



Colonization front of the understorey palm *Astrocaryum sciophilum* in a pristine rain forest of French Guiana

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ABSTRACT

Aims *Astrocaryum sciophilum* (Miq.) Pulle (Arecaceae) is an understorey palm, endemic to north-eastern South America with a patchy distribution. We tested the hypothesis that the spatial distribution of this palm species is not in equilibrium but is slowly colonizing the forest understorey.

Location Inventories and seed dispersal studies were conducted in the undisturbed tropical forest close to the Nouragues research station, French Guiana. Additional data were collected in the entire territory of French Guiana.

Methods We studied the demography of *A. sciophilum* on a 20-ha plot located at the edge of its distribution. The age of the palms was estimated by postulating an exponentially decreasing abundance by age class. Direct seed dispersal experiments were also conducted, to estimate dispersal parameters. The seeds of *A. sciophilum* were dispersed only by rodents. This information was used to parameterize a forest growth simulator, to study the spatial spread of this species.

Results Within the sampling plot, the density of *A. sciophilum* dropped sharply from about 500 individuals per hectare to zero. The maturation age was estimated to be 170 ± 70 years, and over 55 years with 95% confidence. Seed-dispersal experiments yielded an average seed dispersal distance of 11 m and a maximum estimated dispersal distance of 125 m across a generational span of 55 years to maturity. Therefore, the maximal estimated colonization speed is 2.3 m/y.

Conclusions Empirical results and numerical simulations suggest that the boundary of the *A. sciophilum* population is a colonization front, and that the range of this species is slowly expanding. The implications of this result in respect of palaeoenvironmental changes in this region are discussed.

Key words *Astrocaryum sciophilum*, French Guiana, neotropical palaeoecology, palm ecology, population edge, refuges, scatter-hoarding, seed dispersal, spatial pattern.

INTRODUCTION

Small-scale disjunctions are frequent for plants, but several mechanisms may cause these patterns. Spatial environmental heterogeneity is a plausible hypothesis (Ashton, 1969; Gartland *et al.*, 1986), especially of small-sized plants such as pteridophytes (Poulsen & Balslev, 1991; Tuomisto, 1998), epiphytes (Gentry & Dodson, 1987), or some species restricted to swamps (Svenning, 1999). This 'equilibrium' hypothesis postulates situations where species quickly reach a local demographic equilibrium and co-exist by occupying niches

that partition the environmental axes (Grubb, 1977). However, the evidence for habitat specialization is weak or absent for many tree species at the scale of 50 hectares in a forest of Panama (Harms *et al.*, 2001). Indeed, a species that is associated strongly with a given habitat could also be present, although less abundant, in other habitats. A recent survey in the Peruvian Amazon, along the Rio Manu, found that only 25% of the 381 studied species are habitat specialists (Pitman *et al.*, 1999).

Historical factors provide another plausible explanation for the disjunction of species ranges. A species could have gone extinct in certain areas because of sudden environmental changes (drought, fire, outbreak of pathogens) and be in the process of recolonizing these areas from relict populations.

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Such a picture is consistent with non-equilibrium theories for the maintenance of diversity (Hubbell, 1979; Hubbell & Foster, 1986; Hubbell, 2001), suggesting that forest communities are maintained by drifts in species abundance.

In this context, it is interesting to study species that are known to be locally abundant in some areas while totally absent in others. Such a situation could be stable, if the species is a habitat specialist, or it could be related to the spatial dynamics of the population. We have selected the species *Astrocaryum sciophilum* (Miq.) Pulle (Arecaceae), an understorey palm endemic to the Guiana Shield. This species is very common in many areas of the Guianas, but completely absent in others (Kahn & de Granville, 1992). Preliminary observations by Sist (1989a, 1989b) have demonstrated that this palm spends a long time in the immature stage and that its crop is dispersed mainly over short distances.

A demographic study of a population of *A. sciophilum* was conducted on the edge of its distribution. A complete inventory was carried out in 1998 and 2001, in a 20-ha permanent plot located in the pristine lowland rain forest of the Nouragues Research Station, central French Guiana. Additional surveys were performed all around the country to test for habitat specialization. We also present quantitative results on its growth pattern and seed shadow in the core of the population, 1.3 km from the edge. An individual-based forest growth model was used to simulate the spatial dynamics of the population. Our results are discussed in the light of purported palaeo-environmental changes in this region.

METHODS

Study species

We study the palm species *Astrocaryum sciophilum* (Miq.) Pulle. The neotropical genus *Astrocaryum* (Arecaceae) is conspicuous in the Amazonian forest, with over 35 species falling into four taxonomic sections (Kahn & Millán, 1992), which are supported by a recent molecular phylogeny (Pintaud *et al.*, in press). *A. sciophilum* is the only species of section *Munbaca* in French Guiana, and is morphologically and genetically differentiated from the closely related species *A. sociale* in Brazil (Kahn, 2000; Pintaud *et al.*, 2003).

This species is identified easily in the field (Henderson *et al.*, 1995). The different growth stages we use here are based on the morphological criteria selected by Sist (1989a), with slight modifications. We distinguish four juvenile stages, depending upon the life form of the palm, and one adult stage (Charles-Dominique *et al.*, 2001a). Stage 0 begins at germination and includes all individuals with entire leaves. The first leaf reaches 15–20 cm in length, and the most developed individuals in this category can bear up to 11 leaves, 100–120 cm long (mean 66.6 cm, max. 225 cm). Stage 1 includes individuals with leaves bearing one to eight pinnae, still asym-

metrically arranged on either side of the rachis. According to Sist (1989a,b), individuals in this stage bear seven leaves on average (2–12), between 25 and 390 cm in length (mean 156 cm, SD 49 cm). When individuals reach stage 2, the pinnae are arranged symmetrically on either side of the rachis. Individuals display eight leaves on average (mean 8.1, SD 2) that bear between eight and 58 symmetrical pinnae. At this stage, individuals still have at least one pinna larger than the others. Individuals at stage 3 still bear relatively delicate leaves (5–17 leaves, mean 9.7): the rachis is only 26 mm in diameter on average (SD 6.9 mm), while this value reaches 34.1 mm (SD 2.5 mm) for adults.

For adults, the mean length of the leaves reaches 633 cm (SD 154 cm) and the rachis is much sturdier than in Juv 3 individuals. Young adults lack an above-ground stem but none the less show traces of fructification (one or several recent peduncular bracts, or 1–3-year-old remains of infructescence). All older adults have a visible above-ground stem. The tallest individuals had a stem 8.6 m in height.

Site location

We collected most of our data at the Nouragues Research Station in French Guiana (4°05'N, 52°41'W), in an old-growth tropical rain forest (Poncy *et al.*, 1998; Bongers *et al.*, 2001). Rainfall is around 3000 mm/y (14-year average) with a 2-month dry season from September to November (< 100 mm/month), and a short dry season in March. The monthly mean maximum temperature varies between 32.1 and 35.8 °C, and the monthly mean minimum between 19.5 and 20.8 °C. About 95% of French Guiana is lowland wet rain forest. The remaining 5% corresponds to a narrow 3–10 km wide coastal strip of savanna, mangroves and marshes (Boyé *et al.*, 1979). Additional data were collected at the Piste de Saint Elie Research Station and at the Paracou Research Station (Fig. 1).

