Demography and life history of two rattan species, *Eremospatha macrocarpa* and *Laccosperma secundiflorum*, in Côte d'Ivoire

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(*Accepted 26 July 2008*)

Abstract: Two rattans species were studied in Côte d'Ivoire using a stage-classified matrix model to compare their demography and life histories. Respectively 854 and 1009 genets of *Eremospatha macrocarpa* (pleonanthic) and *Laccosperma secundiflorum* (hapaxanthic) were censused every 6 mo over 18 mo. The population growth rates of *E. macrocarpa* ($\lambda = 0.979$) and *L. secundiflorum* ($\lambda = 0.959$) were not significantly different from 1. This indicates that the populations were close to equilibrium. However, the difference between the stable stage distributions and the observed distributions indicated temporal variation in vital rates. Elasticity analysis showed that growth and fecundity had lower contributions to λ than the survival rates for the two species. A Life Table Response Experiment revealed that the survival of the first juvenile stage (all stems < 6 m in length), fecundity, growth of the second juvenile stage (at least one stem > 6 m in length) and adult (reproductive) survival highly contribute to the differences between the demography of the two species. Reproduction is postponed longer for *L. secundiflorum* than for *E. macrocarpa* and the mean remaining life span for adult genets is shorter for *L. secundiflorum* than for *E. macrocarpa*. Finally, our results suggest the existence of two trade-offs within reproduction which suggest that, although the two species have different demographic features, the λ of their populations are not significantly different from 1.

Key Words: age estimation, elasticity, life-table response experiments, non-timber forest products, palm, population growth rate, stage-classified matrix model, tropical forest

INTRODUCTION

Life-history evolution is an important field of modern ecology (Begon *et al.* 2006, Stearns 1977). A useful approach is to compare the life histories of related organisms to determine how evolution has shaped the relationship between different life-history traits. Because the population growth rate is a function of all life-history parameters, changes in these parameters will cause changes in the growth rate (Caswell 2001, Stearns & Hoekstra 2000). In this context, palm trees are suitable models to study perennial plant demography and life history (Barot & Gignoux 1999). In particular, the relatively simple morphology of palm trees makes it is easy to define stages based on morphological traits and size.

Matrix population models have been widely used to analyse the demography of palms (Barot *et al.* 2000,

Bernal 1998, Bullock 1980, De Steven 1986, 1989; Escalante *et al.* 2004, Piñero *et al.* 1984, Rodriguez-Buritica *et al.* 2005, Souza & Martins 2006) and to improve the exploitation of palm populations (Anderson & Putz 2002, Balick 1987, Endress *et al.* 2004, Olmsted & Alvarez-Buylla 1995, Ratsirarson *et al.* 1996). Matrix models constitute useful tools to analyse the persistence of populations, to describe life histories, and to compare the demography of different populations or species (Caswell 2001). For plants, these models are usually stage-classified and require the estimations of the transition probabilities between stages as well as fecundities (Caswell 2001, De Matos & Matos 1998, Ramula & Lehtilä 2005, Silvertown *et al.* 1993). The models also allow the calculation of age-based parameters (Barot *et al.* 2002, Cochran & Ellner 1992) such as the mean ages in different stages.

We present here the first matrix model for the genets of two African rattan species: *Eremospatha macrocarpa* (Mann & Wendl.) Wendl. and *Laccosperma secundiflorum* (P. Beauv.) Kuntze. Despite the existence of over 600

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species of rattan and the fact that rattans constitute one of the main non-timber forest products worldwide, very little is known about their demography and life history. More generally, these species are multiple-stemmed palms, i.e. each individual (genet) produces several stems (ramets) linked by a common rhizome, and the demographic effect of such a type of clonality has seldom been studied. The two species have different flowering types. *Eremospatha macrocarpa* is pleonanthic: inflorescences are developed on axillary buds so that stems go on growing after flowering. *Laccosperma secundiflorum* is hapaxanthic: inflorescences are apical so that ramets die after flowering. We hypothesize here that these two flowering types lead to differences in the ramet dynamics and subsequently in the genet dynamics of the two species. For example, hapaxanthy should lead to higher ramet mortality in *L. secundiflorum* than in *E. macrocarpa*. This could subsequently lead to higher genet mortality in *L. secundiflorum* than in *E. macrocarpa*. In fact, the complete life histories (as defined by the age at first reproduction, fecundity and other life-history parameters) of the two rattan species are likely to have evolved in relation with their flowering types. The two species should thus have different life histories.

In turn, life-history differences should lead to differences between the demography of the two species. Although they live in the same environment and are taxonomically close to each other, their populations should achieve their growth rates through different combinations of demographic parameters. This should be reflected in the pattern of sensitivities of the population growth rate to the demographic parameters and a Life Table Response Experiment comparing the matrix models of the two species. The demographic models we present here have thus three objectives: first to determine the demographic status of the studied palm populations (increasing or decreasing), second to test the hypothesis that the two palm species have evolved different life histories in relation with their flowering types, third to test the hypothesis that the two palm species have different demographic characteristics. It must be added that the flowering type is a life-history parameter among many others, and that all the life-history parameters of the two species and their population dynamics have interacted bidirectionally all through their evolutionary histories. Our rationale is thus valid in retrospect, i.e. at a broad macro-evolutionary scale. Correlations between the flowering type, other life-history parameters and demographic features are thus to be expected but it is difficult to determine the succession of evolutionary pressures that have really been involved. For example, the flowering type of the two rattan species might have evolved before the evolution of different ramet and genet survival rates, but the reverse is also possible.

