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Relationships between ramet and genet dynamics in two clonal palms

Kouadio I. Kouassi [a,b,*], Sébastien Barot [b], Kam-Rigne Laossi [c], Jacques Gignoux [d], Irié A. Zoro Bi [a]

[a] *Laboratoire de Génomique Fonctionnelle et Amélioration Génétique, Université Nangui Abrogoua, UFR des Sciences de la Nature, 02 BP 801 Abidjan 02, Cote d'Ivoire*
[b] *IRD, BIOEMCO (UMR 7618), Ecole Normale Supérieure, 46 Rue d'Ulm, 75230 Paris Cedex 05, France*
[c] *Agronomy Department, Nestlé R&D Centre Abidjan, 01 BP 11356 Abidjan 01, Cote d'Ivoire*
[d] *CNRS, BIOEMCO (UMR 7618), Ecole Normale Supérieure, 46 Rue d'Ulm, 75230 Paris Cedex 05, France*

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ABSTRACT

Eremospatha macrocarpa and *Laccosperma secundiflorum* are two clonal rattan species: through vegetative reproduction each individual, i.e. each genet, may produce several stems that are linked to the same rhizome. To determine the impact of ramet harvest by local human populations in these species, we compared the demography of their ramets and studied the impact of the dynamics of their ramets on the demography of their genets. This also allowed a better analyze of their life-history and demography. Genets were classified in development stages. We counted for each genet the number of alive, new, dead and harvested ramets. We determined the impact of the number of ramets and changes in this number on the genet probability of survival, retrogression and recruitment. Ramet demography differed between the two rattan species. The average numbers of new, harvested and dead ramets are about two times higher in *E. macrocarpa* than in *L. secundiflorum*. Furthermore, ramet demography influenced genet demography in both species. The survival of adult genets in *E. macrocarpa* and juvenile genets in *L. secundiflorum* increased with the initial number of ramets (about 10% between the lower and higher ramet numbers). The genet probability of retrogression increased in *L. secundiflorum* and decreased in *E. macrocarpa* with the initial number of ramets. These results suggest the existence of some physiological integration between the ramets of the two rattan species which leads to some cooperation and competition between ramets, within a genet, and to the compensatory production of new ramets after harvest. Overall, for both species, the links between ramet and genet demography suggest that ramet harvest, at the present harvesting rate, is not detrimental to the studied rattan populations.

1. Introduction

Plants are organized hierarchically and this is most obvious among clonal plants: a genetically homogenous individual grown from a single zygote is composed of functional units, the ramets that have a variable degree of physiological dependence. In particular, some palm species such as rattans are able to generate several ramets (stems) from the same rhizome and are thus described as clonal palms (Sunderland, 2012). In these cases, genets (individuals composed of several stems) can be described as reproducing in a vegetative or asexual way because they produce ramets that are identical from a genetic point of view. The functional significance of clonality depends on the degree of physiological integration between these ramets (Chazdon, 1991): Do they remain linked together? If yes, do they share resources (mineral nutrients, assimilates carbon)? Clonality and the degree of physiological integration between ramets should also have consequences at the level of whole individuals, and subsequently on the population dynamics of these clonal individuals. For example, clonal growth may increase the survival of adult individuals, i.e. genets, sharing the risks of mortality between their ramets: if some ramets die prematurely, the genet stays alive as a clonal individual (Bullock, 1980; de Steven, 1989; Chazdon, 1992). In the case of a significant functional integration between ramets, the number of ramets is an indication of the genet size and the amount of resource (light, water, mineral nutrients) the genet has access to. Thus, genet survival should increase with the number of ramets and could decrease when the number of ramets decreases, because of natural mortality or harvest by human populations. Finally, we can predict that fecundity through sexual reproduction and through the production of new ramets should increase with the number of ramets (de Steven, 1989; Chazdon, 1992; Svenning, 2000). This broad rationale shows that ramet dynamics should strongly influence genet demography in clonal plants.

Due to the flexibility and strength of their stems many rattan species constitute an ideal resource for making furniture and baskets Three rattan genera endemic to Africa, *Eremospatha*,

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* Corresponding author at: Laboratoire de Génomique Fonctionnelle et Amélioration Génétique, Université Nangui Abrogoua, UFR des Sciences de la Nature, 02 BP 801 Abidjan 02, Cote d'Ivoire. Tel.: +225 07 42 13 75.
E-mail address: kouadioignace@yahoo.fr (K.I. Kouassi).

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Laccosperma and *Oncocalamus* (Sunderland, 2012) are important non-wood forest products and are extensively collected for household uses and cash income throughout the humid tropics (Sastry, 2002). In Côte d'Ivoire, Zoro Bi and Kouakou (2004) pointed out an increasing number of industrial and handicraft companies using rattan. This trade is based on the exploitation of wild rattans, which might exhaust their natural populations (Sunderland, 2002; Garcia-Fernandez and Casado, 2005). Indeed, stems are harvested, which can threaten the life of genets, so that both ramets and genets have to be managed. It is therefore important to study the impact of the dynamics of their ramets on the dynamics of their genets. In particular, harvesting stems could decrease the survival of genets and their capacity to produce new ramets (clonal reproduction). However, in case of good physiological integration between the ramets belonging to the same genet, the compensatory production of new ramets in response to harvest has been described (Ticktin et al., 2002; Siebert, 2004; Ticktin, 2004) and may reduce the impact of harvest on rattan populations.