A presence/absence map was constructed for *A. sciophilum* in French Guiana, using botanical inventories (Fig. 1), and by looking for the species *c.* 10 km around the Nouragues research station. Available data are scarce due to the difficult access of the interior; however, we believe that the map provides at least a first approximation. We use this distributional information to help us evaluate our theory that *A. sciophilum* is not limited by edaphic factors or other environmental factors.

Study of the population edge

We first located the distributional border of the population of *A. sciophilum* 4 km to the South-west of the Nouragues Station. On this border, we established a 20-ha permanent plot (500 m × 400 m) perpendicular to the edge of the palm population (Figs 2 and 3). This plot was located in the middle of a

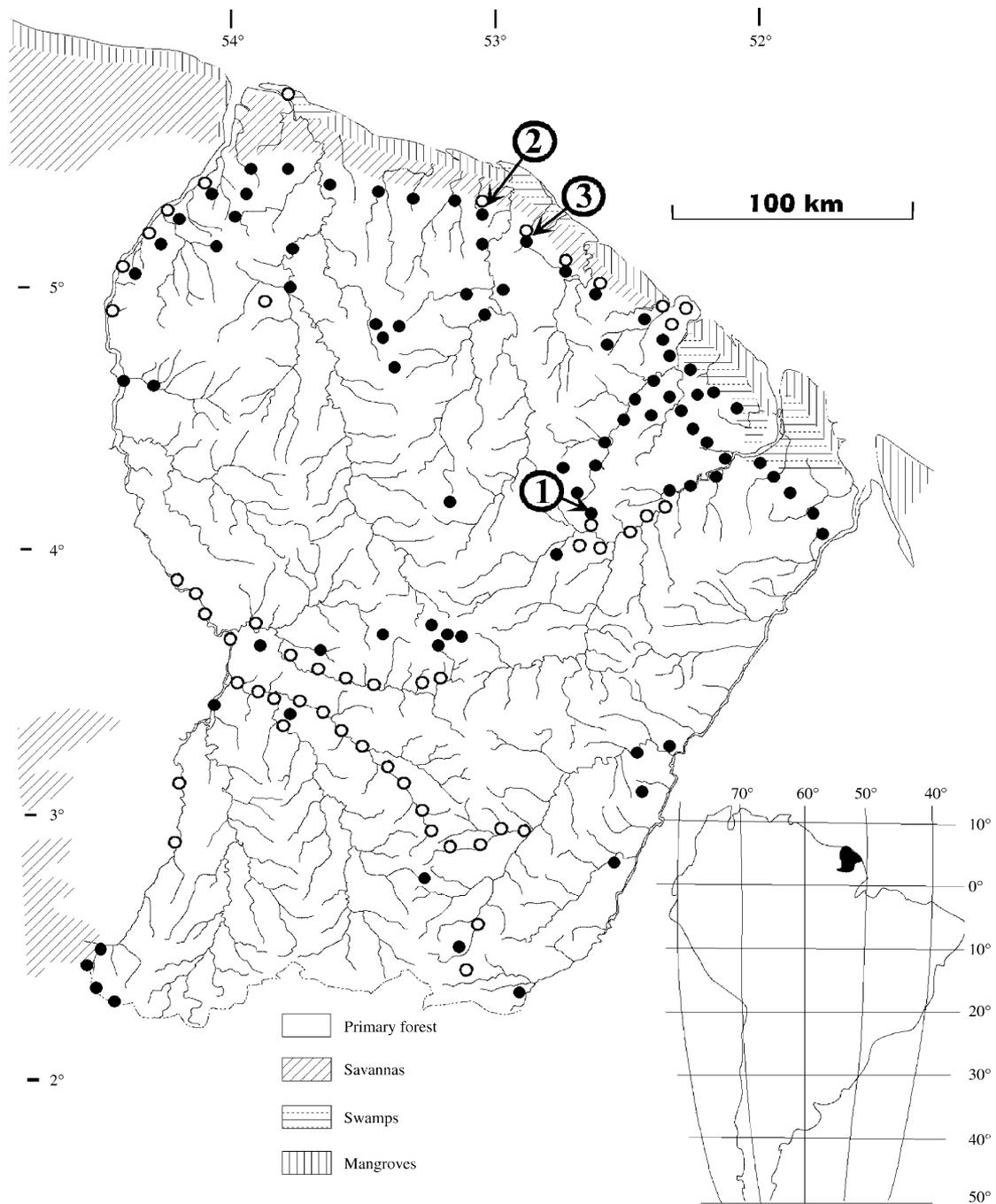


Fig. 1 Map of French Guiana showing the different study areas (1: Nouragues; 2: Piste de St Elie; and 3: Paracou), the distribution of the various habitat types (forest, coastal savanna and swamps and mangroves) and the distribution of *A. sciophilum*: black circle = present, open circle = absent.

plateau in order to avoid hydrographic or topographic effects.

A first census was carried out in October 1998 and a second in October 2001. All adults were recorded over the entire

20 ha, and juveniles were censused in a subsample of 14 ha. Each 1-ha quadrat was subdivided by trails into 20 × 20 m subplots to facilitate the mapping and tagging of each individual. Leaves were counted and measured and the number

