

FRUIT CONSUMPTION, SEED DISPERSAL AND SEED FATE IN
THE VINE *STRYCHNOS ERICHSONII* IN A FRENCH GUIANAN FOREST

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RÉSUMÉ

La consommation des fruits et la dissémination des graines ont été analysées chez trois individus de la liane *Strychnos erichsonii* (Loganiaceae) en forêt mature de Guyane française, pendant la saison de production minimale en fleurs et fruits. Cinq espèces consommatrices, oiseaux ou mammifères diurnes ou nocturnes, ont été observées, alors qu'un rongeur terrestre a été capturé dans des pièges appâtés avec de la pulpe de fruits ou des graines de *S. erichsonii*. Un mammifère diurne et un nocturne ont dispersé les graines à grande distance. Les frugivores arboricoles consommaient les fruits à mesure de leur apparition, et mangeaient également des fruits immatures. L'utilisation de collecteurs a montré que le taux de prélèvement de fruits était plus élevé la nuit chez les lianes les plus productives (productivité « instantanée »). Plus des deux-tiers des graines échantillonnées sur des transects jusqu'à 30 m du pied-mère étaient mortes ou parasitées, sans qu'une relation claire ait pu être établie avec leur localisation (sous ou au-delà de la couronne). La densité de graines chutait dans les premiers mètres à partir du pied-mère, mais restait non négligeable jusqu'à 15 m de la couronne sur certains transects. Les quelques plantules trouvées étaient réparties indépendamment de leur position sous ou au-delà de la couronne. Une mortalité élevée des graines et un faible nombre en même temps qu'un renouvellement rapide des plantules sous et à proximité du pied-mère suggèrent que la dispersion des graines à grande distance est primordiale pour la régénération de la plante. La dispersion à grande distance semble assurée par un petit nombre d'espèces variées. Par sa fructification régulière pendant la période de disponibilité minimale en fleurs et fruits et par sa place privilégiée dans le régime alimentaire de plusieurs mammifères frugivores, *S. erichsonii* constitue probablement une ressource importante pour ces espèces pendant la saison de faible disponibilité alimentaire.

SUMMARY

Fruit removal and seed dispersal of three individuals of the vine *Strychnos erichsonii* (Loganiaceae) were investigated in a mature forest of French Guiana, during the season of minimal flower and fruit production. Five visitor species, birds and diurnal or nocturnal arboreal mammals, were observed, while one terrestrial rodent was collected in traps baited with *S. erichsonii* seeds or fruit pulp. One diurnal and one nocturnal mammal dispersed seeds at long distance. Arboreal frugivores consumed fruits as soon as they became ripe and also ate unripe fruits. Fruit-traps revealed a higher fruit removal during the night for the two more productive vines ('instantaneous' productivity). More than two-thirds of the seeds checked along transects until 30 m for the parent plant were dead or infested, without obvious relationship with the seed localisation (under or beyond the crown). However, the proportion

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of intact vs dead/infested seeds beyond the crown was higher for the more productive plant ('overall' productivity), suggesting predator satiation. Seed density decreased sharply in the first meters from the parent plant, but remained noticeable until 15 m after the crown on some transects. Seedlings were very few and distributed independantly of their position under or beyond the crown. A high seed mortality, a low number and a high turnover of seedlings under and in the vicinity of the parent plant suggest a crucial importance of long distance dispersal for the plant recruitment. Seed dispersal seems to be performed by a small number of varied species. Based on its regular fruiting period during the season of flower and fruit scarcity, and its large place in the diet of several frugivores mammals, *S. erichsonii* is probably an importante resource for these species during the season of food scarcity.

INTRODUCTION

The advantages of seed dispersal or, in other words, the relationships between seed rain and seedling recruitment in a plant species, have been widely debated since the formulation of the 'Janzen-Connell Model'. Both Janzen (1970) and Connell (1971) proposed that juveniles (seeds or seedlings) suffer higher mortality near the parent tree, because high densities of juveniles attract herbivores, seed-eating insects or rodents, and pathogens, or enhance competition between seedlings. Hubbell (1980) reinterpreted Janzen's graphical model and hypothesized, on the contrary, that recruitment reaches its maximum at the parent tree. Seed dispersal was also assumed to allow colonization of sites favourable for seedling establishment, whether these sites are predictable or not in space and time (Howe & Smallwood, 1982). Subsequent field tests of these hypotheses revealed contrasting conclusions (e.g. Fleming & Heithaus, 1981; Clark & Clark, 1984; Forget, 1989, 1991; Burkey, 1994), resulting from the variety and the complexity of the plants and animals traits involved and of their interaction patterns.