Eremospatha macrocarpa (Mann and Wendl.) Wendl. and *Laccosperma secundiflorum* (P. Beauv.) Kuntze are the two mostly exploited species in Côte d'Ivoire (Zoro Bi and Kouakou, 2004). They have distinct flowering types (Baker et al., 2000; Sunderland, 2012). *E. macrocarpa* is pleonanthic: inflorescences are developed on axillary buds so that stems go on growing after flowering. *L. secundiflorum* is hapaxanthic (Sunderland, 2012): inflorescences produced simultaneously in the distal 1–1.8 m portion of ramets so that ramets die after flowering. A previous study of genet dynamics suggests a strong relation between the demographic parameters of genets and flowering type (Kouassi et al., 2008, 2009). Indeed, the reproductive and demographic traits of these two species (diameter and length of stems, shape and seed size, fertility, vegetative reproduction...) might have evolved in relation with their flowering types (Mendoza and Franco, 1998; Sunderland, 2012).

Here we further test the hypothesis that the two species have contrasted life-history strategies, focusing on stems: the two species should be characterized by different ramet dynamics. We also intend to determine the interaction between ramet and genet demography. Specifically, we tested the following hypotheses: (1) Ramet demography is quicker, i.e. higher stem mortality but also higher stem production, in *E. macrocarpa* than in *L. secundiflorum*; (2) Overall, a high number of ramets, a low number of dead ramets and a high number of new ramets should lead to lower genet mortality; (3) The compensatory production of new ramets allows the two species to put up with harvesting. To test these hypotheses we: (1) compared the total number of ramets as well as the numbers of dead, harvested and new ramets between the two species, (2) analyzed the effects of the number of ramets on the production of ramets and their death, (3) determined the effect of the number of stems and variations in this number on the genet probability to survive, to be recruited to the next stage or to retrogress to the previous stage.

2. Data collection and analysis

2.1. Study species

E. macrocarpa and *L. secundiflorum* are multiple-stemmed (or clonal) climbing palms: each individual (genet) produces many stems (ramets) that remain linked to a common belowground rhizome. *E. macrocarpa* is pleonanthic. Its climbing ramets have a small diameter (1–1.8 cm) and are up to 50–75 m long. *E. macrocarpa* fruits are large (2.5 × 2 cm and 15–20 rings of scales). *L. secundiflorum* is hapaxanthic. Its stems have a larger diameter (3–5 cm) and are shorter (25–50 m) (Sunderland, 2007, 2012) than *E. macrocarpa* stems. *L. secundiflorum* fruits are smaller (1.5 × 1 cm and 12 spiral rings of scales) (Sunderland, 2007, 2012) than *E. macrocarpa* fruits.

2.2. Study site and data collection

The study was conducted in the dense, wet and evergreen N'zodji forest (1086 ha) in south-eastern Côte d'Ivoire. This forest is located between 5°33′N and 5°43′N and 3°49′W and 3°56′W. Three 200 × 200 m (4 ha) plots were established in the northern part of N'zodji forest. In this forest, local human populations harvest the stems of the two rattan species. To facilitate the censuses, 100 quadrats 20 × 20 m by plot were established. In each quadrat we counted and labelled all genets and ramets. Genets of the two species were classified into four stages, according to their size and morphology: (1) seedlings (S), recently germinated individuals with no ramet, but having a bipartite or fully developed leaves; (2) juveniles 1 (J1), individuals with all stems smaller than 6 m in length; (3) juveniles 2 (J2), individuals with at least one stems >6 m in length but no sexual reproduction; (4) adults (A), individuals with at least one ramet >6 m in length, bearing flowers or fruits (Kouassi et al., 2008, 2009). It is worth noting that seedlings quickly grow and reach the juvenile stage in less than 6 months. The ramet of juvenile 2 individuals and adults are harvestable. Clumps of ramets were considered as a single individual, i.e. genet. Indeed, it has been shown (Zoro Bi and 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. Genets and ramets were individually and permanently marked to track life stage transitions (such as mortality) both for genets and ramets. The stage of a genet was considered to be the stage of its most developed ramet. Rattan genets and ramets were censused every six months from January 2004 to June 2005. 1856 ramets of *E. macrocarpa* and 1277 ramets of *L. secundiflorum* were censused in January 2004. New ramets, new harvested ramets, and new dead ramets were counted.

It was possible to distinguish ramets that have been harvested by humans (the ramet is no longer present) and ramets that have naturally died (the ramet is still present but dead and dry or broken). The harvest of stems was not controlled. But we measured relatively high harvest rate (between 40% and 50% of the stems in the two species, see results for details). Harvest was due both to traditional harvest for domestic uses and to commercial harvest (stems are sold and transformed in Abidjan, the capital of the Ivory Coast).