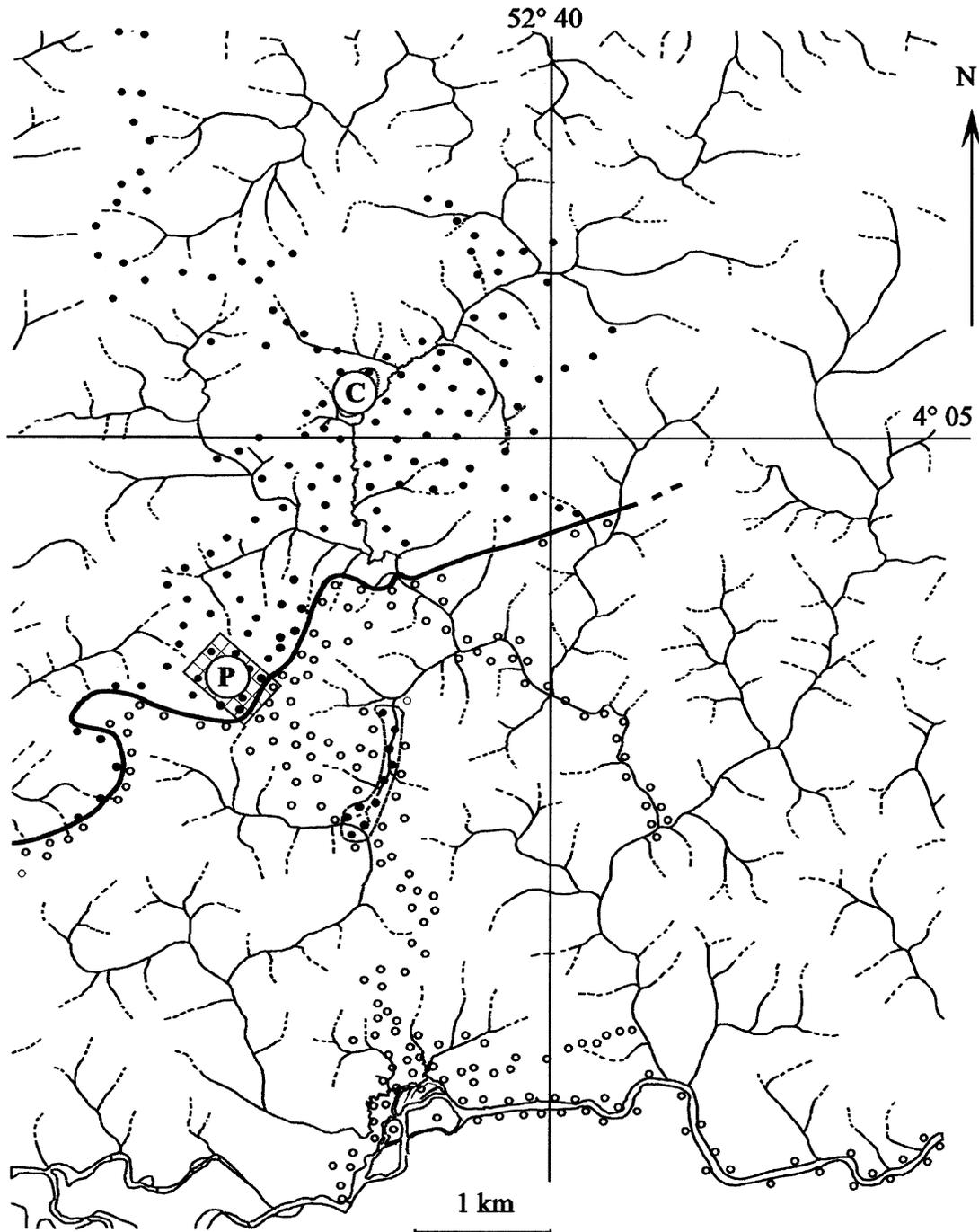


Fig. 2 Map of the Nouragues Station indicating the location of the study plot (P) on the edge of the *A. sciophilum* population and the camp (C). The population edge is drawn as a solid line, black circle = presence of *A. sciophilum*, white circle = absence of *A. sciophilum*. After IGN NB22 II Ib Paris 1983.

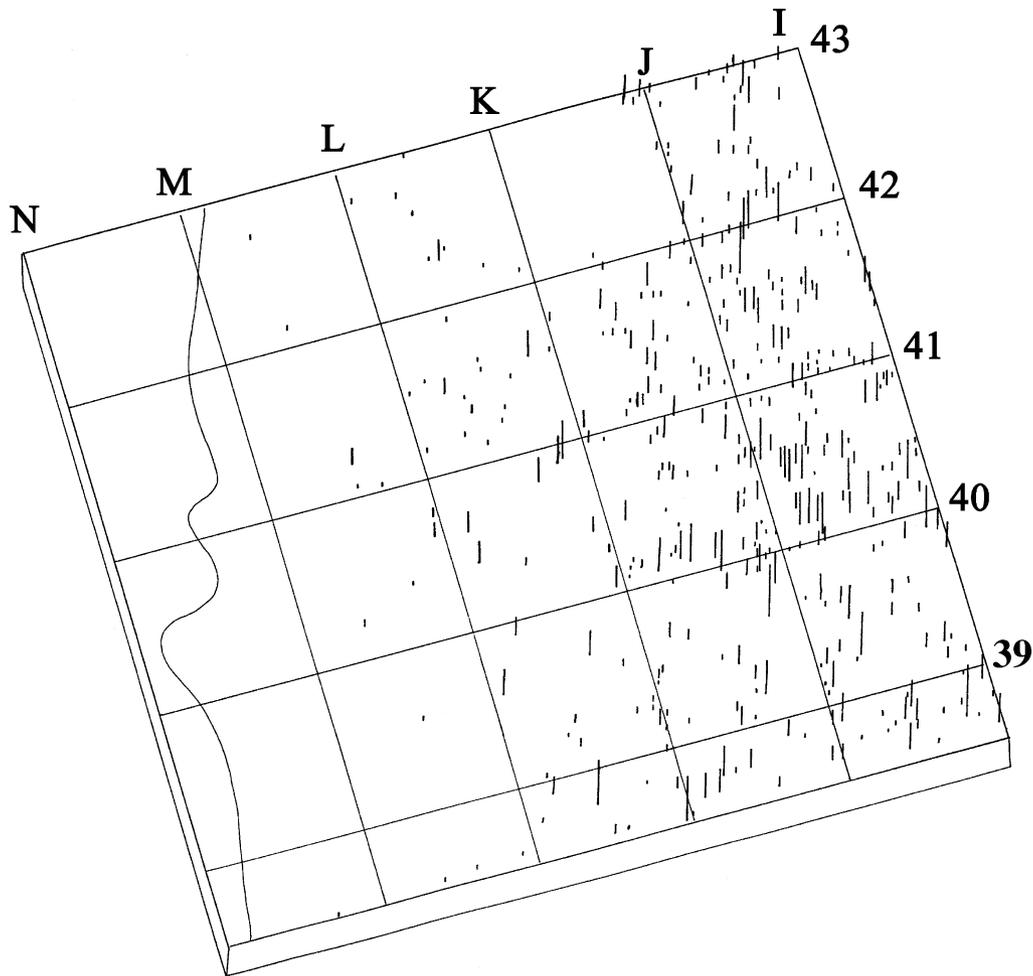


Fig. 3 Distribution of *A. sciophilum* on the study plot (400 × 500 m). Adults were mapped individually (in relation to height). Because juveniles were too numerous to be mapped individually, only the edge of the distribution is shown (solid line between the trails M and N). Numbers (39–43) and capital letters (I–M) indicate the trails.

of pinnae noted. The stem height and phenological state of adults were recorded (inflorescences, infructescences, remains of old infructescences).

Several demographic parameters were collected less than 1000 m from this plot. Every 3–6 months, young unfolded leaves were recorded and measured for juvenile ($n = 325$) and adult ($n = 47$) individuals alike in order to evaluate the phenology of leaf production. A population of 189 adults was examined in the core population (about 1.3 km from the plot) and stem height was recorded.

Age estimation

Different approaches were used to estimate the time needed by a palm to reach the adult stage (Charles-Dominique *et al.*,

2001a). First, if the population is at local equilibrium in age distribution, assuming a constant mortality rate, we expect the number of individuals to decrease exponentially with age class. We then fit the abundance in the juvenile stages to an exponential, which allows us to estimate the time spent in each stage. This analysis was performed on the data available in the core of the palm population, 1.3 km from the edge. Secondly, the count of leaf scars left on the subterranean stem of uprooted palms provides a lower bound estimate of the age of the palm. Indeed, the oldest (and thinnest) part, which corresponds to the earliest phase of the palm's life, is usually decayed or desiccated. We analysed the leaf scars of 35 unearthed stems overall.

A. sciophilum spends its entire life cycle in the understorey. Treefall events are important for this species. The mechanisms

that maintain the terminal bud underground during the entire juvenile phase (Sist, 1989a; Tomlinson, 1990) greatly reduce the risk of complete destruction, which occurs only if a large tree trunk falls directly atop a young individual. To provide the third age estimate, we assume that juvenile mortality is caused only by treefalls. From the fraction of individuals in the juvenile stage we obtain an upper bound of the maturation age, as all the other possible causes of mortality (such as predation) are discarded.

Adult palm age was correlated to adult palm stem height (SE 5%), measured from ground level (at the base of the heap of decomposed leaf-litter accumulated at the foot of each individual) to the base of the oldest leaf still in function.

