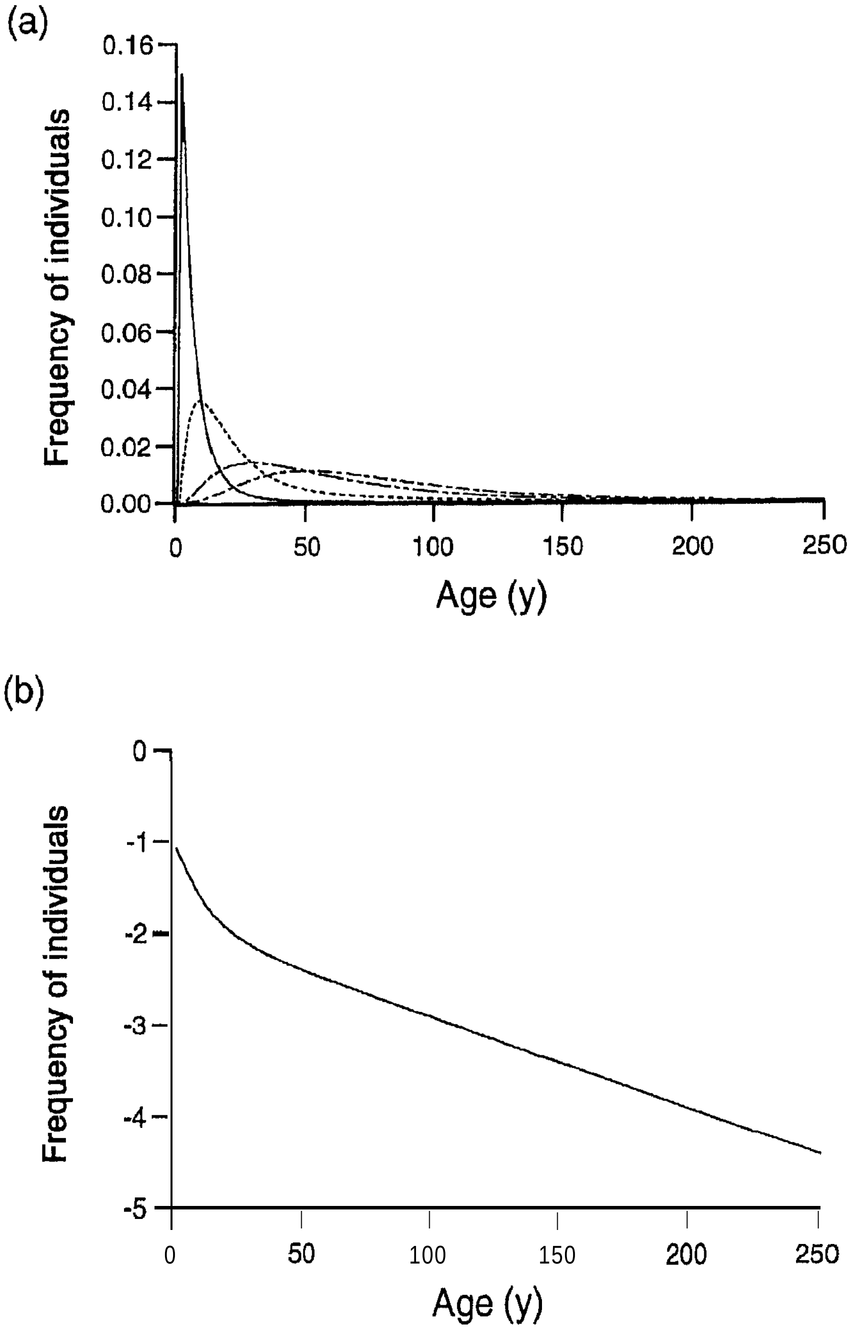

Figure 3. Stable age distributions predicted for the five-stage average *B. aethiopum* model. (a) by stage: ——— EL-seedling, — — — SL-seedling, —— . . juvenile, —— · — adult; (b) in the whole population.

Table 5. Transition *matrices* for the **two types** of savanna and the two **annual** transitions. Stages as in Table 2.