2.3. Statistical analysis

Previously, matrix population models were parameterized for the genets of the two rattan species and the three 6-month periods over which genets and ramets have been censused (Kouassi et al., 2008). The demography of the two species is not significantly different between these 6-month periods and there is no seasonality in the demography of the species. Consequently, we only analyze the interaction between genet and ramet demography over the year and a half period of our study. All statistical analyzes were implemented using SAS version 9.1 (SAS, 1999).

An ANOVA (GLM procedure) was used to estimate the effect of the developmental stage of the genet and species on the number of new, harvested and dead ramets. For significant effects we used multiple comparisons of means (LS means statement of GLM procedure with a level of significance of 0.05) to determine stages that have higher or lower number of new, harvested and dead ramets.

To test the effect of the stage of the genet, species and the interaction on ramet probability to be harvested, to survive and to die a log-linear model was achieved. For these analyzes, the procedure GENMOD was used.

Independently for the two species, an analysis of covariance was used to test the effect of the initial number of ramets by genet, the genet stage and their interaction on variations in the number of new, harvested and dead ramets. The normality and homogeneity of the variance of residuals were checked. When necessary dependent variables (new, harvested and dead ramets) were transformed (square root) before the implementation of the final model we used.

Independently for the two species, a logistic regression (Sokal and Rohlf, 1995) was used to analyze the effect of the initial number of ramets (IR), of harvested ramets (HR), dead ramets (DR) and new ramets (NR) on the probability of recruitment, death, retrogression and survival of genets. The effect of the stage of the genet and the interactions between this stage and the numbers of ramets were also included in these logistic regressions.

3. Results

3.1. Numbers of ramets for each species and stage

In *E. macrocarpa* (Fig. 1 and Table 1), the number of harvested ramets per individual was significantly higher for adults than for juveniles 2 (LS means comparison, $p < 0.05$ for all comparisons in this section). The number of new ramets was significantly higher for juveniles 2 and adults than for juvenile 1 and seedlings. The number of dead ramets per genet was not significantly different between the adult, juvenile 2 and juvenile 1 stages, but was significantly higher in these three stages than in the seedling stage.

In *L. secundiflorum* (Fig. 1 and Table 1), overall, there were a lower number of harvested, new and dead ramets per genet than in *E. macrocarpa* (see details below). The number of harvested ramets was significantly higher for adults than for juveniles 2. The numbers of new ramets was significantly higher for juveniles 2 and adults than for juvenile 1 and seedlings. The number of dead ramets was null for adults. This number of dead ramets was significantly higher for juveniles 2 than for juveniles 1 and seedlings.

The numbers of harvested, new and dead ramets in juveniles 2 and adults were significantly higher for *E. macrocarpa* than for *L. secundiflorum* (significant interaction between stage and species in Table 1), except for dead ramets of juveniles 2 that were more numerous in *L. secundiflorum*. The numbers of harvested and new ramets for juvenile 1 of both species were similar. The number of dead ramets was significantly higher in juveniles 1 for *E. macrocarpa* than for *L. secundiflorum*.

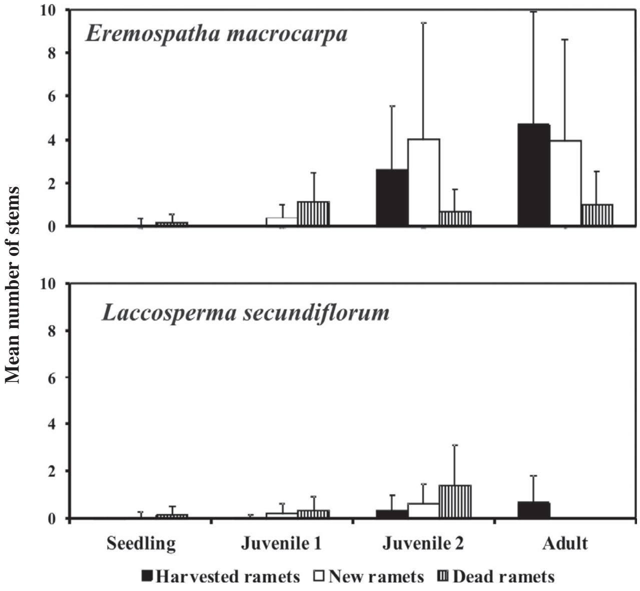

Fig. 1. Average number of new ramets, dead ramets and harvested ramets per genet in the two rattan species and for each stage. Vertical bars correspond to standard deviations.

Table 1
ANOVA comparing the number of harvested (d.f. = 1862), new (d.f. = 1862) and dead (d.f. = 1862) ramets in *Eremospatha macrocarpa* and *Laccosperma secundiflorum* according to the effect of stage, species and the interaction.

Effects	d.f.	Harvested ramets	New ramets	Dead ramets
Stage	3	67.55**	75.04**	106.38**
Species	1	106.99**	119.09**	5.70*
Stage x species	3	38.80**	46.22**	47.06**
R^2		0.44	0.35	0.22

R^2 is the coefficient of determination that denotes the proportion of variability that is accounted for by each model.

* $p < 0.05$.