Seed removal and germination experiments

The seeds of *A. sciophilum* are animal-dispersed. Other means of dispersion can be eliminated easily. In particular, the seed has a specific density greater than 1, and thus it cannot be transported by runoff waters. Its fruits are predated mainly by the squirrel *Sciurus aestuans*, the agouti *Dasyprocta leporina* and the acouchi *Myoprocta exilis*, and to a lesser extent by the spiny rat *Proechimys* spp. Peeling the seed takes a long time, because the animals must gnaw through the endocarp with their incisors, for 10–15 min for the agouti, and nearly 50 min for the squirrel, before reaching the lipid-rich endosperm (personal observation, C.V.). True frugivorous vertebrates such as monkeys (Julliot, 1997), bats and birds (personal observation, P.C.D.) have never been observed to exploit this pulpless species. Similarly, tapirs, known to carry seeds of the palm *Attalea maripa* kilometres away from the site of production (Fragoso, 1997) do not consume this very tough seed (personal observation P.C.D.).

Fruit production is irregular so rodents hide seeds for later use, a scenario already described for other plant–rodent interactions (Kiltie, 1981; Sist, 1989a; Forget, 1991, 1997). Agoutis and acouchis bury the unpredated seeds in small holes 3–9 cm deep (Henry, 1999; Jansen & Forget, 2001), dug carefully and sealed afterwards. Only the buried seeds that have not been dug up and eaten will germinate (Sist, 1989a).

A 2-month seed dispersal experiment was undertaken twice with *A. sciophilum* seeds, during the rainy season (March–June 1998, experiment 1) and during the dry season (September–November 1998, experiment 2). A yellow thread with a coloured flag was affixed to each seed ($n = 600$ for experiment 1; $n = 290$ for experiment 2). Replicates were scattered within the experimental plot. We searched for the seeds that were removed up to 30 m away from each removal experiment plus along four perpendicular 100 m trails radiating from the removal sites.

To analyse the seed dispersal curve we pooled the distance data into bins of 5 m, and fitted the curve by the maximum

likelihood technique using several empirical dispersal kernels (Portnoy & Willson, 1993; Willson, 1993; Turchin, 1998; Clark *et al.*, 1999). We used a decreasing exponential function, a Weibull function (type VII of Turchin, 1998) and a fat-tailed 2Dt function (Clark *et al.*, 1999).

To assess the seed germination potential, we monitored 72 seeds that we buried in the forest, and 19 seeds buried by rodents. This experiment has been followed for 36 months.

Statistical analyses and simulations

We performed correlation analyses to ensure that the population edge was a population front and not a stable limit of the population range. We applied two statistical tests. We tested whether the population increase from the edge of the population was significant (linear regression method). We also tested for the increase in length of juvenile leaves away from the edge using the non-parametric Kruskal–Wallis test (Zar, 1996), applied to palms grouped in 50-m distance classes ($n = 8$ groups). Analyses of variance were not possible, as the distribution of leaf length is markedly leptokurtic. Pairwise comparisons across groups were finally performed using Tukey's test.

The individual-based model TROLL (Chave, 1999, 2001) was used to test the hypothesis of the advance of the *A. sciophilum* population in a primary forest. In this model, each tree is described in three dimensions. Competition for light is also described in three dimensions on the square metre scale, and gap dynamics are modelled. We had previously defined 12 plant functional types for the French Guiana rain forest (Chave, 1999). *A. sciophilum* was introduced as an additional functional type, having the biological characteristics measured in the field.

RESULTS

Edge of the population

Our plot was set out on an edge of the palm population. No palm was encountered further south, except a 'micropopulation' spreading over 100 m east–west and 1000 m north–south and confined to a small wet valley 1200 m to the south. We tested the hypothesis that the gradient corresponds to a true front of colonization. We recorded the individuals as a function of the edge of the population, discarding the last 100 m, which would have induced a sampling bias. Distance classes of 50 m have been used.

The total number of juveniles, subadults and adults increased steadily and significantly from the population edge (Table 1). The total population density varied between 27 and 648 individuals per hectare along the south–north gradient. In the first 100 m, the ratio of juvenile to adults (RJA) was 23, and decreased to 14 from 300 to 400 m of the edge. In the core of the population the RJA was between 10 and 12. The

Table 1 Number of individuals in three different stage classes (juveniles, subadults and adults) as a function of the distance from the population edge. All subadults and adults were sampled in the 400-m-wide strip from the population edge 400 m deep inside the population. Juveniles were censused in a 100-m-wide strip to 400 m inside the population edge. The total number of sampled individuals, their local density (in individuals/ha), the average length and the maximal length of the longest leaf are reported here. For adults, we report the average height and maximal stem height. All dimensions are in cm

Distance class (m)	0–50	50–100	100–150	150–200	200–250	250–300	300–350	350–400
No. of juveniles	7	14	47	66	132	156	225	288
No. per ha	14	28	94	132	264	332	450	576
Average leaf length	136	141	171	140	147	152	123	122
Max. leaf length	240	275	570	430	530	600	560	550
No. of subadults	3	4	19	29	31	46	67	59
No. per ha	1.5	2	9.5	14.5	15.5	23	33.5	29.5
Average leaf length	473	527	579	573	587	573	540	550
Max. leaf length	530	645	790	909	800	810	870	770
No. of adults	1	3	13	19	17	54	75	84
No. per ha	0.5	1.5	6.5	9.5	8.5	27	37.5	42
Average stem height	0	132	84	131	170	141	177	181
Max. stem height	0	240	280	400	650	500	860	680

Kruskal–Wallis test on the leaf length of juveniles showed a significant difference between 50-m distance classes ($n = 8$, $H_c = 1919$, $P < 0.001$). We analysed further the pairwise differences between classes. We found that the six classes from 0 to 300 m were not significantly different (Tukey test with unequal sample size, $Q < 1.22$, $Q_{0.05,7} = 3.03$), while palms from distance 300–400 m had significantly *smaller* leaves ($Q = 3.30$). Pooling subadults with juveniles led to the same result. The differences were marginally significant for stem height ($0.05 < P < 0.10$).

Finally, we tested for the stability of the population edge. If the edge was stable, adult palms located on the population edge should display poorer reproductive success. Of these adult palms, 44% ($n = 34$, 10 ha) were fertile during one year. In the core population, the same experiment gave percentage of fertility of 34% ($n = 161$, 10 ha). Therefore the fertility of the population was slightly higher at the edge of the population than in the core ($\chi^2 = 13.6$, $P < 0.01$). This observation runs against the hypothesis of a stable population edge.

Surveys completed along the coastal savanna/forest boundary near the Piste de Saint Elie Research Station and the Paracou Research Station (Fig. 1) revealed the presence of a population front about 3 km behind the edge of the forest. Counts undertaken along two transects along another population edge at Piste de Saint Elie showed the same general trends as at the Nouragues station: the abundance of adults increased from 25 to 190 individuals per ha in 200 m.

Life history

The time-span between leaf production was 16 months (8–22 months, $SD = 1$, $n = 129$) both for juveniles and adults.