	Tree savanna 199697					Tree savanna 1997-98				
	Seed	**EL-S**	**SL-S**	Juvenile	Adult	Seed	EL-S	**SL-S**	Juvenile	Adult
Seed	0.000	0.000	0.000	0.000	54.9	0.000	0.000	0.000	0.000	81.6
EL-S	0.126	0.863	0.002	0.000	0.000	0.126	0.850	0.034	0.000	0.000
SL-S	0.000	0.037	0.923	0.005	0.000	0.000	0.030	0.900	0.014	0.000
Juvenile	0.000	0.000	0.063	0.989	0.000	0.000	0.000	0.038	0.978	0.000
Adult	0.000	0.000	0.000	0.003	0.959	0.000	0.000	0.000	0.0006	0.926
	Grass savanna 1996-7					Grass savanna 1997-98				
Seed	0.000	0.000	0.000	0.000	69.5	0.000	0.000	0.000	0.000	63.0
EL-S	0.126	0.867	0.031	0.000	0.000	0.126	0.821	0.026	0.000	0.000
SL-S	0.000	0.007	0.936	0.018	0.000	0.000	0.017	0.921	0.015	0.000
Juvenile	0.000	0.000	0.031	0.974	0.000	0.000	0.000	0.040	0.960	0.000
Adult	0.000	0.000	0.000	0.003	0.980	0.000	0.000	0.000	0.005	0.965

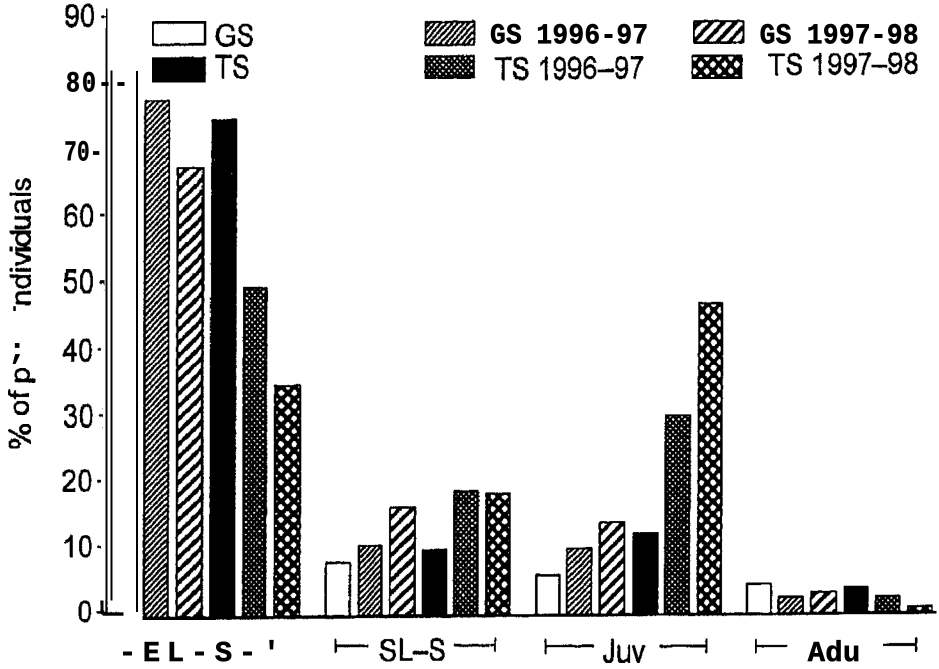

Figure 4. Observed and predicted stable stage distributions of *B. aethiopum* individuals by stages. GS Obs, observed distribution in grass savanna; GS 1996-97, predicted distribution in grass savanna derived from the 1996-97 model; GS 1997-98, predicted distribution in grass savanna derived from the 1997-98 model; TS Obs, observed distribution in tree savanna; TS 1996-97, predicted distribution in tree savanna derived from the 1996-97 model; TS 1997-98, predicted distribution in tree savanna derived from the 1997-98 model. Stages as in Figure 2.

year, $P = 0.58$; interaction, $P = 0.38$). Similarly, both the savanna type and the year were shown to have no effect on the transition matrix (log-linear analysis of variance, df = 3, 49; type of savanna, $P = 0.09$; year, $P = 0.11$; interaction, $P = 0.19$). λ values were, respectively, for TS 1996-97, TS 1997-98, GS 1996-97, and GS 1997-98 models: 1,003, 0.993, 1,007, 1.006. The standard deviations of these asymptotic growth rates were computed (respectively 0.012, 0.019, 0.009, 0.008). These indicate that the rates were not significantly different from 1.0.