MATERIALS AND METHODS

Study site and data

Study site. The study was conduced in the N'zodji forest (1086 ha) in south-eastern Côte d'Ivoire. This forest is located between 5°33′N and 5°43′N and between 3°49′W and 3°56′W. N'zodji forest is dense, wet and evergreen. The climate is wet and subequatorial, with a mean annual precipitation of 1350 mm, and a mean annual temperature of about 25 °C. Soils are ferrallitic and derived from schist rocks.

Study species. *Eremospatha macrocarpa* and *Laccosperma secundiflorum* are multiple-stemmed palms: each individual (genet) produces many stems (ramets) that remain attached to each other by a rhizome. *Eremospatha macrocarpa* stems can reach up to 50–75 m long whereas *L. secundiflorum* stems can reach up to 25–50 m long (Sunderland 2007). In *E. macrocarpa*, the climbing stems have a small diameter (1–1.8 cm). Flowering is pleonanthic (Sunderland 2002): inflorescences are developed on axillary buds. Consequently, ramets can continue their growth after flowering and can thus flower many times. *Laccosperma secundiflorum* is also a multiple-stemmed climbing palm. Its climbing stems have a larger (3–5 cm) diameter than *E. macrocarpa*. Flowering is hapaxanthic: inflorescences are apical so that ramets die after flowering (Sunderland 2002, Tomlinson & Jeffrey 1990). A stem dies after flowering, but the genet it belongs to continues living and producing new stems (Sunderland 2002). *Eremospatha macrocarpa* fruits are larger (2.5 × 2 cm and 15–20 rings of scales) than *L. secundiflorum* fruits (1.5 × 1 cm in height and 12 spiral rings of scales) (Sunderland 2007).

The two rattan species are important non-timber forest products that are used in local handicraft. The exploitation of their natural populations is not controlled, which can potentially threaten these populations. Here, the harvest rate, defined as the number of ramets collected per harvestable ramets (juvenile 2 and adult stages) during a given period, varied according the plot and the species (unpubl. data). These estimates varied from 18% to 23% and from 8.3% to 42.7% over a 6-mo period, respectively for *E. macrocarpa* and *L. secundiflorum*. The harvest rate was on the average higher in *L. secundiflorum*.

Data collection. Three 200 × 200-m (4 ha) plots were established in the northern part of N'zodji forest. In each plot we counted and labelled all genets and ramets. For demographic analyses, genets of the two species were classified in four stages, according to their size and morphology using traditionally used criteria for palm

trees (Bullock 1980, Chazdon 1992, Escalante *et al.* 2004). These stages were established as follows (Figure 1): (1) seedlings (S), recently germinated individuals with no stem, but having a bipartite or fully developed leaves; (2) juvenile 1 (J1), the first juvenile stage, individuals with all stems smaller than 6 m in length; (3) juvenile 2 (J2), the second juvenile stage, individuals with at least one stem > 6 m in length, harvestable but no sexual reproduction; (4) adults (A), individuals with at least one stem > 6 m in length, reproductive adult and bearing flowers or fruits. Here, although the different ramets of a genet remain attached to the same rhizome, we consider the production of new ramets as a form of vegetative reproduction (Tomlinson & Jeffrey 1990). It has been shown from previous studies (Zoro Bi & Kouassi 2004) that ramets growing at more than 25 cm from each other belong to different genets, and those growing closer are linked by a common rhizome. The stage of a genet was considered to be the stage of its most developed ramet. As the model only addresses the demography of genets and since new ramets produced through clonal reproduction remain attached to the parent plants, fecundity was estimated through the count of new genets, i.e. seedlings, germinating from seeds. All genets and ramets were censused every 6 mo over 18 mo (January–June: rainy season; July–December: less-rainy season). During censuses new seedlings as well as new ramets of older genets were labelled.

Matrix analyses

Transition matrix construction. For each species, we designed a genet-based matrix population model with the four stages defined above. Since the population was stage classified, a Levkovitch matrix was used (Caswell 2001). Transition probabilities were calculated according to the proportion of genets in each stage following the three possible fates of surviving individuals. Fecundity was calculated as the number of newly germinating seedlings and attributed to the adults of the considered plot (Menges 1990, Valverde & Silvertown 1998). For each stage (i), a probability of survival in the same stage (Pi), a probability of growth to the next stage (Gi), a probability of retrogression to the previous stage (Ri), and a fecundity (Fi) were estimated (Figure 1). This leads to the following transition matrix:

$$A = \begin{pmatrix} P_s & R_{j1s} & 0 & F_a \\ G_s & P_{j1} & R_{j1j2} & R_{aj1} \\ 0 & G_{j1} & P_{j2} & R_{aj2} \\ 0 & 0 & G_{j2} & P_a \end{pmatrix}$$

Initially, a matrix was estimated for each of the three 6-mo periods using the data collected on the three plots. The 6-mo matrices of each species were compared through a three-way log-linear analysis. This showed that these
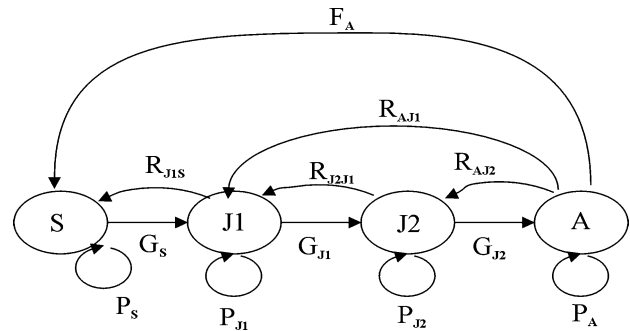

Figure 1. Life cycle diagram to the four-stage matrix model used for *Eremospatha macrocarpa* and *Laccosperma secundiflorum* population. F_i, fecundity in stage i; G_i, probability in stage i of survival and growth to the next stage; P_i, probability in stage i of survival in the same stage; R_i, probability in stage i of survival and retrogression to the precedent stage. Seedling = S; Juvenile 1 = J1, Juvenile 2 = J2, and Adult = A.