However, Van der Steege (1983) found a time-span of 1.1 years for adults in Surinam. In 3 ha (1211 individuals), an average of 49 palms/ha had apparently been damaged by treefalls or branchfalls (12.5% of the total population), 50 palms/ha showed traces of predation (13% of the total) and 18 palms/ha of hydric stress (4.5%). Overall the mortality rate was very low. A small area monitored during 3 years gave the following results: three juveniles of 120 (2.5%) and one adult of 61 (1.6%) died. No lethal predation was recorded on juveniles in this area, although herbivory of this palm by caterpillars of *Brassolis sophorae* (or the closely allied species *B. astyra*) has been observed at the Piste de Saint-Elie station (D. Sabatier & J. Olivier, personal communication).

The methods applied to estimate the maturation age gave the following results. Method 1 (demographic analysis): 180 ± 40 years; method 2 (subterranean stem scars count): 162 ± 88 years; and method 3 (treefall disturbance rate): 300 ± 100 years (about 1% of the forest floor is affected yearly by direct treefalls; Riéra & Alexandre, 1988). Method 3 provides only a very rough estimation of the maturation age. Using only Methods 1 and 2, the time duration of the immature phase is estimated reasonably at about 170 ± 70 years. The error bars should be taken with caution, for they reflect only an average history in one sampled population. The one-sided 95% confidence interval is 55 years, i.e. there is a 95% chance that a palm that reaches maturity is older than 55 years. In the rest of this paper, we retain this value of 55 years as a conservative estimate for the age of maturation.

Concerning the adult phase, stems grew by $27 (\pm 2)$ mm in height with each new leaf (every 16 month). A typical 2-m tall palm is therefore *c.* 270 years old. The tallest recorded individual had a stem 8.6 m in height.

Fruit production and seed dispersal

About 40% of the adults of *A. sciophilum* produced at least one infructescence (mean number 2.2, 1–7), each bearing an average of 65 ripe fruits (SD 177). Because fructification is irregular and depends also on the size of the infructescences, the mean production of ripe fruit can be estimated at 33 fruits/individual/year (see also Sist, 1989a). The dry pulpless fruit is covered by a thin dry and spiny pericarp that can easily be discarded. The size of the endocarp — pear-shaped and rostrate at the apex — has been estimated for $n = 325$ seeds. It measured 44.6 mm in length (28–60 mm, SD = 14.3), 27 mm in diameter (14–39 mm, SD = 6.2), and weighed 14.5 g (4.5–33 g, SD = 4.3). The entire fruit (endocarp plus exocarp) weighed 23 g (8–36 g, SD = 8.5, $n = 300$). Although seeds of this size could, in principle, be eaten by many animal species (van Roosmalen, 1985), the endosperm is protected by an extremely tough and thick endocarp.

Germination studies show that less than one seed per adult palm germinates each year. Seed dormancy is long. After 36 months, 25% of the seeds buried in the experimental plot had germinated ($n = 72$ seeds in total), as had 26.3% of the seeds that had been buried — and not uncovered subsequently — by acouchis ($n = 19$ seeds in total). These percentages are not statistically different.

The 2-month seed dispersal experiments during the rainy season (March–June 1998, experiment 1, $n = 600$ seeds) and during the dry season (September–November 1998, experiment 2, $n = 290$ seeds) gave the following results. We found 247 seeds of 595 removed by rodents during the first experiment: 95.5% ($n = 236$) were scatter-hoarded by acouchis and agoutis; 1.62% ($n = 4$) were eaten by squirrels and 2.83% ($n = 7$) were simply removed and left on the ground. In experiment 2, 80% ($n = 232$) of the seeds we recovered were eaten by rodents, 20% ($n = 58$) were hidden, and none were left *in situ*. These figures reflect the higher predation rate and the lower storage rate during the dry season, with a low food availability. The largest dispersal distance recorded was 40 m (experiment 1) and 21 m (experiment 2). Of the 374 lost seeds, most of them were probably eaten by rodents. However, it is also possible that some seeds were dispersed further away than 40 m. Therefore, we need to model the likelihood of such long-distance dispersal events.

The seed shadow was best fit by an exponential distribution $N(r) = N(0)\exp(-r/l)$ (Fig. 4). The likelihood corresponding to the Weibull function (parametric form $N(r) = \exp(a - br^c)$) was not significantly higher. We found an average dispersal distance of $l = 11$ m (experiment 1) and $l = 7.5$ m (experiment 2). However, to estimate the colonization speed of the population, the mean dispersal is less relevant than the extreme dispersal events. The distance beyond which 5% of the seeds have been dispersed is $r_{95\%} = 33$ m. An even more conservative definition of the extreme dispersal distance is the distance beyond

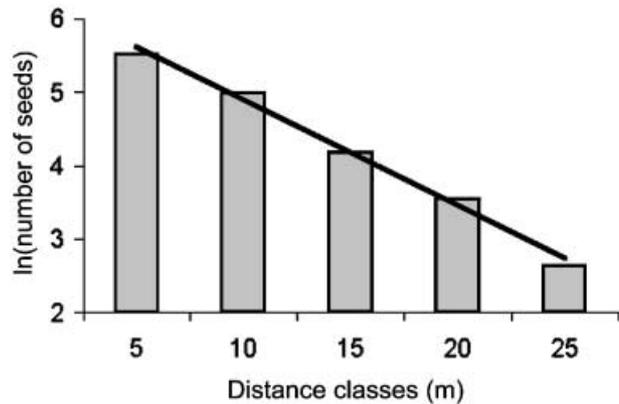


Fig. 4 Seed shadow for *A. sciophilum*; 516 dispersed seeds which were recovered within a distance of 40 m from the removal site. An exponential function fitted the data very well up to 25 m ($r^2 > 0.99$).

which one seed at most has been dispersed during a generation. Suppose a colonization edge comparable to the one at the Nouragues station, where about 50 mature palms contribute to the crop production. The average seed production per mature individual is 33 seeds/individual/year, this gives a total production of about $n = 160\,000$ seeds dispersed during 55 years. We seek the distance such that $N(r_{\max}) = 1$, that is $r_{\max} = \ln(n)l = 125$ m. This value is consistent with the maximum dispersal distance observed for the seeds of *Carapa procera* scatter-hoarded by acouchis at Nouragues (124 m, Jansen *et al.*, 2002).

To model the dynamics of the population edge, we used the TROLL simulator (Chave, 1999, 2001). We took a typical maturation age of 170 years (SD 70 years), and a negative exponential seed shadow, with a 95% dispersal distance of 50 metres. We then conducted two types of computer simulations.

We first started with a ‘forest’ made up only of seedlings (including *A. sciophilum* seeds), and we monitored the forest growth to see how long it took the *A. sciophilum* population to reach demographic equilibrium. The population took almost 1000 years to reach its equilibrium, characterized by around 600 individuals per hectare, in good agreement with the field data. We then performed a second experiment, introducing palm seeds from the edge of a strip of forest (size 2000 × 400 m). During the simulation, we monitored the speed of advance of the population front. Figure 5 shows the patterns observed in this simulation. The colonization front advanced at an average speed of 2 m/year and with a heterogeneous pattern.