Stable stage distributions were different according to the matrix model, and particularly according to the savanna type (Figure 4). For tree savanna, EL-seedlings were much less frequent in the stable stage distribution than in the current distribution (χ^2-test for the equality between observed and predicted distributions, df= 3, $P < 0.001$ for both the 1996-97, and the 1997-98 models). Conversely, juveniles were much more numerous in the predicted stable stage distribution than in the observed population, For grass savanna the predicted stable stage distribution was globally closer to the observed distribution. However, as in the average five-stage model (Figure 2), in both grass and tree savannas there were fewer EL-seedlings and adults, than in the observed distributions (χ^2-test for the equality between observed and predicted distributions, df = 3, $P < 0.001$ for both the 1996-97 and the 1997-98 models). The reverse held for SL-seedlings and juveniles. As in the average five-stage model, the sensitivity of the stable stage distribution was much more important to the recruitment from the juvenile stage to the adult stage than to all other matrix parameters.

DISCUSSION

B. aethiopum demography

B. aethiopum population seems to be very close to the equilibrium: the asymptotic growth rates of the different models are not significantly different from 1.0, and the four five-stage matrices for the two savanna types x two annual transitions are not significantly different. However, *B. aethiopum* populations are not at the stable stage distribution. That suggests either that (1) a past event such as a storm stronger than usual, or a very intense fire has disturbed the stage distribution, which has not yet returned to the stable distribution, or that (2) some vital rates in the transition matrix have changed, for example because of the recent climatic trend, and the new stable stage distribution has not yet been reached. These two cases are possible since the species is long-lived, and since the stable stage distribution should be long to recover from any kind of disturbance or demographic change (Platt et *al.* 1988). However, we do not know of any disturbance, at least since the ecology station has been founded (1962), and the current rainfall irregularity [the total annual rainfall tends to decrease, and the rainy season arrival is often delayed) could have triggered a change in the vital rates (Paturel *et al.* 1995). These rates could also have changed clue to the extinction (in Lamto Reserve) of *B. aethiopum* fruit secondary dispersers (elephants and baboons). In fact, it has been shown that seedling survival and recruitment rates would probably be higher if dispersal distances were longer (Barot et *al.* 1999b). Moreover, the whole palm population dynamics has been predicted to depend strongly on the interaction between environmental heterogeneity, and the palm spatial distribution (Barot *et al.* 1999a). The outcome of this interaction is likely to depend on the primary spatial distribution, i.e. seed spatial repartition. These two mechanisms may explain the observed difference between observed and predicted stable distributions, since the sensitivity of the stable stage distribution to the recruitment rate to the adult stage is very high.

The savanna type did not have any significant effect on the transition matrix. It may be due to the fact that all survival rates are very high, while all recruitment rates are very low: indeed small differences in proportions would be very difficult to highlight unless a lot of individuals were to have been censused. The predicted stable stage distributions present the same trends (within savanna types, and during the two yearly transitions) in comparison to the observed distributions. It suggests that the discrepancy between grass and tree savanna stable stage distributions may arise from an interaction between some general factor of change at the scale of Lamto savanna, and some intrinsic factor to the savanna type, The two savanna types are first characterized by different edaphic conditions, soil being much more humid during the rainy season in grass savannas than in tree savannas. They are also characterized by different adult palm spatial patterns, adults having a random pattern in tree savanna, and a clumped pattern in grass savanna (Barot *et* al. 1999a). That could denote a less intense competition between juvenile or adult palms in grass savanna. These two features (spatial pattern and edaphic conditions) could interact with, for example, a climatic change or a modification in the seed dispersal regime, and produce the observed demographic pattern.

