Population Structure and Reproductive Strategy of Two Multiple-Stemmed Rattans of Côte d'Ivoire

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Life history evolution is an important field of modern ecology (Stearns 1992, Begon et al. 2006). A useful approach is to compare the life histories of related organisms to determine how evolution has shaped the relation between different life-history traits. In this context palms are suitable models to study perennial plant demography and life-history (Barot & Gignoux 1999) because they are monocotyledonous that generally do not branch aerially. Consequently, it is easy to define, observe, and record stages based on morphological traits for palm trees. However, some palm species are able to generate several ramets (stems) from the same rhizome (De Granville 1977). So far this type of clonal behavior has not been frequently studied.

Three rattan genera endemic to Africa belong to this category (Sunderland 2003): *Eremospatha*, *Laccosperma* and *Oncocalamus*. Rattans constitute a large and diverse group of climbing palms, comprising an important assemblage of non-wood forest products that are extensively collected for household uses and cash income throughout the humid Old World tropics (Sastry 2002). Their exploitation generates important income either through industrial or handicraft activities (Siebert 2004, Zoro Bi & Kouakou 2004). In Côte d'Ivoire, Zoro Bi and Kouakou (2004) pointed out an increasing number of industrial and handicraft companies using rattan in Abidjan (capital of Côte d'Ivoire) and its suburbs. This trade is based on the exploitation of wild rattans, which could in the long-term result in the natural populations of these species becoming exhausted (Dransfield 2001). This risk is particularly serious for *Eremospatha macrocarpa* (G. Mann & H. Wendl.) H. Wendl. and *Laccosperma secundiflorum* (P. Beauv.) Kuntze, the two most exploited species (Zoro Bi & Kouassi 2004).

Despite their social and economic importance and the necessary development of sustainable practices of exploitation, very little is known about the ecology and population demography of these species. In this work, we focused our analyses on the population structure and the reproductive strategy of two species: *E. macrocarpa* and *L. secundiflorum*. The two species have distinct flowering types. *E. macrocarpa* is pleonanthic. Inflorescences develop from axillary buds. Consequently, ramets continue their growth after flowering (Sunderland 2003) with multiple flowering. *Laccosperma secundiflorum* is hapaxanthic. Inflorescences are produced simultaneously towards the stem tip and ramets (individual shoots of a clustering plant) die after flowering (Tomlinson 1990, Baker et al. 2000, Sunderland 2002). This suggests that the reproductive and demographic traits of these two species have co-evolved in relation to their flowering types (Stearns 1992, Begon et al. 2006). The two species are thus likely to have developed different demographic strategies and these strategies should lead to different population structures. To test this hypothesis, we describe and compare some demographic traits of the two rattan species as well as their population structure. This is a prerequisite to analyze the demography of the two rattan species and in the long term to implement reliable management strategies to optimize harvesting practices. Such practices should be sustainable and guarantee an income to local populations. They would be usefully implemented in the whole geographic area where our two rattan species grow, but have to be based on solid knowledge about their life-histories. Our study is a first step in that direction.

Materials and Methods

Study site. The study was conducted in the N'zodji forest (1086 ha) in South-Eastern Ivory Coast. 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 an annual mean precipitation of 1350 mm, and an annual mean temperature of about 25°C. Soils are ferrallitic and are derived from schist rocks (Dabin et al. 1960). For the last 11 years,

Table 1. Descriptions of the five stages used in the study

Stages[1]	Leaves[2]	Ramet[3]	Sexual reproduction	Harvestable
Shoots (S)	No (arrowhead)	No	No	No
Rosette (R)	Yes < 15	No	No	No
Juvenile 1 (J1)	Yes	Yes < 6 m	No	No
Juvenile 2 (J2)	Yes	Yes > 6 m	No	Yes/No[4]
Adult (A)	Yes	Yes > 6 m	Yes	Yes

[1] J2 and A genets are only found in clumps while the three other stages can be in the two biological forms (solitary or clump).