One interaction step concerns fruit selection by frugivores. Studies on fruit selection at the plant species level are numerous, and several point out that fruit choice may be influenced by numerous co-occurring factors (Martin, 1985; Janson *et al.*, 1986; Leighton, 1993). Conversely, those few studies performed at the plant individual level point out that patterns of fruit selection and seed dispersal may also greatly vary from one plant to another within the same species. For instance, the number of visits, the number of fruits eaten, or the proportion of fruits removed on a single plant by a 'feeding assemblage', may be influenced by the crop size (Howe & Vande Kerckove, 1979; Jordano, 1989), the mean pulp/seed ratio (Howe & Vande Kerckove, 1980; Jordano, 1984), the vicinity of fruiting conspecifics (Manasse & Howe, 1983; Sargent, 1990), the number of seeds per fruit (Hedge *et al.*, 1991) or the rate of infestation by insects (Manzur & Courtney, 1984). Ultimately, the reproductive success of an individual plant may considerably vary according to its 'fruiting environment' or crop characteristics.

However, none of these studies have attempted to link at the individual plant level the overall impact of fruit eaters and seed dispersers and the composition of the 'feeding assemblage'. More recently, the accent was paid on the necessity to focuse on the complex 'missing link' between seed dispersal and seedling recruitment, i.e. to link all aspects of a dispersal system, from the behaviour of the dispersers to the establishment of the new reproductive plant (Houle, 1995; Schupp & Fuentes, 1995).

This study presents some traits in plant-animal relationships related to the vine *Strychnos erichsonii* (Loganiaceae). Fruit production, fruit consumption,

identity and impact of frugivores, seed dispersal, seed fate and seedling recruitment were investigated at the individual plant level. The aim was (1) to explore the interaction system between frugivores and a fruiting plant, with an attempt to link disperser behaviour and seedling recruitment, and (2) to examine the influence of the size of the food patch at the individual plant level in fruit use, seed dispersal and seedling establishment.

STUDY SITE, MATERIAL AND METHODS

The study site was located at the Nouragues field Station (4° 05' N, 52° 40' W), about 100 km south of Cayenne, French Guiana. The forest type is primary lowland evergreen rainforest. The topography is characterized by low hills (50-200 m above sea level), separated by small streams. Mean annual rainfall (records 1987-1996 at the field station) is 2 980 mm distributed on 310 days, with great annual variations. This study was conducted in July and August 1991, during the transition between the rainy and the dry (September-November) season. Extensive observations indicated that fruit production was very low during these two months. Flowering was also reduced in July, while the annual peak in flowering started in mid-August (personal observations). These phenological patterns were in accordance with previous censuses conducted in another mature forest in French Guiana (Sabatier, 1985; Julien-Laferrière & Atramentowicz, 1990). The same fruiting pattern was observed during two other annual cycles at the study site, with an order of magnitude of ca. 1 to 5 in the number of fruiting species between the minimum (July-November) and the maximum (January-May; Zhang & Wang, 1995; Julliot, 1996).

Strychnos erichsonii (Loganiaceae) is a large, woody canopy vine that typically grows on well drained soils in 'terra firme' mature forests (Bordenave, in press). The fruit is a subglobose (diameter \times height [mean \pm SD]) $32 \pm 6 \times 28 \pm 6$ mm at maturity, weight 15.6 ± 7.5 g, $N = 29$), indehiscent berry with a variable (range 2-14) number of seeds, more frequently 2 or 4 (54 % occurrence on 48 fruits). The seeds are fairly large and slightly cone-shaped (length \times width \times height $18 \pm 1 \times 14 \pm 2 \times 8 \pm 2$ mm, $N = 10$; weight 1.1 ± 0.2 g, $N = 30$). Ripe fruit is dull yellow and easy to open with teeth. A soft yellow-orange mesocarp covers the inner part of the epicarp and goes on by thin walls between the seeds. The seeds are easy to pull off from the mesocarp. They are covered with a thin (< 1 mm) edible whitish coat. This coat is fairly nutritious, since it contains 6.8 % dry weight in protein ('*Strychnos* sp. 2' of Simmen & Sabatier, 1996; see Atramentowicz, 1988 for comparison).