Our transition matrices are more complicated than the ones used by De Matos & Silva Matos (1998) since there is some retrogression. Anyhow, our sensitivity and elasticity results follow the general pattern they found in Lefkovitch matrices: sensitivities to recruitment are higher than to survival, whereas the reverse holds for elasticities. The elasticity to fecundity is very small, which seems to be a common property of a Lefkovitch matrix (elasticities to fecundities are bound to be smaller than the greatest elasticity to recruitment rate) (De Matos & Silva Matos 1998). As far as both relative sensitivities (elasticities) and sensitivities are concerned, the most sensitive stage is the juvenile stage: (1) the vital rate that limits mostly (sensitivity) the growth rate of the palm population is the recruitment rate from the juvenile stage to the adult stage, i.e. juvenile growth rate that is very low; (2) the relative increase (elasticity) in a vital rate that would lead to the strongest increase in λ would be an increase in juvenile survival. This pattern may partly be explained by fire that each year burns the palm leaves up to several metres, and forces palms to invest in new leaves, and probably into defences (thick highly sclerotic tissues). Moreover, there seems to be an intense intraspecific competition between juveniles (probably for light) that decreases their growth rates (Barot *et al.* 1999a). The lack of nutrients in Lamto savanna soils could also be a factor limiting juvenile growth and their recruitment to the adult stage: nutrients have a very patchy distribution that has led to a particular root foraging strategy that involves the development of a wide root system (Mordelet *et* al. 1996). Fire, intraspecific competition, and the lack of soil nutrients are probably the main proximate causes of the observed very low recruitment rate to the adult stage. In this way, this recruitment rate constitutes a kind of demographic bottleneck that constrains the whole palm demography.

The elasticity of λ to the sex ratio is small. That is due partly to the fact that the sex ratio is used to compute G_4, the recruitment to the female adult stage, for which the elasticity is also very small. That is also due to the fact that fecundity was supposed not to depend on males (pollination is not taken into account). A two-sex model (Caswell & Weeks 1986, Meagher & Antonovics 1982) would be more relevant, but data on the role of males in the fecundity are difficult to obtain. Data on the mechanism of sex determination (environmental, or purely genetic) (Bierzychudek & Eckhart 1988) and a mean to determine the sex of non-reproducing individuals would also be very useful to deal with this issue.

B. aethiopum *life-history*

As already suspected, *B. aethiopum* is very long-lived (Barot & Gignoux 1999). The most striking feature is that, according to the assessed age-based parameters, reproduction is highly delayed (first reproduction on average at 114 y), while the reproductive period before death is quite short (about 22 y on average), and much shorter than expected (Barot & Gignoux 1999). *B. aethiopum*, a savanna palm tree, seems to delay its reproduction more than forest palms for which age at first reproduction has been assessed through growth models and counts of leaf scars (Bullock 1980, Enright & Watson 1992, Olmsted & Alvarez-Buylla 1995, Pinard 1993, Piñero et *al.* 1984). Standard deviations of age-based parameters are very high. It *is* due to the fact that survival rates are quite high in *all B. aethiopum* stages, whereas recruitment rates are very low, that allows individuals to remain for a very long time in the same stage, without dying and without recruiting to the next stage. That denotes that the relation between age and stage (or size) is weak in *B. aethiopum* and that there is a strong growth plasticity in the species. Moreover, retrogression (recruitment of individuals to a precedent stage) increases the standard deviation of age-based parameters and is another clue of plasticity.

As stated in the method section, adult and juvenile stages were preliminarily divided into size classes. When the juvenile stage was divided into four height classes and the adult stage into two classes according to the number of leaves (height was measured less precisely for adults than for juveniles), it appeared that mortality decreases in the first three juvenile classes, and increases from the third juvenile class to the second adult class. Moreover, fecundity is higher for the first adult stage than for the second (results not detailed here). Dividing adult and juvenile stages in size classes enabled the building of a nine-stage matrix model that was also used to compute age estimations. As pointed out by Enright *et* al, (1995) these age estimations depend on the number of stages used in the model, Yet, the nine-stage model led to age estimations c. 15 y higher than the five-stage model (for age at first reproduction): that reinforces the conclusion that *B. aethiopum* begins to reproduce very late.

The results showing that fecundity (seed production) decreases in successive adult stages, and that mortality increases as early in the life-cycle as in the juvenile stage are consistent with previous results (Barot & Gignoux 1999) pointing out a clear senescence period in *B. aethiopum* life-cycle: numbers of leaves are maximum for the younger adults, fecundities assessed by seedling counts are higher for the younger females, They support the fact that senescence begins as soon as sexual maturity is reached.