[2] Leaves of the J2 and A stages are longer than those of the J1 and R stages

[3] J2 ramets are green; A ramets are brown

[4] Peasants harvest J2 ramets when A ramets become scarce

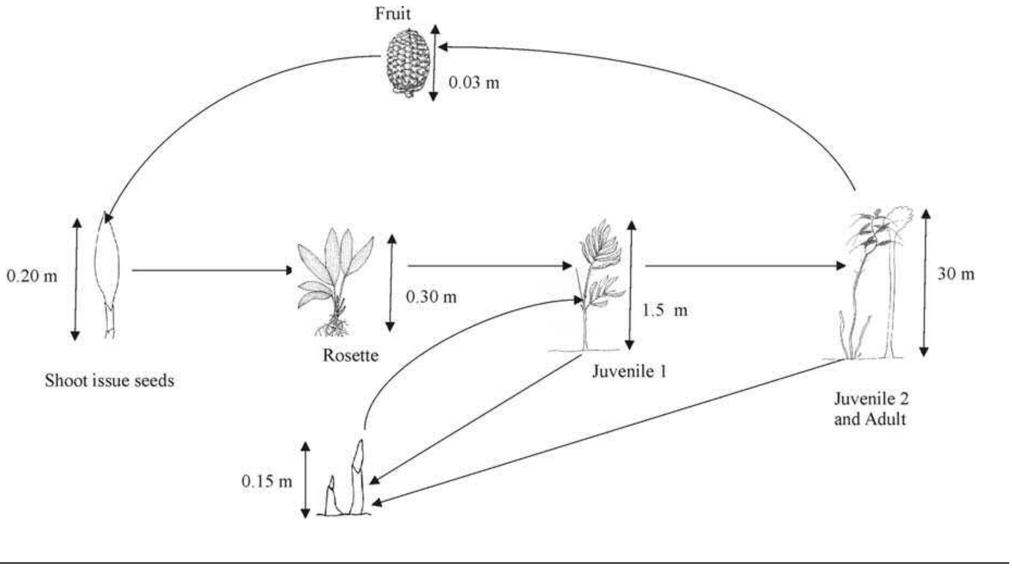
the area of the N'zodji forest has been opened by the SODEFOR (the main institution involved in the monitoring and management of forests in Côte d'Ivoire) to the public for timber and other forest products. The site is covered by an evergreen forest dominated by *Musanga cecropioïdes*, *Tarrietia utilis* and *Diospyros gabunensis*. Forest canopy height averages 20–30 m.

Three 200 × 200 m (4 ha) plots were established in the northern part of N'zodji forest. The first plot (Plot 1: 5°42′N, 3°52′W) is located on the outskirts of the forest. It corresponds to a secondary forest growing on well drained soils (mean soil moisture of 21%). In this plot, canopy trees have moderate heights (20 m). The second plot (plot 2: 5°41′N, 3°52′W) is located 3 km inside the forest. It is a semi-secondary forest growing on well drained soils (mean soil moisture of 17%). Canopy trees are of variable heights (20–30 m). The last plot (plot 3: 5°41′N, 3°51′W) is located 7 km inside the forest. It is a primary forest, less drained (mean soil moisture of 44%), with high canopy trees (30 m). The average altitude of the plots is 122 m. In this forest, five rattan species have been identified: *Calamus deërratus* (G. Mann & H. Wendl.), *E. macrocarpa*, *E. hookeri* (G. Mann & H. Wendl.) Wend., *L. laeve* (G. Mann & H. Wendl.) Drude and *L. secundiflorum* (Zoro Bi & Kouassi 2004). The plots are representative of the whole forest as far as rattan densities are concerned.

Study species. In Africa, *L. secundiflorum* and *E. macrocarpa* are distributed from Liberia to Angola. *Eremospatha macrocarpa* is an example of multiple-stemmed rattan with as many as 50 ramets (stems) per genet (genetically distinct individual) (Sunderland 2007). The climbing stem, with sheaths devoid of spines, can reach up to 30 m and have a small diameter (1–1.8 cm). Flowering is pleonanthic (Sunderland 2003). *Laccosperma secundiflorum* is also a multiple-stemmed climbing palm. Here, although the different ramets from a genet remain attached to the same rhizome we consider the production of new ramets as a form of vegetative reproduction (Tomlinson 1990). The climbing stems have spiny sheaths and can reach up to 30 m. They have a larger diameter than *E. macrocarpa* stems (3–5 cm diameter). Flowering is hapaxanthic. The fruits of these rattans are ellipsoidal and one-seeded. Those of *E. macrocarpa* are larger (2.5 cm in diameter, 2 cm in height and 15–20 rings of scales) while those of *L. secundiflorum* are relatively smaller (1.5 cm in diameter, 1 cm in height and 12 spiral rings of scales). These species are found in secondary or primary forest and often grow in canopy gaps (Sunderland 2003). Here, the harvest rate, defined as the number of ramets collected every six months per harvestable ramet (juvenile 2 and adult stages), varied according to the plot and the species. These estimates were 18–23% and 8–42% for *E. macrocarpa* and *L. secundiflorum,* respectively. The harvest rate was on the average higher in *L. secundiflorum* (Gore Bi 2004).