Environmental constraints

Our explorations have underlined the omnipresence of *A. sciophilum* along a 100-km-wide strip on the northern coastal edge forest, from Saint-Georges de l’Oyapock, eastwards, to

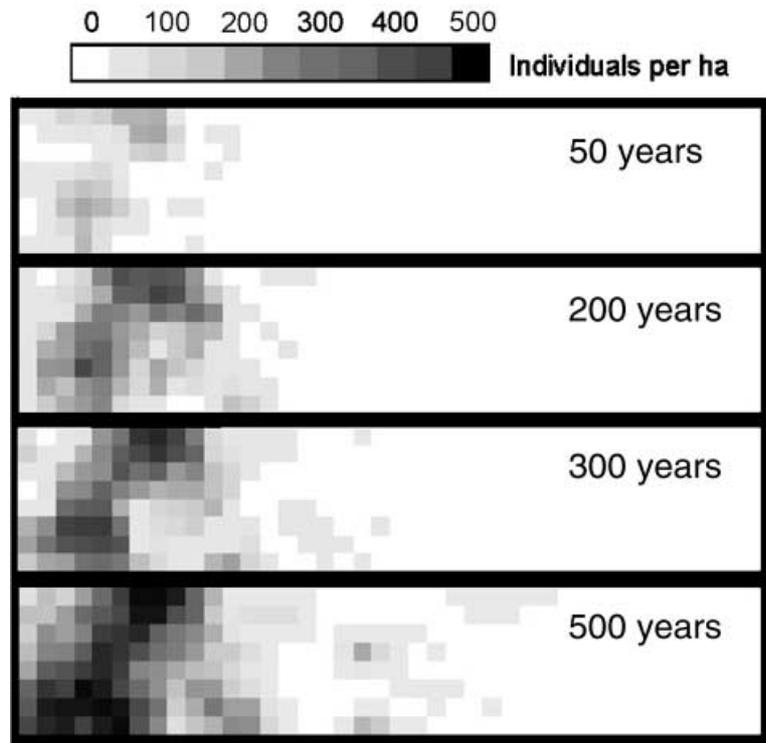


Fig. 5 Simulated pictures of a 'virtual forest' using the individual-based model TROLL. *A. sciophilum* seeds were introduced at the left extremity. The size of the simulation is 2000×400 m, and the density of *A. sciophilum* stems is recorded in quadrats of size 25×25 m (white: no individual, black: more than 500 individuals per hectare). After 500 years, we observe a progression of about 500 m and a heterogeneous pattern of distribution, close to the situation presently observed in the field.

near St Laurent du Maroni, north-westwards (Fig. 1). The species is absent, however, from the first 3 km of the coastal forest. The Nouragues population (100 km from the coast) and the 'coastal' population, present throughout the coastal region, are both part of a single continuous population. Incidentally, the palm *Geonoma oldemanii* exhibits the same spatial distribution (de Granville, 1989). The continental edge of the *A. sciophilum* population lies a few kilometres to the south of the Nouragues station, following roughly an east-west direction (Figs 1 and 2). No *A. sciophilum* populations were found to the south of this borderline for several dozen kilometres, excepted one isolated population in the area of the Mont Chauve, about 25 km south of the edge (C. Sarthou, personal communication). Other localized populations were found southwards, in the central and southern regions of French Guiana, on a rugged landscape of granite outcrops as well as on tabletop mountains on basic bedrock (Sabatier & Prévost, 1987; Kahn & de Granville, 1992; personal observation, J.J.dG. and P.C.D.). North-eastwards, the population extends towards the Venezuelan Guiana (Galeano, 1992). As mentioned above, the populations encountered in the region of Manaus probably belong to another species, *A. sociale* (Kahn, 2000; Pintaud *et al.*, 2003).

No obvious change in the physiognomy of the forest can explain the heterogeneity of the distribution of *A. sciophilum*. The palm can be found on a wide variety of soil types: latosols (lateritic soils), the summits of table mountains with

an underlying lateritic base, podzols, soils on granite, gneiss and schist. All these soil types are encountered along the coast, where the species is widespread (Boyé *et al.*, 1979; Charles-Dominique *et al.*, 2001b). Moreover, where the species is present, it can be found in valleys, near poorly drained areas, as well as on the well-drained slopes and ridges of hills, and it is abundant (on the order of 500 individuals per hectare). About 1300 m to the south of the Nouragues station, the edge of the coastal population crosses the middle of a plateau, then runs diagonally across a valley and up the other side onto another plateau.

DISCUSSION

We have shown that *A. sciophilum*, unlike most other congeneric species, is a slow-growing palm, with a maturation age of over 170 years (over 55 years with 95% confidence). This slow growth rate is consistent with C14 dating of large trees (Chambers *et al.*, 1998) and direct diameter growth measurements (Worbes, 1989; Condit *et al.*, 1999). If trees reach maturity above 10 cm d.b.h., with an average growth rate of *c.* 1 mm/year, their typical maturation age compares with that of *A. sciophilum*.

This species is dispersed only by scatter-hoarding rodents over short distances. Dispersal by water is highly improbable as the fresh seed sinks in water. Our seed-dispersal experiments and supporting calculations suggest an extreme dispersal

distance of 125 m in the 55 years estimated for individuals to reach reproductive maturity. Therefore, the upper-bound speed of a front of *A. sciophilum* palms is $125/55 = 2.3$ m/year. Thus, *A. sciophilum* can be considered as a poor colonist (Clark *et al.*, 1999). This holds only if we can positively exclude long-distance dispersal events, i.e. seed movements well beyond 125 m. They would enhance the invasion speed considerably, and this has been suggested as a probable mechanism to explain the rapid advance of vegetation in temperate areas after the last glacial (e.g. Clark *et al.*, 1999). However, we have found no direct evidence of any long-distance transport for *A. sciophilum*, and the present study suggests that long-distance seed dispersal is unlikely to be related to secondary dispersal by scatter-hoarding rodents.

The spatial distribution of *A. sciophilum* is highly aggregated. Several hypotheses could explain this clumping, and we shall discuss four of these: (1) the current range of *A. sciophilum* could be limited by edaphic constraints; (2) it could be related to human settlements; (3) it could be highly sensitive to present-day climatic fluctuations; (4) finally, we could witness a slow, continuous, invasion stage, lasting since the last major climatic disturbance.

The regional survey performed all around French Guiana showed consistently that *A. sciophilum* is a habitat generalist. Hence, hypothesis (1) can be rejected. Anthropogenic influence (hypothesis 2) should not be dismissed (Bush *et al.*, 2000), since *A. sciophilum* has been recorded as a useful palm in Venezuela (Galeano, 1992) and in Suriname (Wessels Boer, 1965). However, several lines of evidence suggest that this hypothesis is incorrect. *A. sciophilum*'s only recorded use is in the production of oil, which results in the destruction of the seeds. Several other species of the same genus are much more common and convenient for oil production (e.g. *A. vulgare*, *A. paramaca*). Hence, we also reject this hypothesis. Temperatures are relatively uniform throughout French Guiana, but rainfall does vary. However, current rainfall distribution cannot explain the sharp edge observed near the Nouragues, or that in the central and southern landscapes of French Guiana (the spatial distribution of the species does not overlap with the isohyet lines). Therefore, we also reject the third hypothesis.

While current climatic restrictions cannot explain *A. sciophilum*'s present spatial distribution, former environmental stresses have probably contributed to it. This idea was the starting point of the refuge hypothesis (Haffer, 1969; Prance, 1973; Granville, 1982). Although this hypothesis has been criticized strongly for the Neotropics (Nelson *et al.*, 1990; Bush, 1994; Colinvaux *et al.*, 2000), it is generally acknowledged that recurrent climatic events may have modified the species composition of neotropical forests during the Holocene, while maintaining a closed canopy (Bush *et al.*, 2000; Colinvaux *et al.*, 2000, 2001). It is therefore reasonable to suggest that the observed heterogeneous distribution of the species could be

related to past disturbances from which the species is recovering at a slow pace. In our study of the population front, we found that the individuals located on the population edge are as fit as those in the bulk of the population. Moreover, the greater proportion of young individuals found there suggests that we are observing a true population advance within the forest.