The U-shaped mortality pattern that has been found for *B. aethiopum is* frequent among trees (Harcombe 1987) and palms (Enright & Watson 1992, Olmsted & Alvarez-Buylla 1995, Piñero *et al. 1984).* Causes of mortality are hardly known, but juveniles usually seem to die progressively, after spending several years with very few leaves, i.e. they seem to die from resource exhaustion. The whole mortality pattern would thus be linked to the resource allocation pattern (into roots, stem and leaves) and to some environmental constraints, mostly the global lack of nutrients in the savanna soils, and the annual fire (as stated above). Young palms that are too far from nutrient-rich patches, or that are too densely clumped are likely to die slowly just because they do not find enough resources to survive and grow (Barot *et al.* 1999a). Adults' death is in 80% of cases linked to an obvious senescence, i.e. they die when only three or four very small leaves remain without having reproduced for some years. Twenty per cent of adults' death are due to uprooting that can be viewed as a kind of frequent accident. However, uprooted palms are usually senescent (S. Barot, *pers. obs.*), and the obvious decrease in their number of leaves is likely to be concomitant with a decrease in the root system extension, which is of paramount importance for adult palm mechanical stability.

Thus, all results are consistent and point to an extreme case of the perennial strategy: reproduction is highly delayed, and its onset coincides with a strong senescence. Three savanna features are likely to be very important for plant dynamics, and are consequently likely to have shaped their life-histories (Skarpe 1992): fire (that burns Lamto savanna each year), the lack of mineral nutrients in soils (especially nitrogen), the lack of water (at least during the dry season). A fourth factor, herbivoty, plays an important role in savanna vegetation dynamics, but is probably not very important for palm trees: no herbivore is known to have a strong influence on *B. aethiopum* survival. For this palm, fire, the lack of nutrients (Mordelet *et al,* 1996), and possibly the lack of water during certain periods of the year are likely to weaken seedlings and juveniles, and to reduce their growth. As far as fire is concerned, a slow growth–high investment into aerial protective structure strategy seems to have been selected for *B. aethiopum*: protection of the terminal bud, thick sclerotic tissues, probably very rich in silica (Tomlinson &Jeffrey 1990). Moreover, for *B. aethiopum* it would probably not be advantageous to reproduce before a certain height has been reached, otherwise flowers (male and female) or young fruits may get burnt before becoming mature; flowers usually begin to develop during the dry season before the annual fire and fire often climbs up very high along palm stems (S. Barot, *pers. obs.*).

CONCLUSION

The main result of our study is that the studied palm populations are very close to the demographic equilibrium. However, a long-term study would be necessary to verify this conclusion. The asymptotic growth rates being very close to 1.0 may be due to the intraspecific competition formerly pointed out between juveniles (Barot *et* al. 1999a). Our model takes globally into account the effect of this density dependence on vital rates, and that leads to the observed vital rates, and to the consequent λ values: for example, the measured recruitment rate from the juvenile stage to the adult stage results partly from intraspecific competition between juveniles. Density dependence could be explicitly included in matrix population models (Silva Matos *et al.* 1999), but it was not possible here, since all palm populations have roughly the same density in Lamto savannas.

It must also be emphasized that matrix models do not take into account differences between individuals of the same stage. Such differences are particularly important for plants since plant individuals of a given population at least differ from each other in their spatial location, environment being often heterogeneous, and spatial distribution of individuals being usually uneven (Crawley 1986, Pacala & Silander 1985). Such space-related processes are suspected to play a particularly important role in *B. aethiopum* demography (Barot *et al.* 1999a). The matrix models and the computed λ values globally result from all these processes, without taking them explicitly into account as for density dependence. In fact, juvenile vital rates are probably density dependent, but since juveniles are highly clumped the negative interaction between them is strictly local (a few metres in scale) (Barot et *al.* 1999): it cannot be modelled easily with a matrix model. To understand how spatial processes—local competition, seed dispersion, favourable patches-interact, and what is their relative importance for the persistence of *B. aethiopum* populations, spatially explicit individual-based model should be built (Bolker & Pacala 1997, Huston 1992, Huston *et* al, 1988).

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