** $p < 0.01$.

3.2. Effects of the stage on ramet transition probabilities

The survival probability of ramets did not vary significantly with the species, but varied with the stage (Table 2 and Fig. 2). The interaction between stage and species was also significant. On average, for both species, the survival probability of ramets was high in the adult stage (between 40% and 50%). The fate of juvenile 1 ramets was not significantly different between the two species (log-linear model). The significant interaction between stage and species thus came from the difference between the two species for juvenile 2: the survival probability of juvenile 2 ramets was higher for *E. macrocarpa* than for *L. secundiflorum* (Fig. 2). The probability of being harvested did not vary with the species and the interaction between stage and species (Table 2 and Fig. 2). However, it varied with the stage. In both species the probability that a ramet is harvested increased with the stage (from seedling to adults, Fig. 2).

3.3. Effect of the initial number of ramets on the number of new, dead and harvested ramets

In *E. macrocarpa* the higher the initial number of ramets, the higher was the production of new ramets for adults and juveniles 2 (Table 3, significant effect of the new ramets, stage and interaction). This effect was stronger for juveniles 2 than adults (as shown by the model parameters not displayed in Table 3). For juveniles 1, the higher the number of ramets, the lower was the number of new ramets. The number of harvested ramets followed the same pattern. The number of dead ramets was affected positively by the initial number of ramets in the three stages. This effect was stronger in juveniles 1 than in juveniles 2 and adults (as shown by the model parameters not displayed in Table 3).

Table 2
Log-linear analysis of the effect of stage, species and the interaction on the probability to be harvested (d.f. = 3123) and to survive (d.f. = 3123) of ramets in *Eremospatha macrocarpa* and *Laccosperma secundiflorum*.

Effects tested	d.f.	Probability to survive	Probability to be harvested
Stage	3	77.87**	95.68**
Species	1	0.11	3.20
Stage x species	3	43.10**	1.64

** $p < 0.01$.

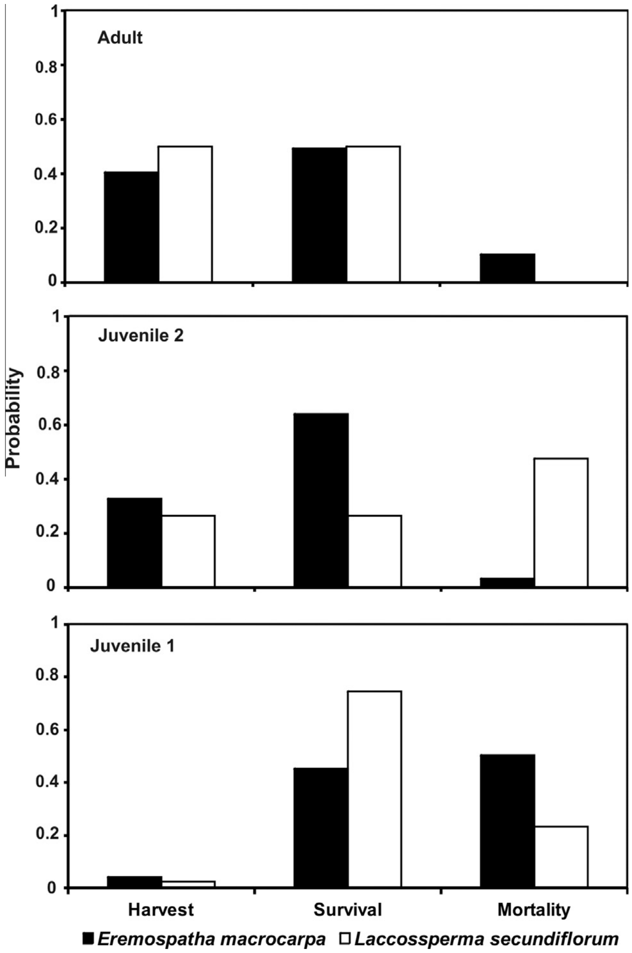

Fig. 2. Ramet probability to be harvested, to survive and to die naturally according to the genet stage and for the two rattan species.

In *L. secundiflorum* the number of harvested ramets increased significantly with the initial number of ramets for juveniles and adults (Table 3, significant effect on the number of ramets, stage and interaction). This effect was stronger in adults (as shown by the model parameters not displayed in Table 3). In this species there was no significant effect on the production of new ramets and ramet mortality.

3.4. Effects of numbers of ramets on genet demography

For *E. macrocarpa*, for juveniles 2, the genet probability of recruitment to the next stage increased significantly with the initial number of ramets, the numbers of harvested, dead and new ramets (logistic regression, Table 4). In juveniles 1, the lower the number of dead ramets and the number of new ramets, the higher was the probability of recruitment. For *L. secundiflorum* the probability of recruitment increased significantly with the number of ramets, the number of dead ramets and the number of new ramets for the juveniles 1 and 2 (Table 4).

For *E. macrocarpa*, the higher the initial number of ramets, the lower was the genet probability of death for adults (logistic regression, Table 4). In juveniles 1, the probability of death increased with the number of dead ramets and decreased with the number of new ramets. For *L. secundiflorum*, in juvenile 1, the probability of death decreased with the initial number of ramets and increased with the number of dead ramets (Table 4). There was no significant effect in adults.

For *E. macrocarpa*, in juveniles 1, the genet probability of retrogression to the previous stage increased with the number of dead ramets (logistic regression, Table 4). No effect was observed for juveniles 2 and adults. For *L. secundiflorum*, in juvenile 1 and 2, the genet probability of retrogression increased with the initial number of ramets, the number of dead and new ramets (Table 4). For adults, there was no significant effect.