6-mo matrices are not significantly different and that we were not able to detect any seasonality in the matrices. Consequently, the arithmetic mean of the parameters of the three 6-mo matrices was then calculated to get an average matrix for each species (Caswell 2001, Silva Matos *et al.* 1999).

Transition matrix analyses. The average matrix of each species was used in all analyses. We computed the asymptotic growth rates (λ), stable stage distributions and the elasticities of λ to the matrix parameters (Caswell 2001). The estimation of the confidence intervals of λ was based on the approach described by Caswell (Caswell 2001). The variance of λ was estimated as the sum of the variances of all matrix parameters weighted by the squared sensitivities of λ to the parameters. Confidence intervals were then computed assuming a normal distribution for λ. This allowed testing whether the estimates were significantly different from 1. Moreover, the observed stage distributions were compared with the stable stage distributions predicted by the models using Chi-square tests. The fecundities (number of new seedlings per adult in the plot) of the two species were compared through a GLM repeated-measures model using the three plots as repetitions and the three 6-mo periods as within-subjects factor. The matrices of the two species were compared through a three-way log-linear analysis of variance (Caswell 2001).

Stage-based matrix models allow estimating age-based parameters, exploiting the idea that, even if the matrix model does not take explicitly age into account, age is implicitly present in the model since the transition matrix is computed on a yearly base (or any fixed time step) (Barot *et al.* 2002, Cochran & Ellner 1992). For each stage, we calculated: the mean age of residence in the ith stage (S_i), the conditional remaining life span of genets in the ith stage (Ω_i), the mean time to reach the ith stage from the

shoot (first stage) ($\tau_{s,i}$) (Barot *et al.* 2002, Cochran & Ellner 1992).

Sensitivity analysis. We used elasticity and Life Table Response Experiments (LTRE) to compare the life cycles of the two studied species and to explore the relative importance of the different matrix entries in the population growth rate. The first method consisted of calculating the elasticities of λ (asymptotic growth rate). Elasticity analyses evaluate the relative contribution of matrix entries to λ by providing information on how much λ would change if matrix entries were modified. Elasticities are a measure of proportional sensitivity of λ to proportional change in a_{ij} (De Kroon *et al.* 2000). Elasticities have been considered a useful tool to identify vulnerable life cycle stages on which to focus conservation and management strategies. We also used Silvertown's approach (Silvertown *et al.* 1992, 1993). This method consists in characterizing the life cycle by summing the elasticities of λ (asymptotic growth rate) to fecundities (*F*), growth rates (*G*) and survival rates (*L*) (Silvertown *et al.* 1992).

Secondly, to determine the differences between the transition matrices of the two species that are responsible for the different demographic behaviours of the two species and the difference in their asymptotic growth rates, a LTRE was conducted (Caswell 1996a). To do so, the arithmetic mean of the two matrices was calculated and the sensitivity of its asymptotic growth rate to each parameter was computed. These sensitivities were then multiplied by the difference between the corresponding parameters of the two species. This results in a contribution matrix taking into account both the effect of each demographic parameter on the population growth rate and the amplitude of the difference between the parameters of the two species. If a demographic parameter is very influential for the population growth rate but has similar values in the two species or if a parameter has highly different values in the two species but is not influential for the population growth rate it will have a low contribution in the LTRE matrix (and vice versa).

Matrix analyses were performed using the ULM software (Legendre & Clobert 1995) and some specially designed SAS routines using SAS/IML particularly for the age estimations. Statistics were also implemented in the SAS statistical package.

RESULTS

Average four-stage matrix model

In total 854 genets and 1853 ramets of *E. macrocarpa* were labelled in the three plots (Table 1). One thousand and

Table 1. Number of individuals of *Eremospatha macrocarpa* and *Laccosperma secundiflorum*, censused by stage in three plots (12 ha) in N'zodji forest of Côte d'Ivoire.

	Eremospatha macrocarpa		*Laccosperma secundiflorum*	
	Genets	Ramets	Genets	Ramets
Seedling	603	818	788	987
Juvenile 1	183	368	204	266
Juvenile 2	23	415	14	19
Adult	45	252	3	3
Total	854	1853	1009	1275

Table 2. Average 6-mo transition matrix for *Eremospatha macrocarpa* and *Laccosperma secundiflorum* computed for three plots and two 6-mo matrices.