Data collection and statistical analysis. We defined five development stages for the two

1. Life cycle of *Eremospatha macrocarpa* and *Laccosperma secundiflorum*.



species (Fig. 1): (*i*) shoot (S); (*ii)* rosette (R); (*iii*) juvenile 1 (J1), (*iv*) juvenile 2 (J2) and (*v*) adult (A). These stages were described using criteria traditionally (Tab. 1) used for palms (Bullock 1980, Chazdon 1992, Bernal 1998, Barot & Gignoux 1999). Shoots (S) are buds with undeveloped leaves. Rosettes (R) are plantlets bearing fully-developed leaves (< 15 leaves). It is worth noting that shoots quickly grow into rosettes (in less than 6 months). Juveniles 1 (J1) are individual ramets with green-colored stems, up to 6 m long. Juveniles 2 (J2) are individual ramets with harvestable green-colored stems. Adults (A) are sexually reproductive genets, characterized by brown ramets. In this study, clumps were considered as a single genet. Indeed, it has been shown from preliminary 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 always linked by a common rhizome. The stage of a genet was considered to be the stage of its more developed ramet.

The study was conducted in January 2004. A total of 1856 ramets of *E. macrocarpa* and 1277 ramets of *L. secundiflorum* were counted and described in all the plots.

To assess the effect of soil humidity on the abundance of rattans, each plot was divided in 25 (40 × 40 m) quadrats. In each quadrat, we assessed the percentage of moisture (H) on one soil sample collected in June, i.e. during the rainy season, between 0 and 15 cm, P1 being the weight of the fresh sample and P2 being the weight of the dried sample, H was calculated as follows: H = (P1-P2) / P1. In each quadrat, the abundance of the genets and ramets of the two species was also measured.

Fecundity by sexual reproduction was estimated during three successive six-month periods as the number of newly germinated seedlings and rosettes. These shoots were attributed to the adults of the considered plot to assess the number of newly produced individuals by adult genet (Menges 1990).