Observations were conducted on three *S. erichsonii* individuals located about 100 m apart. Five other *S. erichsonii* were located after fruits fallen on the 40 ha surveyed, but their fruit production was over or at the very end of the fruiting period. For this reason, they were not included in the sample. Seven out of the eight individuals were located on an area of 11 ha. Arboreal frugivores were identified and their feeding behaviour and impact on seed dispersal determined by direct observation from under or into the crown of the three vines (17 hrs during 7 diurnal bouts and 32 hrs during 10 nocturnal bouts between July 3 and 22, plus August 12). Observations were concentrated on the first part of the day (0615-1230) and the night (1900-0130). Terrestrial granivores (rodents) were censused by live-trapping with 5 'Tomahawk' live-traps ($41 \times 13 \times 13$ or $53 \times 18 \times 18$ cm)

baited with fruit pulp or seeds, and placed in the vicinity of the fruiting vines. Traps were placed on July 11 and checked each morning until July 28.

Instantaneous (daily or weekly) fruit production was evaluated by gathering fallen fruits in 1 m² collectors made of wire-mesh polyethylene. Five fruit-traps were laid 1 m high on a circle located at mid-distance between the center and the edge of the crown of each vine. Fruits fallen in fruit-traps were collected twice daily at dusk and dawn between 8-28 of July, to evaluate diurnal and nocturnal consumption respectively. They were next collected biweekly until the end of August. Collected fruits and seeds were counted and weighed. Fruit productions were evaluated by extrapolating fresh weight values to the crown areas. The crown areas were measured by mapping the projection area of the crowns to the ground. The use of fruit-traps allowed to evaluate simultaneously the fruit consumption by arboreal frugivores, as observations pointed out that all fallen fruits had been opened in situ by arboreal frugivores, who dropped large fruit pieces representing most part of each fruit eaten, together with part of the seeds. Fruit maturity was estimated externally after fruit size, color, and hardness, unripe fruits were clearly smaller, greener and/or harder than ripe ones, and seeds were difficult to pull off from the mesocarp.

To assess for the patterns of seed distribution and plant recruitment on the vicinity of the parent plant, one transect 1 m wide and 60 m long was delimited from each of the three vines (30 m north and 30 m south from the base of each). As the census was performed during the last part of the fruiting season, the survey involved most of the yearly seed fall, and was used to evaluate the overall fruit productivity including the whole fruiting period. Each seed and seedling was counted by m². Total numbers of seeds and seedlings present were extrapolated by 2 m-wide rings from the base of the parent plant to 30 m distance. The state of the seeds (presumed alive, empty, infested by insect larvae or fungi, or germinating) was recorded from external observation. The seedlings were numbered with white plastic labels. The transects were censused in August 1991, at the end of the fruiting period. Seedlings were re-censused in March and November 1993.

To confirm seedling determination and evaluate the germination time, 25 freshly fallen seeds were collected shortly before the end of the field study, placed in a heated and lighted with a 12L/12D plant-light greenhouse at the laboratory, and checked each two weeks during 8 months. Seventeen seeds germinated, 11 of which produced seedlings. The first two germinations began to occur one to two weeks after seed sowing, the next nine four to six weeks after sowing. The last germination began to occur 20 weeks after sowing.

RESULTS

FRUGIVORE SPECIES AND THEIR ROLE IN SEED DISPERSAL

Three frugivore species were seen visiting *S. erichsonii* for fruits during the day and two during the night (Table I).

Observation of feeding and control of fruit parts fallen on the ground during the visits showed that both Kinkajous (*Potos flavus*) and Capuchin Monkeys (*Cebus apella*) opened the fruits with teeth and swallowed the seeds intact, but dropped part of the seeds during fruit handling. During the capuchin visits, only

TABLE I

Diurnal and nocturnal arboreal consumers of fruits of three Strychnos erichsonii. The duration of the observations is indicated in parentheses.

Species	# of visits	# of individuals	% of observation time present	# of visits with seed fall and/or defecation	# of visits with unripe fruits eaten
Day (17.3 hrs)					
<i>Deroptylus accipitrinus</i> (Red-fan Parrot)	3	11	19.7	2	1
<i>Cebus apella</i> (Capuchin Monkey)	2	6	2.4	2	1
<i>Trogon melanurus</i>	1	1	1.1	?	?
Night (31.8 hrs)					
<i>Potos flavus</i> (Kinkajou)	7	11	35.9	6	3
<i>Caluromys philander</i> (Bare-tailed Woolly Opossum)	2	2	4.6	?	0

unripe to nearly ripe fruits were available and eaten by the monkeys. During 3 out of 7 visits, kinkajous fed on unripe fruits, and on nearly ripe fruits during one. Moreover, during 6 visits, *P. flavus* defecated *S. erichsonii* seeds while feeding in the vine. Two individuals radio-tracked during this study visited one vine at 4 occasions and defecated seeds 5 times at long distance, at 70, 160, 170, 250 and 250 m from the parent plant. The Red-fan Parrots (*Deroptylus accipitrinus*) opened the fruits and ate the mesocarp as well as the coat surrounding the seeds by gently grasping it with their beak, then dropped the seeds on the ground. Before choosing the fruit, they 'tested' it by gently biting it. If not chosen, the fruit was left intact.