4. Discussion

4.1. Comparison of ramets demography between the two species

The production of new ramets was higher in *E. macrocarpa* than in *L. secundiflorum*. This difference can be interpreted as the existence of a trade-off (Stearns et al., 2000) between the number of ramets produced and their size (Svenning, 2000). Indeed, the production of ramets could be related to the large diameter of *L. secundiflorum* ramets (3–5 cm), and the smaller diameter of

Table 3
Analyze of covariance examining the effect of the initial number of ramets by genet (IR), its stage and the interaction on variations in the number of ramets (number of new ramets, harvested ramets and naturally dead ramets) in *Eremospatha macrocarpa* ($n = 251$) and *Laccosperma secundiflorum* ($n = 221$). For the simple effects of the initial number of ramets and stage the significance of the test is given. For interactions between the initial number of ramets and stage, the direction of the effect is given for each stage: + denotes a positive effect (the considered variation in ramet number- new, harvested or dead ramets- increases when the number of ramets increases) while – denotes a negative effect. ns, no significant effect; Juv 1, juvenile 1; Juv 2, juvenile 2. The number of new, harvested and dead ramets was transformed (square root) before applying the statistical model.

Dependent variable	Explanatory variable	Stage	*E. macrocarpa*	*L. secundiflorum*
New ramets	IR		***	ns
	Stage		**	ns
	IRXstage	Juv 1	–	ns
		Juv 2	+	ns
		Adult	+	ns
Harvested ramets	IR		***	***
	Stage		***	***
	IRXstage	Juv 1	–	+
		Juv 2	+	+
		Adult	+	+
Naturally dead ramets	IR		***	ns
	Stage		*	ns
	IRXstage	Juv 1	+	ns
		Juv 2	+	ns
		Adult	+	ns

[*] $p < 0.05$.
[**] $p < 0.01$.
[***] $p < 0.001$.

Table 4
Logistic regressions testing the effects of the initial number of ramets by genet (IR), the numbers of harvested (HR), naturally dead (DR) and new (NR) ramets, the stage and interactions between stage and numbers of ramets on the genet probability of recruitment to the next stage, death and retrogression. For the effects of numbers of ramets and their interactions with stage, + denotes a positive effect (the considered probability increases when the number of ramets increases) while – denotes a negative effect. For the interactions between numbers of ramets and stage, the direction of the effect (positive or negative) is given separately for each relevant stage. Statistics are given for each species: EM (*Eremospatha macrocarpa*, $n = 251$) and LS (*Laccosperma secundiflorum*, $n = 221$). ns, no significant effect; Juv 1, juvenile 1; Juv 2, juvenile 2.

Explanatory variable		Recruitment		Death		Retrogression	
		EM	LS	EM	LS	EM	LS
Stage		***	ns	ns	ns	ns	ns
IR		ns	+	–	–	–	ns
HR		ns	ns	+	ns	ns	ns
DR		ns	ns	+	+	+	+
NR		ns	+	–	ns	ns	+
IR X stage	Juv 1	ns	+	ns	–	ns	+
	Juv 2	+	+	ns	ns	ns	+
	Adult			–	ns	ns	ns
HR X stage	Juv 1	ns	ns	ns	ns	ns	ns
	Juv 2	+	ns	ns	ns	ns	ns
	Adult			ns	ns	ns	ns
DR X stage	Juv 1	–	+	+	+	+	+
	Juv 2	+	+	ns	ns	ns	+
	Adult			ns	ns	ns	ns
NR X stage	Juv 1	–	+	–	ns	ns	+
	Juv 2	+	+	ns	ns	ns	+
	Adult			ns	ns	ns	ns

*** Denotes a significant effect of stage ($P < 0.001$).

E. macrocarpa (1–2 cm) (Sunderland, 2007). The lower the diameter, the lower is the resource the clonal individual must invest to produce a ramet, resulting in a higher number of new ramets. This confirms that *E. macrocarpa* is characterized by a high potential for vegetative reproduction compared to *L. secundiflorum*: ramet production starts earlier for *E. macrocarpa* (for 10 year old individuals) than for *L. secundiflorum* (for 15 year old individuals) (Kouassi et al., 2008) and *E. macrocarpa* produces more ramets than *L. secundiflorum*. This recalls the well documented trade-off within sexual reproduction between fecundity and the size of offspring/propagules. The same type of results has already been documented for clonal reproduction in other clonal palms (de Steven, 1989; Enright, 1992; Mendoza and Franco, 1998; Svenning, 2000). Nevertheless, this trade-off is much better described for sexual than for clonal reproduction.