Charcoal analyses undertaken at the Nouragues research station (Tardy, 1998) showed that areas that are covered nowadays with a mature wet tropical forest were burnt several times during the Holocene (Charles-Dominique *et al.*, 1998). These analyses indicate a less diverse tree community between 12 000 and 6000 years BP in comparison to the period 5000 years BP to the present day. In addition, taxa such as *Tabebuia* and *Swartzia*, now conspicuous in the semideciduous forest of Venezuela, were abundant in French Guiana between 12 000 and 6000 years BP. It is likely that such fires modified the spatial distribution of many slowly dispersing species, such as *Eperua* spp. or *Vouacapoua americana* (Caesalpinaceae). In addition, local blowdowns might have played an important role in these forests (Nelson *et al.*, 1994). However, as juveniles of *A. sciophilum* possess a well-protected subterranean apex, short fire episodes probably did not affect this population greatly. In a 25-ha block of forest that was clear-cut in 1976 at Piste de Saint Elie (ARBOCEL plot), a mean of 210 individuals/ha *A. sciophilum* had resprouted in 1994, some with leaves over 6 m high (P. Chareyre, unpublished report). In addition, the rapid regeneration of this palm in abandoned slash-and-burn areas (personal observation, P.C.D.) suggests that the absence of *A. sciophilum* from certain areas of French Guiana is probably related more to disturbances that lasted long enough to impede the regeneration of this species.

The reconstitution of the forest in response to long-term regional climatic change and for species such as this palm probably from a few scattered locales, has probably occurred at a variable pace depending on the species colonization ability, thus leading to a non-linear increase in diversity over time. Such 'within-forest invasions' might hold the key to variations in plant diversity in tropical forest ecosystems (ter Steege & Hammond, 2001). Complementary research should include genetic work on this species, as well as on other species (Caron *et al.*, 2000; Dutech *et al.*, 2000).

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REFERENCES

- Ashton, P.S. (1969) Speciation among tropical forest trees: some deductions in light of recent evidences. *Biological Journal of the Linnean Society London*, **1**, 155–196.
- Bongers, F., Charles-Dominique, P., Forget, P.-M. & Théry, M., eds (2001) *Nouragues: dynamics and plant–animal interactions in a neotropical rainforest*. Kluwer Academic Publishers, Dordrecht.
- Boyé, M., Cabaussel, G. & Perrot, Y. (1979) *Atlas des départements Français d'outre-mer. La Guyane*. CNRS-ORSTOM, Paris.
- Bush, M.B. (1994) Amazonian speciation: a necessarily complex model. *Journal of Biogeography*, **21**, 5–17.
- Bush, M.B., Miller, M.C., De Oliveira, P.E. & Colinvaux, P.A. (2000) Two histories of environmental change and human disturbance in eastern lowland Amazonia. *Holocene*, **10**, 543–553.
- Caron, H., Dumas, S., Marque, G., Messier, C., Bandou, E., Petit, R.J. & Kremer, A. (2000) Spatial and temporal distribution of chloroplast DNA polymorphism in a tropical tree species. *Molecular Ecology*, **9**, 1089–1098.
- Chambers, J.Q., Higuchi, N. & Schimel, J.P. (1998) Ancient trees in Amazonia. *Nature*, **391**, 135–136.
- Charles-Dominique, P., Blanc, P., Larpin, D., Ledru, M.P., Riéra, B., Rosique, T., Sarthou, C., Servant, M. & Tardy, C. (2001b) Palaeoclimates and their consequences on forest composition. *Nouragues: dynamics and plant–animal interactions in a neotropical rainforest* (ed. by F. Bongers, P. Charles-Dominique, P.-M. Forget and M. Théry), pp. 79–88. Kluwer Academic Publishers, Dordrecht.
- Charles-Dominique, P., Blanc, P., Larpin, D., Ledru, M.P., Riéra, B., Sarthou, C., Servant, M. & Tardy, C. (1998) Forest perturbations and biodiversity during the last ten thousand years in French Guiana. *Acta Oecologica*, **1**, 295–302.
- Charles-Dominique, P., Chave, J., Vezzoli, C., Dubois, M.-A. & Riéra, B. (2001a) Growth strategy of the understorey palm *Astrocaryum sciophilum* in the rainforest of French Guiana. *Life forms and dynamics in tropical forests* (ed. by G. Gottsberger and S. Liede), pp. 153–163. *Dissertationes Botanicae* 346, Berlin/Stuttgart.
- Chave, J. (1999) Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. *Ecological Modelling*, **124**, 233–254.
- Chave, J. (2001) Spatial patterns and persistence of woody plant species in ecological communities. *American Naturalist*, **157**, 51–65.
- Clark, J.S., Silman, M., Kern, R., Maklin, E. & HilleRisLambers, J. (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**, 1475–1494.
- Colinvaux, P.A., de Oliveira, P.E. & Bush, M.B. (2000) Amazonian and neotropical plant communities on glacial time-scales: the failure of the aridity and refuge hypotheses. *Quaternary Science Reviews*, **19**, 141–169.
- Colinvaux, P.A., Iron, G., Rasanen, M.E., Bush, M.B. & De Mello, J. (2001) A paradigm to be discarded: geological and paleoecological data falsify the Haffer & Prance refuge hypothesis of Amazonian speciation. *Amazoniana*, **16**, 609–646.
- Condit, R., Ashton, P.S., Manokaran, N., LaFrankie, J.V., Hubbell, S.P. & Foster, R.B. (1999) Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50-ha plots. *Philosophical Transactions of the Royal Society of London B*, **354**, 1739–1748.
- Dutech, C., Maggia, L. & Joly, H.I. (2000) Chloroplast diversity in *Vouacapoua americana* (Caesalpinaceae), a neotropical forest tree. *Molecular Ecology*, **9**, 1427–1432.
- Forget, P.-M. (1991) Scatterhoarding of *Astrocaryum paramaca* by *Proechymis* in French Guiana: comparison with *Myoprocta exilis*. *Tropical Ecology*, **94**, 255–261.
- Forget, P.-M. (1997) Effect of microhabitat on seed fate and seedling performance in two rodent-dispersed tree species in rain forest in French Guiana. *Journal of Ecology*, **85**, 693–703.
- Fragoso, J.M.V. (1997) Tapir-generated seed shadows: scale dependent patchiness in the Amazon rain forest. *Journal of Ecology*, **85**, 519–529.
- Galeano, G. (1991) *Las Palmas de la Region de Araracuara*. Studies on the Colombian Amazon 01 (ed. by J.G. Saldarriaga and T. van der Hammen). Tropenbos-Colombia, Bogota, 180pp.
- Gartland, J.S., Newbery, D.McC., Thomas, D.W. & Waterman, P.G. (1986) The influence of topography and soil phosphorus on the vegetation of Korup Forest reserve, Cameroun. *Vegetatio*, **65**, 131–148.
- Gentry, A.H. & Dodson, C. (1987) Diversity and phytogeography of neotropical vascular epiphytes. *Annals of the Missouri Botanical Garden*, **74**, 205–233.
- de Granville, J.-J. (1989) La distribución de las palmas en la Guyana francesa. *Acta Amazónica*, **19**, 115–138.
- Grubb, P.J. (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **53**, 107–145.
- Haffer, J. (1969) Speciation in Amazonian forest birds. *Science*, **165**, 131–137.
- Harms, K., Condit, R., Hubbell, S.P. & Foster, R.B. (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology*, **89**, 947–959.
- Henderson, H., Galeano, G. & Bernal, R. (1995) *Field guide to the palms of the Americas*. Princeton University Press, Princeton.
- Henry, O. (1999) Frugivory and the importance of seeds in the diet of the orange-rumped agouti (*Dasyprocta leporina*) in French Guiana. *Journal of Tropical Ecology*, **15**, 291–300.
- Hubbell, S.P. (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, **203**, 1299–1309.
- Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Monographs in population biology. Princeton University Press, Princeton.
- Hubbell, S.P. & Foster, R.B. (1986) Biology, chance and history and the structure of tropical rain forest tree communities. *Community Ecology* (ed. by J. Diamond and T.J. Case), pp. 314–329. Harper & Row, New York.
- Jansen, P.A. & Forget, P.M. (2001) Scatter hoarding and tree regeneration. *Nouragues: dynamics and plant–animal interactions in a neotropical rainforest* (ed. by F. Bongers, P. Charles-Dominique, P.M. Forget & M. Théry), pp. 275–288. Kluwer Academic Publisher, Dordrecht.
- Jansen, P.A., Bartholomeus, M., Bongers, F., Elzinga, J.A., Den Ouden, J. & Van Wieren, S.E. (2002) The role of seed size. Dispersal by