	Seedling	Juvenile 1	Juvenile 2	Adult
Eremospatha macrocarpa				
Seedling	0.866	0.062	0.000	0.096
Juvenile 1	0.057	0.804	0.000	0.011
Juvenile 2	0.000	0.017	0.587	0.090
Adult	0.000	0.000	0.397	0.881
Laccosperma secundiflorum				
Seedling	0.863	0.031	0.000	2.139
Juvenile 1	0.064	0.919	0.190	0.000
Juvenile 2	0.000	0.011	0.619	0.000
Adult	0.000	0.000	0.071	0.750

nine (1009) genets and 1275 ramets of *L. secundiflorum* were recorded in the plots (Table 1). In general, the structure of the population was dominated by the seedling stages in the two species.

The average transition matrices of both species (Table 2) were characterized by very high survival rates, and low retrogression rates between stages. For *E. macrocarpa*, the growth rates were higher in the adult stage than in the other stages while for *L. secundiflorum* the higher growth rate was observed in the seedling and adult stages.

For *E. macrocarpa*, the mortality rate in 6 mo (mortality $= 1 - g_i - p_i - r_i$) was higher in the seedling and juvenile 1 stages (respective mortalities for seedling, juvenile 1, juvenile 2, adult: 0.077, 0.113, 0.016, 0.020). For *L. secundiflorum*, mortality was higher in the seedling, juvenile 2 and adult stages (respective mortalities for seedling, juvenile 1, juvenile 2, adult: 0.074, 0.039, 0.119, 0.250). For *E. macrocarpa*, the lowest mortality rates were observed for the juvenile 2 and adult stages, while for *L. secundiflorum* these two stages had higher mortality rates. The growth rate in 6 mo of the juvenile 2 stage was very low for *L. secundiflorum* (0.071) and much higher for *E. macrocarpa* (0.397). Moreover there was a high retrogression rate in 6 mo for *E. macrocarpa* from the adult to the juvenile 2 stage, while for *L. secundiflorum* the highest retrogression rate was from the juvenile 2 to the juvenile 1 stage.

The asymptotic growth rate was slightly lower than 1.0 for the two species ($\lambda = 0.979$ for *E. macrocarpa* and $\lambda = 0.959$ for *L. secundiflorum*). The standard deviation of λ, due to the uncertainty in matrix parameters, was 0.048 for *E. macrocarpa* and 0.046 for *L. secundiflorum*. Assuming a normal distribution for λ, led to the following 95% confidence intervals: 0.885–1.073 for *E. macrocarpa* and 0.870–1.048 for *L. secundiflorum*. Thus the asymptotic growth rates of the two species were not significantly different from 1.0.

There was a significant difference between the average matrices of the two species (log-linear analysis of variance, model df $= 1$, P < 0.001). This difference comes from all stages (log-linear analysis of variance comparing the fate of genets between the two species, separately for each stage, model df $= 1$, respective Ps: < 0.001, < 0.001, 0.027 and < 0.001 for the seedling, juvenile 1, juvenile 2 and adult stages). The average fecundity for *E. macrocarpa* and *L. secundiflorum* was 0.10 new individuals per adult genet per 6-mo period for *E. macrocarpa* and 2.14 for *L. secundiflorum*. The difference between these total fecundities was significant (repeated-measures ANOVA, F $= 12.90$, df $= 5$; P $= 0.023$ for the between-subjects effect).

Stable stage distribution analysis

The proportions of individuals in each stage were, respectively for *E. macrocarpa* and *L. secundiflorum*: seedling (0.504, 0.351), juvenile 1 (0.232, 0.622), juvenile 2 (0.060, 0.020) and adult (0.204, 0.007). For the two species, the observed stage distribution was different from the predicted stable stage distribution (Figure 2; Chi-square test for the equality between observed and predicted distributions, $\chi^2 = 9.49$, df $= 4$, P < 0.05). If the observed transition rates were constant in time, the proportion of adults in the whole population would decrease, while the proportion of seedlings and juveniles would increase for the two species.

Elasticity analysis

Generally, in the two species, elasticities of λ for the survival rates were higher than for the growth and retrogression rates (Table 3). In *E. macrocarpa*, the highest elasticity was observed in the adult survival while in *L. secundiflorum*, it was observed in juvenile 1 survival. This suggests that the critical stage was the adult stage in *E. macrocarpa* and the juvenile 1 stage in *L. secundiflorum*. The elasticity of λ for fecundities was very low in the two species.

The decomposition of elasticities in *F*, *G* and *L* led to 0.004, 0.084 and 0.911 for *E. macrocarpa*, and
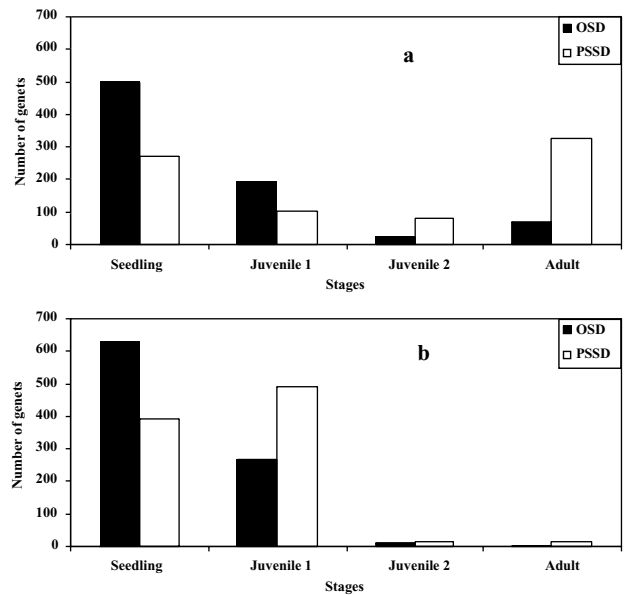

Figure 2. Comparison of observed stage distribution (OSD) and predicted stable stage distribution (PSSD) for *Eremospatha macrocarpa* (a) and *Laccosperma secundiflorum* (b).