The production of new ramets increased along genet development stages till the adult stage in *E. macrocarpa* but only till the juvenile 2 stage in *L. secundiflorum*. In parallel, this production increased with the initial number of ramets in adults and juveniles 2 of *L. secundiflorum*. This confirms the hypothesis that clonal ramet production is linked to the size of genets (Mendoza and Franco, 1998; Verburg and Grava, 1998) because the number of ramets is a good proxy for the genet size and therefore the quantity of resource it can absorb and allocate to the production of new ramets (de Steven, 1989; Mendoza and Franco, 1998). This suggests some physiological integration between ramets: resources appear to be managed at the genet scale. The effect of genet size on ramet production was not significant in *L. secundiflorum*, probably due to the lower number of ramets per genet in this species (see above). Finally, the negative effect of the number of ramets on the production of new ramets at the juvenile 1 stage in *E. macrocarpa* suggests that, at this stage, the ramet number is not a good indicator of the quantity of resources that can be allocated to the production of new ramets (Ticktin et al., 2002; Siebert, 2004; Ticktin, 2004). In fact, in clonal plants, in early stages, resources are often allocated preferentially to the development of a storage system (rhizome) and to increase ramet size. Once a critical physiological state or size is achieved, the genet starts to favour the production of new ramets (Cheplick, 1995).

Ramet natural mortality was higher in *E. macrocarpa* than in *L. secundiflorum*. There are two main causes of natural death for rattan genet: competition for light with trees and lianas (Ewers and Fisher, 1989) and accidents such as branch and tree falls (Chazdon, 1992). However, in most cases, genet mortality is low owing to the high mechanical resistance of ramets (Parren and Bongers, 2001). According to Ebanyenle (Ebanyele and Oteng-Amoako, 2003), the high proportion of thick-walled fibres and smaller diameter metaxylem vessels suggests that the ramets of the genus *Laccosperma* are mechanically more resistant than the ramets of *Eremospatha*. This difference in ramet resistance between the two species is strengthened by the difference in ramet diameter (Sunderland, 2007; Kouassi et al., 2009). Overall, this would explain the difference in ramet mortality between the two species. This interpretation also shows that the fact that *E. macrocarpa* is pleonanthic while *L. secundiflorum* is hapaxanthic does not determine the hierarchy in the mortality of their ramets. This probably happens because flowering and the consecutive mortality only occurs on old and tall ramets in *L. secundiflorum*.

Moreover, ramet natural mortality increased from the juvenile 2 to the adult stage in *E. macrocarpa* but decreased between the same stages in *L. secundiflorum*. In parallel, the number of dead ramets increased for the three stages with the initial number of ramets for *E. macrocarpa* but not for *L. secundiflorum*. It is difficult to interpret these results because ramet harvesting interacts with natural mortality. Thus, the absence of ramet mortality (natural mortality) observed in the adult stage of *L. secundiflorum* could be partly due to the high percentage (50%) of ramets harvested at this stage. For *E. macrocarpa*, the increase in the number of dead ramets with the number of ramets may be explained by a simple quantitative effect (the higher the number of ramets, the higher the potential number of dead ramets) but also by competition between ramets for access to resources (water, mineral nutrients, photosynthates) and by the fragility of the ramets of this species. The intensity of competition may indeed increase with the number of competitors, i.e. the ramets, which might cause the death of the smaller ramets (Bernal, 1998; Siebert, 2000).

4.2. Relationship between ramet and genet demography

The majority of results can be intuitively interpreted: in both species, the increase in the number of ramets is favourable to genet demography and vice versa. Overall, the probability of recruitment increased with the number of ramets (initial, produced, harvested, and dead) in both species. Meanwhile, survival increased with the initial number of ramets and the production of new ones, and decreased with the harvest and mortality of ramets. Moreover, the probability of retrogression increased with the number of dead ramets. These results suggest that a genet with more ramets “is larger”, has accumulated more resources that can be used to grow more ramets and limit the risk of mortality (large rhizome, large root system). Such results confirm that the ramet number is a good indicator of the vigour of a genet. This also confirms (see above) that resources are exchanged between the ramets of the two rattan species studied: the clonal individuals behave as a single unit allowing the allocation of photosynthates form the larger to the smaller ramets (Hutchings and Wijesinghe, 1997; Gardner and Mangel, 1999).

4.3. Impact of ramet harvesting

The probability that a ramet is harvested was quite similar in both rattan species: between 40% and 50% for adult genets.

However, the number of harvested ramets was higher in *E. macrocarpa* than in *L. secundiflorum*, partially because *E. macrocarpa* produces more ramets (see above) and because the ramets of this species are necessary in large numbers to make baskets while the *L. secundiflorum* ramets are only used to make furniture frames (Zoro Bi and Kouakou, 2004).

Ramet harvest had no negative effect on the survival of genets of the two species at the current harvest rates. This is in keeping with the results of Siebert (2004): the harvest of rattan (*Calamus zollingeri* and *Daemonorops robusta*) does not increase the genet mortality, whatever the frequency or intensity of ramet harvesting. This confirms that clonal palms are resistant to harvesting (Chazdon, 1991). Ramet harvest was not detrimental to genet survival but survival probability increased with the number of ramets. This suggests that ramet harvest stimulates ramet production through a kind of compensatory growth (Siebert, 2000). It must be noticed that the absence of negative effect of harvest on genet survival and this compensatory ramet production occur while the studied populations have been exploited for years. Probably, this compensatory mechanism is very efficient and does not lead to the exhaustion of genet resources. Through this mechanism, ramet harvest stimulates the production of the future harvest (Siebert, 2000). The mechanisms explaining these effects are probably related to the physiological integration between ramets. Harvesting ramets decreases the number of competitors for resources. More resources thus become available for the growth of remaining ramets and the production of new ramets. Ramet harvest could also suppress apical dominance, subsequently stimulating bud and ramet production (Siebert, 2004).