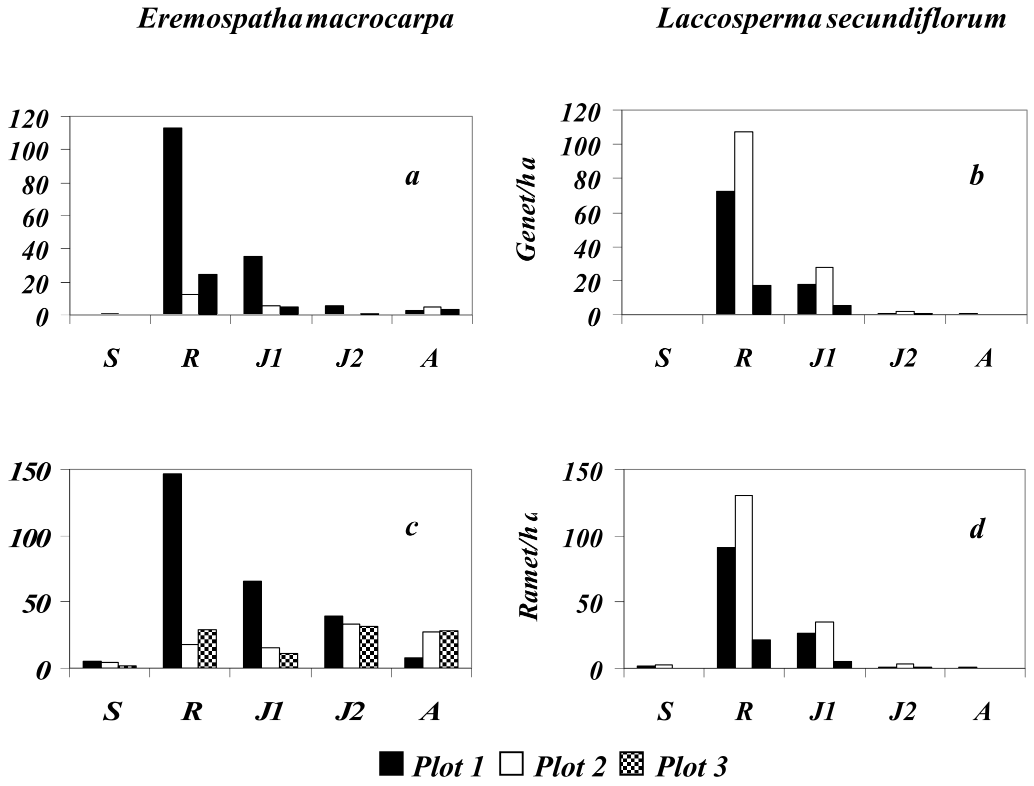
Statistical analyses were implemented with the SAS statistical package (SAS 1999). We described the genet and ramet stage distributions, the ramet number by genet in each stage or all stages pooled together. Distributions were compared using log-likelihood tests. The effect of soil moisture on the abundance of the two rattan species was tested using PROC GLM procedure and the 25 quadrats of each plot as repetitions. The fecundities of the two species were compared through a GLM Repeated measured model using the three plots as repetitions (SAS 1999).

Results

Genet and ramet density. An average of 154.5 ± 94.42 and 106.08 ± 72.46 ramets per hectare was found respectively for *E. macrocarpa* and *L. secundiflorum*. Ramet densities vary from 98 (plot 2) to 263.5 (plot 1) for *E. macrocarpa*, and from 27.50 (plot 3) to 170.25 (plot 2) for *L. secundiflorum*. An average density of 71.17 ± 74.26 and 83.92 ± 57.85 genets per hectare was found respectively for *E. macrocarpa* and for *L. secundiflorum*. Genet densities also vary from 33 (plot 3) to 156.75 (plot 1) for *E. macrocarpa*, and from 22.75 (plot 3) to 137.15 (plot 2) for *L. secundiflorum*.

Table 2. Log-likelihood ratio test (G) to compare the population structures of the two rattan species

Structures	Plots	df	*G*	*P*
Genet distribution	Plot 1	3	16.67	0.003
	Plot 2	4	85.13	< 0.001
	Plot 3	3	17.20	< 0.001
Ramet distribution	Plot 1	4	125.87	< 0.001
	Plot 2	4	591.01	< 0.001
	Plot 3	4	145.11	< 0.001
Percentage of genets with more than one ramet	Plot 1	1	7.51	0.006
	Plot 2	1	50.70	< 0.001
	Plot 3	1	5.82	0.016