Table 3. Elasticity matrices for the four-stage average *Eremospatha macrocarpa* and *Laccosperma secundiflorum* matrix models (Table 2).

	Seedling	Juvenile 1	Juvenile 2	Adult
Eremospatha macrocarpa				
Seedling	0.043	0.001	0.000	0.004
Juvenile 1	0.006	0.031	0.000	0.001
Juvenile 2	0.000	0.005	0.110	0.068
Adult	0.000	0.000	0.073	0.657
Laccosperma secundiflorum				
Seedling	0.223	0.014	0.000	0.011
Juvenile 1	0.025	0.631	0.004	0.000
Juvenile 2	0.000	0.015	0.027	0.000
Adult	0.000	0.000	0.010	0.038

0.011, 0.051 and 0.939 for *L. secundiflorum*. This decomposition was not significantly different between the two species (Kruskall–Wallis test, taking the three periods as repetitions, model df $= 1$, respectively $\chi^2 = 1.19$, P $= 0.26$; $\chi^2 = 0.05$, P $= 0.83$; and $\chi^2 = 0.05$, P $= 0.83$).

Life-table response experiments (LTRE)

Figure 3 shows that the differences in the demographic parameters that most contribute to the differences between the demography of the two species are: fecundity, juvenile 1 survival, juvenile 2 growth and adult survival. While juvenile 1 survival and the fecundity are higher in *L. secundiflorum* than in *E. macrocarpa* and increase the population growth rate of *L secundiflorum* relatively to that of *E. macrocarpa*, it is the reverse for juvenile 2 growth and adult survival.
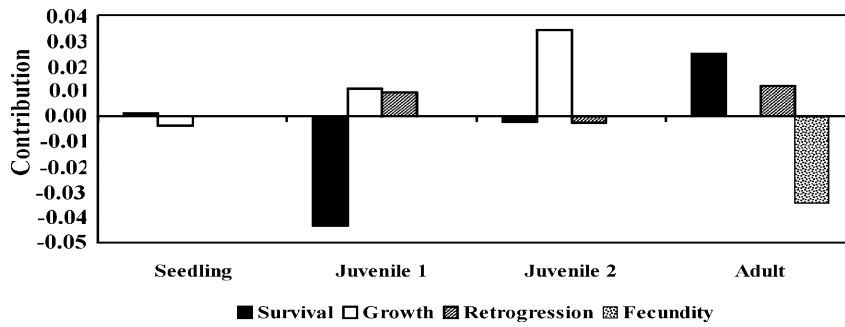
Figure 3. Life Table Response Experiment (LTRE) comparing the two rattan species. For each matrix parameter the product of the sensitivity of the asymptotic growth rate of the average matrix to this parameter and the difference between the parameters of the two species was calculated. Positive contributions correspond to demographic parameters that are higher in *Eremospatha macrocarpa* than in *Laccosperma secundiflorum* (and vice versa).

Table 4. Age-based (y) life-history parameters corresponding to the four-stage average matrix model for *Eremospatha macrocarpa* and *Laccosperma secundiflorum*. Values are mean $\pm$ SD. S_i = mean age of residence in the ith stage; Ω_i = conditional remaining life span of genets in the ith stage; $\tau_{seedling,i}$ = mean time to reach the ith stage from the first stage.

	S_i	Ω_i	$\tau_{seedling,i}$
Eremospatha macrocarpa			
Seedling	4.95 ± 5.43	6.56 ± 133	0.58 ± 0.95
Juvenile 1	8.15 ± 7.74	6.65 ± 180	4.47 ± 4.17
Juvenile 2	23.8 ± 19.7	21.4 ± 504	9.92 ± 7.01
Adult	28.0 ± 20.1	21.0 ± 498	9.23 ± 5.42
Laccosperma secundiflorum			
Seedling	5.99 ± 7.25	8.33 ± 162	0.69 ± 1.54
Juvenile 1	12.5 ± 9.61	10.0 ± 185	4.22 ± 3.46
Juvenile 2	13.8 ± 9.67	6.68 ± 141	12.5 ± 9.09
Adult	15.8 ± 9.82	2.00 ± 10.2	14.3 ± 9.67

Age-based parameters

The growth to the adult stage occurred earlier in *E. macrocarpa* than in *L. secundiflorum* (Table 4): respectively in the two species, mean age of residence in the adult stage 28.0 y, 15.8 y (S_{adult}); mean time to reach the adult stage, 9.2 y, 14.3 y ($\tau_{seedling, adult}$). For both species, $\tau_{seedling, adult}$ value was coherent with the S_{adult} value. That was also related to the asymptotic growth rate value being slightly lower than 1.0: few young individuals had been produced in the recent cohort.

The stable age distributions by stage (Figure 4a, c) had three characteristics for the two species: (1) frequencies of individuals decreased from the seedling stage to the adult stage for the two species; (2) age distributions were increasingly symmetric with increasing stage order; (3) the variability of age inside each stage increased with the stage order. This is also clear in Table 4 where all the standard deviations increased from the seedling to the juvenile 2 stage, for all the parameters estimated for *E. macrocarpa* and *L. secundiflorum* (with some exceptions for the later species). The stable age distribution of adults

showed two parts in *E. macrocarpa* (Figure 4b): first a steep slope depending on the high mortality rates in the first stages, second a milder slope depending on adult survival rate. In contrast, due to a higher mortality in the adult stage, the stable age distribution of *L. secundiflorum* presented a constant steep slope (Figure 4d).