Harvesting ramets could still have negative effects on *E. macrocarpa* and *L secundiflorum* especially if it becomes very intense (Endress et al., 2004; Siebert, 2004; Zuidema et al., 2007; Widayati and Carlisle, 2012): decreasing the number of ramets frees resources for other ramets but also decreases the capacity of genets to absorb new resources (reduction of photosynthetic area). This is shown by the positive effect of the ramet number on the production of new ramets in *E. macrocarpa*. We can predict that a more intensive harvesting, beyond a certain threshold, would ultimately lead to a situation where ramet harvest slows ramet production, instead of simulating it. This would threaten the survival of genets and the sustainability of the rattan exploitation. This threshold remains to be determined to optimize the harvest.

5. Conclusion

We have successfully tested the three hypotheses put forwards in the introduction: (1) Ramet demography is quicker in *E. macrocarpa* than in *L. secundiflorum*; (2) The number of ramets is a good proxy for genet size and the genet survival probability increases with its number of stems; and (3) Probably because of compensatory production of stems, harvesting is not harmful to the studied rattan populations, at least at the actual harvest rate. There is probably a high level of physiological integration between the ramets that are linked together by a common rhizome: (1) Ramets cooperate with each other and the number of ramets is a good indicator of genet size and the quantity of resources it may mobilize (probable increase in the root system size and water and nutrient absorption, increase in photosynthetic and light absorption); (2) Ramets are competing for elaborated resources (photosynthates). We have exemplified, for clonal reproduction, two relations that are classical for sexual reproduction between the size of parents, the size of offspring and the number of offspring (Stearns, 1992): "clonal fecundity" (number of new ramets) increased with the size of genets and decreased with the size of ramets (stem diameter).

Both rattan species were poorly sensitive to harvesting, which has already been suggested by demographic data focussing on genet demography (Kouassi et al., 2008). However, the intensification of ramet harvest may have a negative impact on ramet demography and subsequently on genets if a certain threshold of harvest intensity (still to be determined) is reached. Ramet harvest could also have a negative effect on sexual reproduction (Siebert, 2001). In the future, such interactions deserve to be studied in rattans. Finally, while stage-classified matrix population models are popular for palm trees (Barot et al., 2000; Escalante et al., 2004; Kouassi et al., 2008; Trimiño et al., 2011), such models do not allow taking into account explicitly the complex interactions between genet and ramet dynamics we have described. New models should thus be designed to account for these interactions and ramet harvesting. Such models are required to optimize harvesting strategies.

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References

Baker, W.J., Hedderson, T.A., Dransfield, J., 2000. Molecular phylogenetics of *Calamus* (Palmae) and related rattan genera based on 5S nrDNA spacer sequence data. Mol. Phylogenet. Evol. 14, 218–231.

Barot, S., Gignoux, J., Legendre, S., Vuattoux, R., 2000. Demography of a savanna palm tree in Ivory Coast (Lamto): population persistence, and life history. J. Trop. Ecol. 16, 637–655.

Bernal, R., 1998. Demography of the vegetable ivory palm *Phytelephas seemannii* in Colombia, and the impact of seed harvesting. J. Appl. Ecol. 35, 64–74.

Bullock, S.H., 1980. Demography of an undergrowth palm in littoral Cameroon. Biotropica 12, 247–255.

Chazdon, R.L., 1991. Effects of leaf and ramet removal on growth and reproduction of *Geonoma congesta*, a clonal understorey palm. J. Ecol. 79, 1137–1146.

Chazdon, R.L., 1992. Patterns of growth and reproduction of *Geonoma congesta*, a clustered understory palm. Biotropica 24, 43–51.

Cheplick, G.P., 1995. Life history trade-offs in *Amphibromus scabrivalis* (Poaceae): allocation to clonal growth, storage and cleistogamous reproduction. Am. J. Bot. 82, 621–629.

de Steven, D., 1989. Genet and ramet demography of *Oenocarpus mapora* ssp. *mapora*, a clonal palm of Panamian tropical moist forest. J. Ecol. 77, 579–596.

Ebanyele, E., Oteng-Amoako, A., 2003. Anatomy and identification of indigenous rattan species of Ghana. Ghana J. Forest. 11, 77–90.

Endress, B.A., Gorchov, D.L., Peterson, M.B., Serrano, E.P., 2004. Harvest of the palm *Chamaedorea radicalis*, its effects on leaf production, and implications for sustainable management. Cons. Biol. 18, 822–830.

Enright, N.J., 1992. Factors affecting reproductive behaviour in the New zealand nikau palm, Rhopalostylis sapida Wendl. & Drude. New Zeal. J. Bot. 30, 69–80.

Escalante, S., Montana, C., Orellana, R., 2004. Demography and potential extractive use of the liana palm, *Desmoncus orthacanthos* Martius (Arecaceae), in southern Quintana Roo. Mexico Forest Ecol. Manag. 187, 3–18.