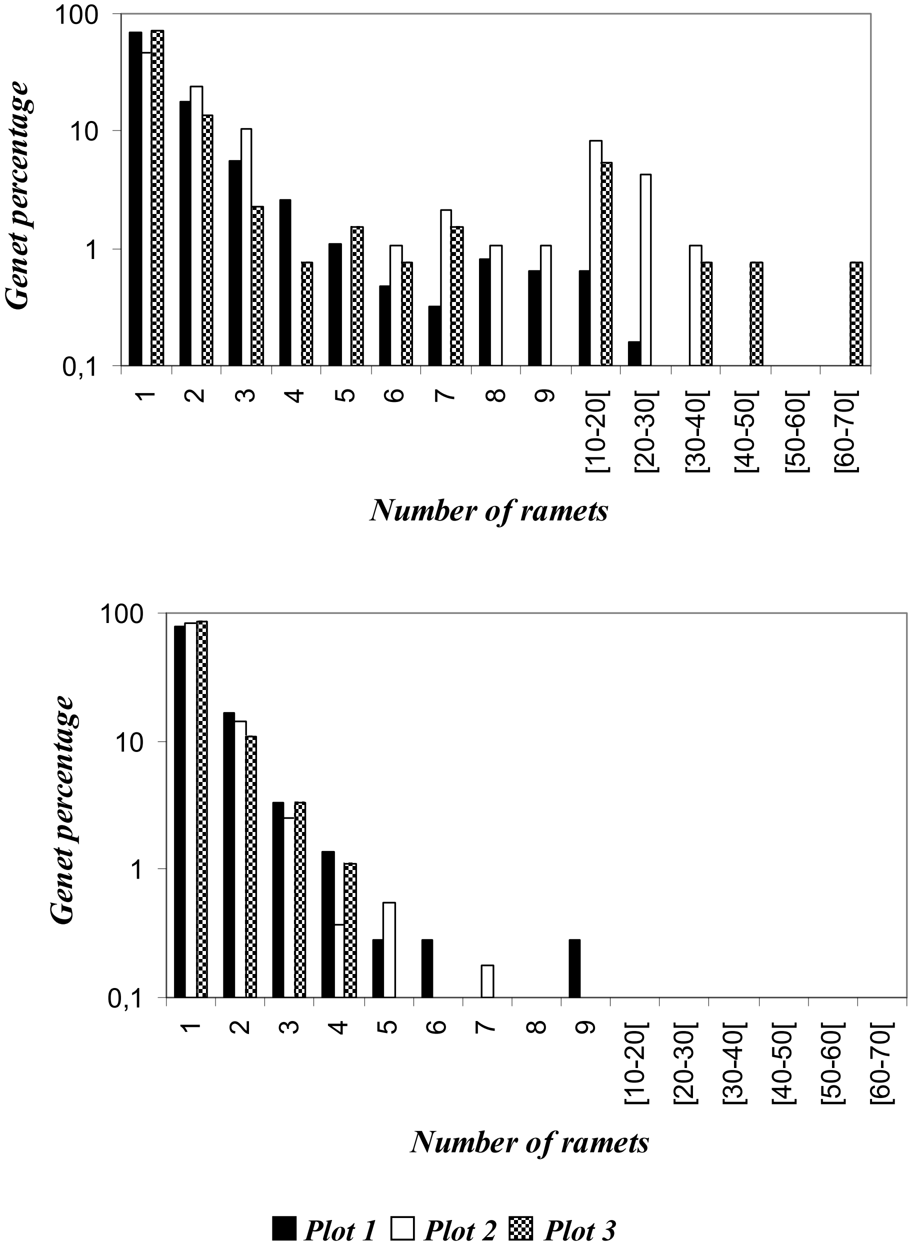
2. Genet and stem distribution by stage (S: shoots; R: rosette; J1: juvenile; J2: juvenile 2; A: adults) for the two rattan species and the three studied plots.

Genet stage distribution. For *E. macrocarpa*, the rosette stage was the most abundant and genet proportion gradually decreased from the rosette to the juvenile 2 stage and slightly increased at the adult stage in the plots 2 and 3 (Fig. 2a). *Laccosperma secundiflorum* (Fig. 2b) presented the same pattern, but the frequency of genets did not increase from the juvenile 2 to the adult stage. For each plot, the genet stage distributions of the two species were significantly different (Tab. 2).

Ramet stage distribution. For the two rattan species the percentage of genets and ramets in the shoot stage is very low, probably due to a low residence time of ramets in this shoot stage. Genet and ramet stage distributions were very similar for *L. secundiflorum* and *E. macrocarpa* (Figs. 2). For this species, the ramet percentage per stage decreased from the rosette to the adult stage less than the genet percentage. While the ramet stage distributions of the two species were significantly different ($P < 0.001$) in all plots (Tab. 2) percentages of genets and ramets per stage are highly variable between plots.

Number of ramets per genet. The percentage of genets in the different classes of ramet number was a decreasing function of the ramet number (Fig. 3). It decreased respectively from 71.96 to 0.76% and from 82.2 to 0.18% for *E. macrocarpa* and *L. secundiflorum*. Approximately 63 and 82% of genets has only one ramet for *E. macrocarpa* and *L. secundiflorum* respectively. The maximum numbers of ramets per genet were respectively 70 and 9 for *E. macrocarpa* and *L. secundiflorum*. The mean number of ramets per genet of the adult stage is much higher for *E. macrocarpa* (2.17 ramets) than for *L. secundiflorum* (1.26 ramets). Log-likelihood test showed that in two plots (1 and 2) the distribution of the number of ramets per genet of the two species were significantly different (plot 1: $G = 7.02$, $P = 0.009$; plot 2: $G = 34.81$, $P < 0.001$; plot 3: $G = 2.91$, $P = 0.094$).