The mean age to reach maturity ($\tau_{seedling,adult}$) was higher in *L. secundiflorum* than in *E. macrocarpa*. However, the relative duration of the reproductive stage (Ω_{adult}) in comparison with the time to reach sexual maturity ($\Omega_{adult}/\tau_{seedling,adult}$) was higher for *E. macrocarpa* (2.23) than for *L. secundiflorum* (0.14). *Eremospatha macrocarpa* lives longer than *L. secundiflorum*: the conditional total life span of individuals that had reached the adult stage was higher for *E. macrocarpa* (30.2 y) than for *L. secundiflorum* (16.3 y).

DISCUSSION

Life histories of *Eremospatha macrocarpa* and *Laccosperma secundiflorum*

The standard deviations of the age-based parameters were high. This was due to the fact that survival rates were higher than growth and retrogression rates in all stages. This allows genets to remain in the same stage during a long period without dying, being recruited or retrogressing (Barot *et al.* 2000). For this reason, the relation between age and stage becomes looser and looser over successive stages. According to Barot *et al.* (2000), the non-null retrogression probabilities found for the two rattan species are also likely to increase the variability of the age-based parameters and were a sign of plasticity. The variability in the mean age of residence, the conditional remaining life span and the total conditional life span are much higher in *E. macrocarpa* than in *L. secundiflorum*. This is explained by the lower adult mortality rate and the higher retrogression rates from the adult to the juvenile 1 and 2 stages in *E. macrocarpa* than in *L. secundiflorum*.
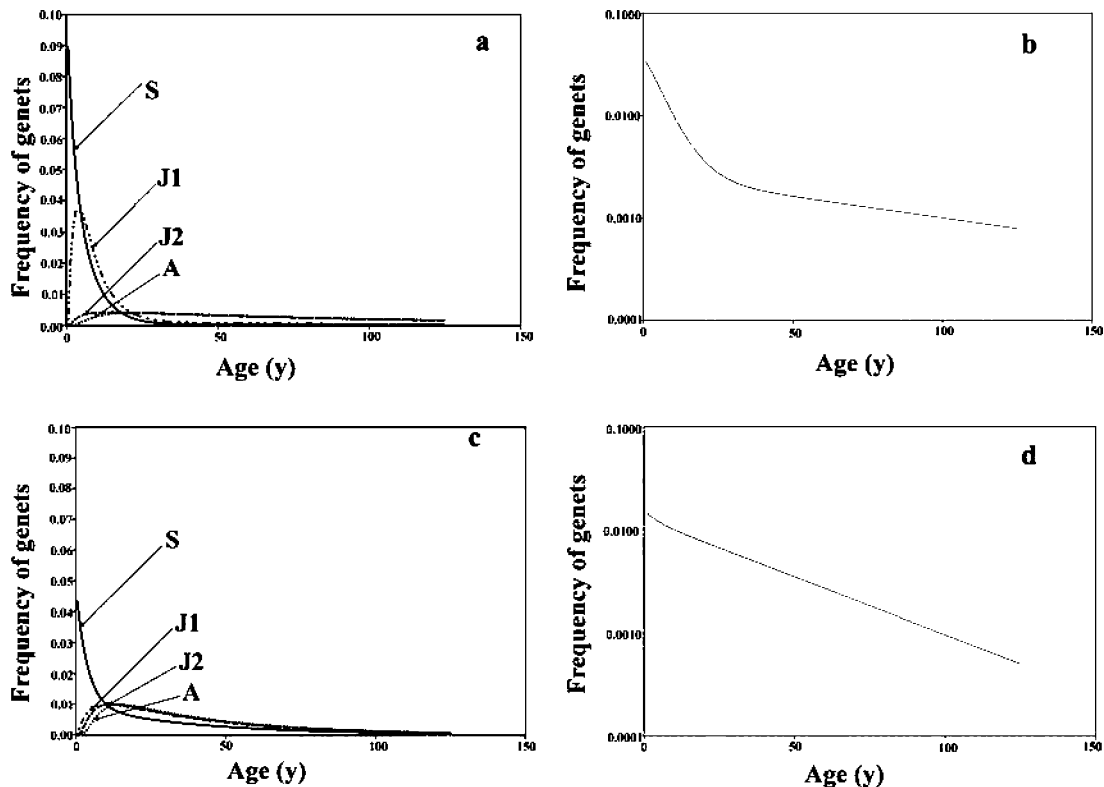
Figure 4. Stable age distribution by stage (a and c), S: Seedling, J1: Juvenile 1, J2: Juvenile 2, A: Adult, and for the whole population (b and d) as predicted by the four-stage average *Eremospatha macrocarpa* (a and b) and *Laccosperma secundiflorum* (c and d) model.