- a scatter-hoarding rodent. *Seed dispersal and frugivory: ecology, evolution and conservation* (ed. by D.J. Levey, W.R. Silva and M. Galetti), pp. 209–225. CABI Publishing, Wallingford.
- Julliot, C. (1997) Impact of seed dispersal of red howler monkeys *Alouatta seniculus* on the seedling population in the understorey of tropical rain forest. *Journal of Ecology*, **85**, 431–440.
- Kahn, F. (2000) Two Amazonian palm species revalidated: *Astrocaryum farinosum* and *A. Sociale*. *Palms*, **45**, 29–36.
- Kahn, F. & de Granville, J.-J. (1992) *Palms in forest ecosystems of Amazonia*. Ecological Studies 95. Springer-Verlag, New York.
- Kahn, F. & Millán, B. (1992) *Astrocaryum* (Palmae) in Amazonia, a preliminary treatment. *Bulletin de l'Institut Français d'Etudes Andine*, **21**, 459–531.
- Kiltie, R.A. (1981) Distribution of palm fruits on a rain forest floor: why white-lipped peccaries forage near objects. *Biotropica*, **13**, 234–236.
- Nelson, B.W., Ferreira, C.A.C., da Silva, M.F. & Kawasaki, M.L. (1990) Endemism centres, refugia and botanical collection density in Brazilian Amazonia. *Nature*, **345**, 714–716.
- Nelson, B.W., Karpos, V., Adams, J.B., Oliveira, W.J., Braun, O.P.G. & do Amaral, I.L. (1994) Forest disturbance by large blowdowns in the Brazilian Amazon. *Ecology*, **75**, 1994.
- Pintaud, J.-C., Second, G. & Kahn, F. (in press). Species relationships and species concepts in Amazonian *Astrocaryum* (Palmae): an evaluation based on cladistic and phenetic analyses of morphological and DNA (AFLP) characters. *American Journal of Botany*, in press.
- Pitman, N.C.A., Terborgh, J., Silman, M.R. & Nuñez, V.P. (1999) Tree species distribution in an upper Amazonian forest. *Ecology*, **80**, 2651–2661.
- Poncy, O., Riéra, B., Larpin, D., Belbenoit, P., Jullien, M., Hoff, M. & Charles-Dominique, P. (1998) The permanent field research station 'Les Nouragues' in the tropical forest of French Guiana: current projects and preliminary results on tree diversity, structure and dynamics. *Measuring and Monitoring Tropical Forest Diversity: a Network of Biodiversity Plots*. Man and the biosphere series (ed. by F. Dallmeier and J. Comiskey), pp. 398–414. UNESCO and Parthenon Publishing Group, Carnforth, Lancashire.
- Portnoy, S. & Willson, M.F. (1993) Seed dispersal curves: behavior of the tail of the distribution. *Evolutionary Biology*, **7**, 25–44.
- Poulsen, A.D. & Balslev, H. (1991) Abundance and cover of ground herbs in an Amazonian rain forest. *Journal of Vegetation Science*, **2**, 315–322.
- Prance, G.T. (1973) Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. *Acta Amazônica*, **3**, 5–28.
- Riéra, B. & Alexandre, D. (1988) Surface des chablis et temps de renouvellement en forêt dense tropicale. *Acta Oecologica*, **9**, 211–220.
- Sabatier, D. & Prévost, M.F. (1987) *Une forêt à cacaoiers sauvages sur le haut-camopi, en Guyane Française*. ORSTOM, Paris.
- Sist, P. (1989a) Peuplement et phénologie des palmiers en forêt guyanaise (Piste de Saint-Elie). *Revue d'Ecologie (Terre et Vie)*, **44**, 113–151.
- Sist, P. (1989b) Demography of *Astrocaryum sciophilum*, an understorey palm of French Guiana. *Principes*, **33**, 142–151.
- ter Steege, H. & Hammond, D.S. (2001) Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology*, **82**, 3197–3212.
- Svenning, J.-C. (1999) Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology*, **87**, 55–65.
- Tardy, C. (1998) Paléoincendies naturels, feux anthropiques et environnements forestiers de Guyane Française, du Tardiglaciaire à l'Holocène récent, *Approches Chronologique et Anthracologique*. Thèse de Doctorat, Université de Montpellier II.
- Tomlinson, P.B. (1990) *The structural biology of palms*. Clarendon Press, Oxford.
- Tuomisto, H. (1998) What satellite imagery and large-scale field studies can tell about biodiversity patterns in Amazonian forests. *Annals of the Missouri Botanical Garden*, **85**, 48–62.
- Turchin, P. (1998) *Quantitative analysis of movement*. Sinauer, Sunderland, MA.
- Van der Steege, J.G. (1983) *Bladproductie En Bladfytomassa Van Een Aantal Palmsoorten Van Het Tropisch Regenbos Van Suriname*. CELOS rapporten no. 138. Universiteit van Suriname, Paramaribo.
- Van Rosmalen, M.G.M. (1985) *Fruits of the Guianan flora*. Institute of Systematic Botany, Utrecht University, Drukkerij Veenman B.V., Wageningen.
- Wessels Boer, J.G. (1965) *The indigenous palms of Suriname*. E.J. Brill, Leiden, the Netherlands.
- Willson, M.F. (1993) Dispersal mode, seed shadows, and colonization patterns. *Vegetatio*, **107/108**, 261–280.
- Worbes, M. (1989) Growth rings, increment and age of trees in inundation forests, savannas and a mountain forest in the neotropics. *IAWA (International Association of Wood Anatomists) Bulletin*, **10**, 109–122.
- Zar, J.H. (1996) *Biostatistical Analysis*, 3rd edn. Prentice Hall, Englewood Cliffs.

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