Percentage of genets in clump. For the two species and in all the plots, the percentage of genets in clump, i.e. having already started vegetative reproduction, increased from the rosette to the adult stage where it reached 100% (Fig. 4). For each plot, the percentage of genets in clump by stage was significantly higher for *E. macrocarpa* than for *L secundiflorum* (Tab. 2). This percentage increased more quickly along



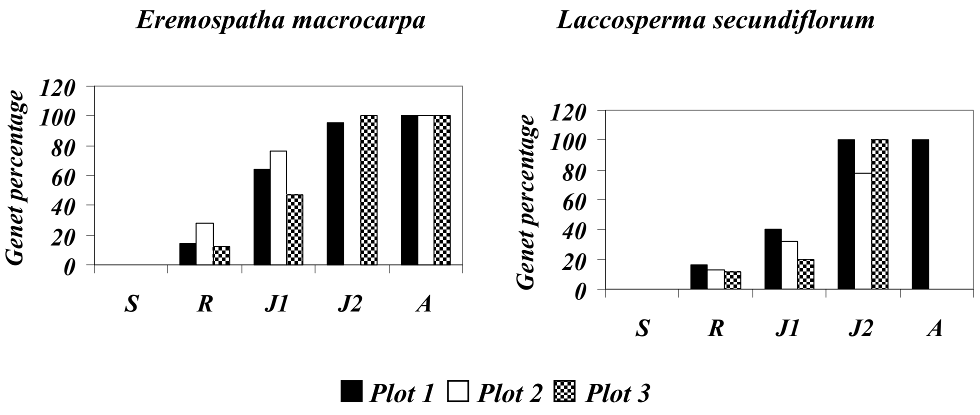
3. Distribution of the number of ramets per genet for the two rattan species in the three studied plots. Upper graph shows data for *Eremospatha macrocarpa*; lower graph shows data for *Laccosperma secundiflorum*. The y-axis has a logarithmic scale.

the successive stages for *E. macrocarpa* than for *L. secundiflorum*. This suggests that vegetative reproduction starts earlier in *E. macrocarpa* than in *L. secundiflorum*.

Sexual fecundity. The average fecundity was 0.12 ± 0.09 new individuals (shoots and rosettes) per year per adult genet for *E. macrocarpa* and 0.89 ± 0.92 for *L. secundiflorum*. The difference between the two species for this parameter was significant (repeated-measures ANOVA, F = 14.13, P = 0.023).

Discussion

Genet and ramet densities. We did not find a clear relationship between harvest rates and ramet or genet densities. This could be due to a weak effect of ramet harvesting on survival and growth of rattan genets (Siebert 2004).



4. Percentage of genets growing in clumps per genet stage for the two rattan species in the three studied plots (S: shoots; R: rosette; J1: juvenile; J2: juvenile 2; A: adults).

Siebert (2004) showed that ramet harvesting seems to stimulate the production of new ramets and that a repeated harvest only reduces the average ramet length. The harvest rate of *L. secundiflorum* ramets was higher in plot 2 (43%). For *E. macrocarpa*, this rate was higher in plot 1 (23%). The high densities of *L. secundiflorum* and *E. macrocarpa,* in plots 1 and 2 respectively, are likely to make harvesting more attractive and efficient in these plots and could also lead to the high harvesting rates of these plots. This suggests that human exploitation does not threaten the studied population of the two rattan species, at least for the moment, after 11 years of exploitation.