Mortality follows a U-shaped distribution in *L. secundiflorum*: high mortality in the first stage, low mortalities in intermediate stages, higher mortality in the adult stage. It is the general case for long-lived plants (Hall & Bawa 1993) and palm trees (Barot *et al.* 2000, Enright & Watson 1992, Olmsted & Alvarez-Buylla 1995, Piñero *et al.* 1984). In contrast, in *E. macrocarpa*, mortality remains low in the adult stage. Interpreting this difference in mortality rates is difficult only using the demographic censuses that did not give much information on mortality causes. One of our hypotheses can however help explaining this pattern. The mortality difference between *E. macrocarpa* and *L. secundiflorum* could be due to their different reproductive behaviours. Pleonanthic clonal palm species such as *E. macrocarpa* are potentially immortal, especially when they produce many ramets. Hapaxanthy in *L. secundiflorum* is likely to cause a high mortality rate in adult ramets which should lead to higher genet mortality. However, the link between ramet and genet demography has been poorly documented in palm trees. In our case it would be particularly useful to determine the effect of ramet harvesting on genet mortality. The fall of branches and trees is another potential source of ramet and genet mortality that should also be studied.

Table 5 sums up the life-history features (flowering type, stem diameter, vegetative reproduction, adult

Table 5. Synthetic description of the life histories of the two rattan species.

Demographic characteristics	*Eremospatha macrocarpa*	*Laccosperma secundiflorum*
Flowering mode	Pleonanthic	Hapaxanthic
Stem diameter	Smaller	Larger
Vegetative reproduction	Production of many ramets	Production of fewer ramets
Adult mortality	Lower	Higher
Fecundity	Lower	Higher
Adult remaining life span (Ω_{adult})	Higher	Lower
Mean time to reach the adult stage ($\tau_{seedling,adult}$)	Lower	Higher

mortality, fecundity and age-based parameters) of the two rattan species. It contains information obtained in the present study and unpublished results (stem diameter, vegetative reproduction). Despite the variability in the age of individuals of each stage, which is inherent to long-lived plant species, it appears that *E. macrocarpa* individuals tend to start reproducing earlier ($\tau_{seedling,adult}$; 9 y) than *L. secundiflorum* individuals ($\tau_{seedling,adult}$; 14 y). Ramet diameter is thinner in *E. macrocarpa* than in *L. secundiflorum*, which leads to a lower resource investment per ramet for *E. macrocarpa*. For this reason, *E. macrocarpa*

ramets probably grow quicker than *L. secundiflorum* ramets. These results show that *E. macrocarpa* has a much stronger potential for growth and vegetative reproduction than *L. secundiflorum*. Consequently, our results also suggest the existence of a trade-off between the ramet diameter and the number of produced ramets.

There is a low fecundity by genet (as estimated by the production of new offspring by sexual reproduction) for both *E. macrocarpa* and *L. secundiflorum*. However, this fecundity seems to be lower for *E. macrocarpa* than for *L. secundiflorum*. Our data thus suggest that *E. macrocarpa* produces fewer seeds per genet (and ramet) than *L. secundiflorum*. Consequently, since *E. macrocarpa* individuals produce more ramets than *L. secundiflorum* individuals, this suggests the existence of a trade-off between sexual and vegetative reproduction. However, data on the production of seeds per adult and germination rates would be needed to better characterize the demographic strategies of the two species and to understand how *E. macrocarpa* can produce fewer offspring (ramets) per individual (tuft of ramets) than *L. secundiflorum*.

As hypothesized, our results (Table 5) clearly show that the two rattan species have different life histories. The higher adult mortality and the lower adult remaining life span in *L. secundiflorum* are probably linked to hapaxanthy. It is more difficult to interpret the whole pattern of differences between the life histories of the two species and to link this pattern to the two flowering types. This is due to the fact that individuals must distribute their resource among at least three functions (maintenance, reproduction and growth) and that there are many potential combinations. However, trade-offs between and within these functions are likely to limit the number of possible combinations of resource allocation. Here, our results suggest the existence of two trade-offs within reproduction: between vegetative and sexual reproductions and between the diameter of offspring (by vegetative reproduction) and the number of offspring. More generally, pleonanthy and hapaxanthy should have evolved in relation with the other life-history features. This might have led to distinct demographic syndromes. Whether pleonanthic and hapaxanthic palms tend to have the same demographic syndromes as *E. macrocarpa* and *L. secundiflorum* (lower potential for vegetative reproduction and higher production of offspring through sexual reproduction in hapaxanthic species than in pleonanthic species) remains an open issue.

Demography of *Eremospatha macrocarpa* and *Laccosperma secundiflorum*

The matrix model approach used here has been applied earlier to describe the dynamics of many palm species (Barot *et al.* 2000, Bernal 1998, Bullock 1980, De Steven 1986, 1989; Escalante *et al.* 2004, Piñero *et al.* 1984, Rodriguez-Buritica *et al.* 2005, Souza & Martins 2006). In general, the value of λ obtained for the studied species was close to 1.0, likely because the environment of these studies was not much disturbed by human activities or natural ecosystem dynamics. In the case of the studied populations of *E. macrocarpa* and *L. secundiflorum*, in spite of the exploitation of the ramets of the two species, the estimated λ values were not significantly different from 1.0. This suggests that exploitation by local human population does not threaten these rattan populations. This also shows that the populations of the two species achieve comparable growth rate despite clear differences in their life histories. However, the uncertainty on λ was higher and the estimated λ was lower for *L. secundiflorum* than for *E. macrocarpa*. This was due to a lower number of adult palms (Table 1) and to a higher mortality rate in juvenile 2 and adults (respectively 0.119 and 0.250) for *L. secundiflorum* than for *E. macrocarpa*.