Ewers, F.W., Fisher, J.B., 1989. Variation in vessel length and diameter in stems of six tropical and subtropical lianas. Am. J. Bot. 76, 1452–1459.

Garcia-Fernandez, C., Casado, M.A., 2005. Forest recovery in managed agroforestry systems: the case of benzoin and rattan gardens in Indonesia. Forest Ecol. Manag. 214, 158–169.

Gardner, S.N., Mangel, M., 1999. Modeling investments in seeds, clonal offspring, and translocation in a clonal plant. Ecology 80, 1202–1220.

Hutchings, M.J., Wijesinghe, D.K., 1997. Patchy habitats, division of labour and growth dividends in clonal plants. Trends Ecol. Evol. 12, 390–394.

Kouassi, K.I., Barot, S., Gignoux, J., Zoro Bi, I.A., 2008. Demography and life history of two rattans species, *Eremospatha macrocarpa* and *Laccosperma secundiflorum*, in Côte d'Ivoire. J. Trop. Ecol. 24, 493–503.

Kouassi, K.I., Barot, S., Zoro Bi, I.A., 2009. Population structure and reproductive strategy of two multiple-stemmed rattan species of Côte d'Ivoire. Palms 53, 38–48.

Mendoza, A., Franco, M., 1998. Sexual reproduction and clonal growth in *Reinhardtia gracilis* (Palmae), an understory tropical palm. Am. J. Bot. 85, 521–527.

Parren, M.P.E., Bongers, F., 2001. Does climber cutting reduce felling damage in southern Cameroon? Forest Ecol. Manag. 141, 175–188.

SAS, 1999. SAS/ETS User's Guide, Vers. 6, 4th ed. SAS Inst, Cary, NC.

Sastry, C.B., 2002. Rattan in the twenty-first century – An outlook. In: Dransfield, J., Tesoro, F.O., Manokaran, N. (Eds.), Rattan: Current Research Issues and Prospects for Conservation and Sustainable Development. FAO, Rome (Italy), pp. 237–244.

Siebert, S.F., 2000. Abundance and growth of *Desmoncus orthacanthos* Mart. (Palmae) in response to light and ramet harvesting in five forest sites in Belize. Forest Ecol. Manag. 137, 83–90.

Siebert, S.F., 2001. Nutrient levels in rattan foliage and cane, and implications for harvesting. Biotropica 33, 361–363.

Siebert, S.F., 2004. Demographic effects of collecting rattan cane and their implications for sustainable harvesting. Cons. Biol. 18, 424–431.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. W.H. Freeman and Company, New York (USA).

Stearns, S.C., 1992. Number and size of offspring. In: Stearns, S.C. (Ed.), The Evolution of Life Histories. Oxford University Press, Oxford, pp. 150–179.

Stearns, S.C., Ackermann, M., Doebeli, M., Kaiser, M., 2000. Experimental evolution of aging, growth, and reproduction in fruitlies. Proc. Natl. Acad. Sci. 98, 3309–3313.

Sunderland, T.C.H., 2002. Hapaxanthy and pleonanthy in African rattans (Palmae: Calamoideae). J. Bamboo Rattan 1, 131–139.

Sunderland, T.C.H., 2007. Field Guide to the Rattan Palms of Africa. Kew Publishing, Royal Botanic Gardens, Kew.

Sunderland, T.C.H., 2012. A taxonomic revision of the rattans of Africa (Arecaceae: Calamoideae). Phytotaxa 51, 1–76.

Svenning, J.-C., 2000. Growth strategies of clonal palms (Arecaceae) in neotropical rainforest, Yasuni, Ecuador. Aust. J. Bot. 48, 167–178.

Ticktin, T., 2004. The ecological implications of harvesting non-timber forest products. J. Appl. Ecol. 41, 11–21.

Ticktin, T., Nantel, P., Ramirez, F., Johns, T., 2002. Effects of variation on harvest limits for nontimber forest species in Mexico. Cons. Biol. 16, 691–705.

Trimiño, C.G., Bernal, R., Bittner, J., 2011. Demography of the clonal palm *Prestoea acuminata* in the Colombian Andes: sustainable household extraction of palm hearts. Trop. Conserv. Sci. 4, 386–404.

Verburg, R., Grava, D., 1998. Differences in allocation patterns in clonal and sexual offspring in a woodland pseudo-annual. Oecologia 115, 472–477.

Widayati, A., Carlisle, B., 2012. Impacts of rattan cane harvesting on vegetation structure and tree diversity of conservation forest in Buton. Indonesia Forest Ecol. Manag. 266, 206–215.

Zoro Bi, I.A., Kouakou, K.L., 2004. Etude de la filière rotin dans le district d'Abidjan (Sud Côte d'Ivoire). BASE 8, 199–209.

Zoro Bi, I.A., Kouassi, K.I., 2004. Rattan abundance and collection in N'zodji forest (South Eastern Côte d'Ivoire). Revue Ivoirienne des Sciences et Technologie 5, 185–197.

Zuidema, P.A., de Kroon, H., Werger, M.J.A., 2007. Testing sustainability by prospective and retrospective demographic analyzes: evaluation for palm leaf harvest. Ecol. Appl. 17, 118–128.