Differences observed between species abundances can be explained by their reproductive biology and/or their growth requirements (Siebert 1993). For many rattan species, higher light intensities generally result in higher growth rates (Bøgh 1996, Siebert 2005, Sunderland 2007). According to Sunderland (2007) *E. macrocarpa* is extremely light demanding, occurring naturally in forest gaps and forest margins. *L. secundiflorum* is more shade tolerant and is present as slender climbers under the canopy of mature forests. Thus, the paucity of genets and stems of *E. macrocarpa* in plot 3 might be related to its high light requirement, given that tree density and canopy height are higher in this plot than in the two others. Besides, rattans are generally more abundant on well drained soils (Bøgh 1996, Siebert 2000, Siebert 2004). However, no effect of soil moisture on the abundance of the two rattan species was found. This suggests that the level of drainage in our plots is sufficient to provide suitable conditions to the two rattan species. Other differences observed between the abundances of the two rattan species in the three plots remain difficult to explain. Of course, censuses of the two rattan species in many plots of different forests are necessary to determine with certainty the factors influencing their densities. It would also be useful to study rattan abundance at a lower spatial scale (10 × 10 m), i.e. the scale at which the local structure of the forest determines the availability of light and the presence of suitable trees to support the climbing rattan ramets.

Demographic strategies of the two species. Genet and ramet distributions of many palm species have been reported (Bernal 1998, Barot & Gignoux 1999, Siebert 2000, Escalante et al. 2004, Barot et al. 2005, Widyatmoko et al. 2005). Authors showed that genet densities and frequencies by stage decrease overall from the juvenile to the adult stage. This general pattern in plants is due to the high mortality rates usually found in the first stages. Such a high mortality could be explained by the effect of environmental stress and intraspecific competition that should be higher for less developed stages characterized by smaller genets storing less resources.

Eremospatha macrocarpa has more ramets per genet (individual) than *L. secundiflorum.* This explains why the ramet and genet stage distributions are different for *E. macrocarpa* but identical for *L. secundiflorum*. Genet stage distribution is slightly bimodal for *E. macrocarpa* in plot 2 and 3, i.e. more adults than juveniles 2, but not for *L. secundiflorum.* A bimodal distribution was already mentioned

Table 3. Various demographic characteristics of *Eremospatha macrocarpa* and *Laccosperma secundiflorum*

	E. macrocarpa	*L. secundiflorum*
Flowering mode	Pleonanthic	Hapaxanthic
Stem diameter	Thin (1.0–1.8 cm)	Large (3–5 cm)
Fecundity by sexual reproduction	Lower	Higher
Vegetative reproduction	Higher	Lower
Fruit size	2.5 cm long x 2 cm diam.	1.5 cm long x 1 cm diam

for several solitary and clumping palms (Enright 1985, De Steven 1986, De Steven 1989, Eguiarte et al. 1993, Bernal 1998, Barot & Gignoux 1999, Siebert 2000, Escalante et al. 2004, Widyatmoko et al. 2005). Enright (1985) showed that the accumulation of slow-growing individuals in the larger stages was the cause of size bimodality in *Rhopalostylis sapida*. This structure would be due to relatively high genet survival rates in larger size classes (here the adult stage) and relatively high recruitment rates to the adult stage. In the case of *E. macrocarpa*, adults having survived in the first stages grow quickly and accumulate in the multi-stemmed adult stage. The unimodal stage distribution for *L. secundiflorum* genets could be due to a higher mortality rate at the adult stage. This high death rate could be due to the hapaxanthic flowering of this species, if a higher ramet mortality leads to a high genet mortality. Similarly, *E. macrocarpa* has a bimodal ramet distribution (more adults and juveniles 2 than juveniles 1 in plot 2 and 3) while *L.* secundiflorum has a unimodal ramet distribution. This suggests that ramet survival is higher for *E. macrocarpa* than for *L. secundiflorum*. This should again be due to their different flowering modes.

The average number of ramets per genet varies between plots but is higher for *E. macrocarpa* than for *L. secundiflorum*. Such an interspecific variation in the number of ramets by genets has already been highlighted (De Steven 1989, Siebert 2000, Escalante et al. 2004, Widyatmoko et al. 2005). Using these published studies, we have tried to test whether high or low numbers of ramets per genet could be respectively associated with pleonanthic and hapaxanthic palms. However, no general rule was found. Nevertheless, the difference observed between *E. macrocarpa* and *L. secundiflorum* should be explained by a higher ramet survival (pleonanthic flowering vs. hapaxanthic) and/or by a more intense vegetative reproduction (higher rate of stem production) of *E. macrocarpa* compared to *L. secundiflorum*.