The difference between the predicted stable stage distributions and the observed stage distributions suggests that the demographic parameters included in the matrices have changed in the recent past because of some changes in environmental conditions, driven or not by human activities such as harvesting. Our evaluation of the demographic parameters was carried out over an 18-mo period. Because transition probabilities (survival, growth and retrogression) and fecundity are likely to vary in time much more quickly than stage distributions, estimating these parameters over a longer period could lead to more accurate stable stage distributions and to a better correspondence between the observed distributions and the predicted stable distributions (Enright & Ogden 1979). Our matrix models explain the different population structures observed and predicted respectively for *E. macrocarpa* and *L. secundiflorum* (Figure 2): for *E. macrocarpa* there are more adults than juveniles 2. This can be explained by the higher adult survival observed for *E. macrocarpa* than for *L. secundiflorum*, which could allow the accumulation of individuals in the adult stage in *E. macrocarpa*.

Elasticity results follow the general pattern found in Lefkovitch matrices: the asymptotic growth rate was more sensitive to survival rates than to growth rates and elasticities to fecundities were very small (Caswell 2001, De Matos & Matos 1998). The very large contributions of survival rates to the elasticity matrices found for *E. macrocarpa* and *L. secundiflorum* is typical of long-lived species (Silvertown *et al.* 1993, 1996). Since elasticities measure the relative influence of the demographic parameters on the population growth, conservation measures should concentrate on the demographic parameters with high elasticities (Caswell 1996b, Menges 1990). We obtained the highest elasticities for adult

survival in *E. macrocarpa* and for juvenile 1 survival in *L. secundiflorum*. This suggests that conservation practices, or practices aimed at a sustainable and more productive exploitation of these natural populations (thus approaching a kind of in situ cultivation) should focus on these demographic parameters. The high elasticity for adult survival in *E. macrocarpa* suggests that this species is more sensitive than *L. secundiflorum* to the exploitation of adult ramets, at least if this exploitation increases genet (individual) mortality. The high elasticity obtained for juvenile 1 survival in *L. secundiflorum* suggests that protecting juvenile 1 would be an efficient way to protect the *L. secundiflorum* population or to allow an intensification of the exploitation of adult ramets. The difference in the critical stage of the two rattan species could probably be explained by the lower adult retrogression rate for *L. secundiflorum* than for *E. macrocarpa* and a lower adult mortality rate for *E. macrocarpa* compared to *L. secundiflorum*.

The LTRE analysis gives complementary information. It confirms the importance of juvenile 1 survival for *L. secundiflorum* but shows that demographic parameters, such as fecundity, that are not very influential for the asymptotic growth rate may determine the difference between the demography of the two rattan species. The LTRE analysis also suggests that the two species achieve relatively similar asymptotic growth rate (neither is significantly different from 1) with different combinations of demographic parameters: *L. secundiflorum* through a higher juvenile 1 survival and fecundity, *E. macrocarpa* through a higher juvenile 2 growth and adult survival. This also shows that, while the asymptotic growth rates are mostly sensitive to survival rates, the fecundity and growth rates must be taken into account to explain the differences between the demography of the two species. Taken together, the differences between the elasticity patterns of the two species and the LTRE results are due to differences in their demographic parameters and confirm the hypothesis that the two rattan species have distinct demographic features. This in turn reflects the fact they have different life histories. The description of these life histories suggests the existence of two trade-offs within reproduction. These trade-offs and probably other ones between survival and reproduction would explain that, although the two species have different life histories, the growth rates of their populations are not significantly different from 1.

Comparison with other clonal palm species and lianas

Elasticity patterns found in this study are similar to those obtained for other clonal palm species (Bullock 1980, Escalante *et al.* 2004, Rodriguez-Buritica *et al.* 2005, Souza & Martins 2006), a clonal liana (Nabe-Nielsen 2004) and, more generally, to other long-lived perennial plant species (Silvertown *et al.* 1993). The high elasticity for stasis of large plants and the low elasticities for sexual reproduction and growth are typical for woody polycarpic plants (Caswell 2001, Silvertown *et al.* 1993). The high total elasticity of stasis for *E. macrocarpa* and *L. secundiflorum* is comparable with that of long-lived tropical trees (Alvarez-Buylla *et al.* 1996). The elasticity pattern and high longevities suggest that both clonal climbing palms and clonal lianas (Bullock 1980, Escalante *et al.* 2004, Nabe-Nielsen 2004, Rodriguez-Buritica *et al.* 2005, Souza & Martins 2006) achieve, through clonality and the production of many shorter-lived ramets, the same type of life-cycle as long-lived perennials such as the trees among which they are living.

Conclusion

The present study has allowed the description of the demography of two rattan species. Our results suggest that the two studied populations are not threatened by the exploitation of ramets by local human populations but that *E. macrocarpa* should be more sensitive to this exploitation. However, to better understand the effect of the exploitation of adult ramets on the demography of the two rattan species more data are needed. First, the production of seeds and their germination rate should be assessed for the two species. This would allow incorporating the seed stage into the model and assess the influence of seed production, seed survival and germination on the two species growth rates. This is important, as manipulating seeds would be an easy way to enhance the demography of the two palms and increase the sustainability of ramet exploitation. Second, determining the effect of ramet natural mortality and exploitation on genet mortality and further ramet production is essential to design optimal harvesting strategies (percentage and frequency of ramet harvesting). More generally, such data linking the demography of ramets and genets in long-lived clonal plants is so far very sparse and should allow us to better understand the role of clonality in the demography of perennial plants.

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