Although *L. secundiflorum* and *E. macrocarpa* are two multiple-stemmed palms growing in the same environment they have different life-history characteristics (Tab. 3). Ramet diameter ranges respectively between 1 and 1.8 cm for *E. macrocarpa* and 3 and 5 cm for *L. secundiflorum*. Moreover, according to Sunderland (2007), the relatively higher proportion of thick-walled fibers and narrower diameter of metaxylem vessels in the ramets of the *Laccosperma* genus suggests they have a greater density and hence are mechanically more resistant than the ramets of *Eremospatha.* Together with their smaller diameter, this suggests that *E. macrocarpa* ramets are less costly to be produced than *L. secundiflorum* ramets but are probably more fragile. Indeed, increasing stem diameter and producing physically resistant structures decreases the risk of stem bending or breaking (through branch and tree falls) for understory palms (Svenning, 2000).

Genets must distribute their resources between the basic biological functions (growth, maintenance, reproduction). If they increase the resource allocation to a function, they must decrease the resource allocated to the other functions. This leads to the concept of trade-off (Stearns & Hoekstra 2000, Saenz & Guariguata 2001) and obliges species to adopt different allocation strategies and thus different demographic strategies. The ramet diameter of *E. macrocarpa* is thin and corresponds to a lower resource investment than for *L. secundiflorum*. For this reason, *E. macrocarpa* ramets probably grow more quickly than *L. secundiflorum* ramets and *E. macrocarpa* starts reproducing vegetatively earlier in its life-cycle. This would be a hint of a trade-off between the ramet diameter and the number of produced ramets. Such a trade-off would be the equivalent for vegetative reproduction of the classical trade-off between offspring size and fecundity (Stearns & Hoekstra 2000). Of course, complementary data would be necessary to support further the hypothesis of such a trade-off. It would for example be useful to be able to assess the biomass of whole ramets to measure more accurately the resource investment in each ramet.

Our results suggest that there is a low fecundity by sexual reproduction for both *E. macrocarpa* and *L. secundiflorum* (numbers of new individuals in the shoots stage). However, this fecundity seems to be lower for *E. macrocarpa* than for *L. secundiflorum*. This suggests that there is a trade-off between vegetative and sexual reproduction. Besides, the fruits of the two species contain 1–3 seeds but those of *E. macrocarpa* are larger than those of *L. secundiflorum* (Sunderland 2003). The lower fruit size and the higher fecundity of *L. secundiflorum* push this species towards the *r* pole in the continuum between *r* and *K* demographic strategies. On the contrary, the lower potential for vegetative reproduction of *L. secundiflorum* seems to push this species towards the *K* pole. This apparent contradiction could result from the suggested trade-off between sexual reproduction and vegetative reproduction. These results cast some doubts on the applicability of a theory classifying demographic strategies on a unique *r–K* axis, especially for species with both sexual and vegetative reproductions. However, it can be argued that the production of new ramets in the two rattan specie does not correspond to vegetative reproduction: it does not increase the number of genets. Moreover, a high potential for new ramet production, as in *E. macrocarpa*, can be considered as a strategy to increase individual size and longevity. It allows colonizing local canopy gaps but does not directly help colonizing a whole forest. Moreover, pleonanthy is likely to increase further the longevity of ramets and genets of this species. In this way, *L. secundiflorum* (lower longevity and individual size, higher fecundity by sexual reproduction) would be closer to the *r* pole than *E. macrocarpa*.

Finally, the different life-history strategies observed for our two rattan species are probably linked evolutionarily to their different flowering types. However, the life-cycle of other multi-stemmed palms should be studied to test whether pleonanthic and hapaxanthic palms are characterized by the same demographic syndromes as *E. macrocarpa* and *L. secundiflorum* and to study the precise nature of underlying trade-offs. As a test of these hypotheses, it remains to compare directly the quantity of seeds produced by the genets of the two species, as well as the rate of germination of their seeds. It also remains to estimate the ramet and genet survivals in the different stages. This would also help construct population matrix models. These models would allow us to describe in a synthetic way the demographic strategies of the two rattan species and to evaluate better the relative importance of the sexual and vegetative reproductions of these two species for the growth rate of their populations (Caswell 2001). In the long term, constructing and parameterizing these models should also help in designing sustainable harvesting practices optimized for the demographic strategies of the two rattan species.

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