No terrestrial frugivore or granivore was seen using fallen fruits or seeds. However, two Spiny Rats (*Proechimys* sp.) were trapped, one in a trap baited with fruit pulp, the other in a trap baited with seeds. All the fruit pulp and seeds had been eaten when the rodents were checked.

FRUIT PRODUCTION AND CONSUMPTION BY ARBOREAL FRUGIVORES

This study took place during the decreasing phase of fruit production (vine 1) or at the end of the fruiting period (vines 2 and 3; Fig. 1). Production was much higher in vine 1 at the beginning of the census, but decreased constantly afterwards. Instantaneous fruit production by the three plants tended toward zero at the end of the census.

The mean part of fruits eaten daily and during the night varied between the three vines (Table II). Fall of fruits eaten was more important during the night for the two more productive plants (instantaneous productivity; ANOVA F-test between day and night, N = 17: vine 1, F = 4.75, P < 0.05, vine 2, F = 7.93,

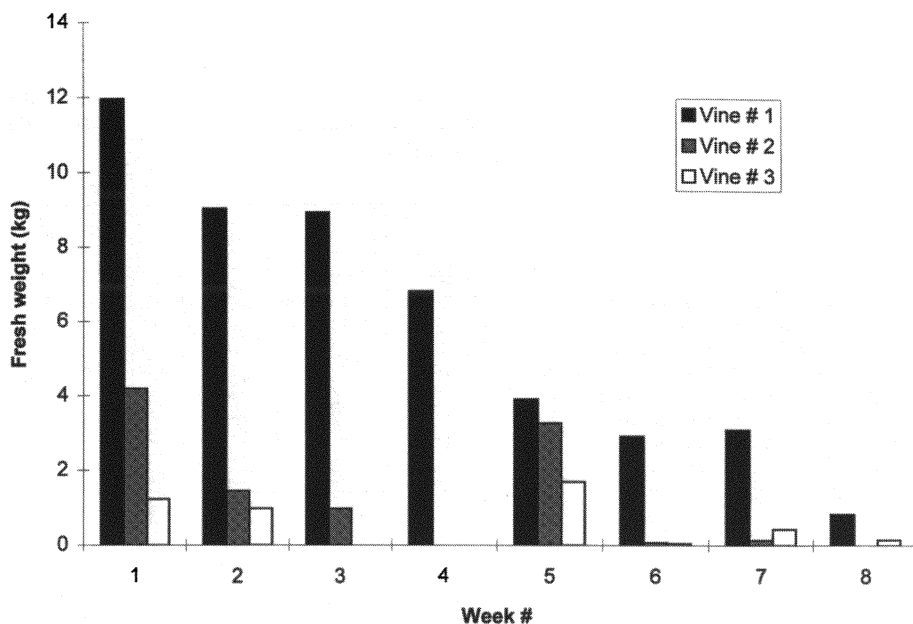


Figure 1. — Relative weekly fruit production and consumption by arboreal frugivores, evaluated from fruit traps in three *Strychnos erichsonii*: 5 m² of collectors, extrapolated to the crown area. The first week is 8-14 July, the last one is 26-31 August.

TABLE II

*Mean diurnal, nocturnal and daily fruit consumption (mean ± SD, kg/day in fresh weight) evaluated by fruit-traps in three S. erichsonii from July 9 to 24. ANOVA F-test, *: P < 0.05, **: P < 0.01.*

Vine #	1	2	3
Consumption by day	0.33 ± 0.45*	0.01 ± 0.01**	0.11 ± 0.20
Consumption by night	0.92 ± 0.88	0.34 ± 0.48	0.04 ± 0.09
Total/24 hrs	1.25 ± 0.95	0.35 ± 0.48	0.15 ± 0.21
Total production	19.49	5.56	2.21

P < 0.01) whereas no significant difference between night and day appeared for the less productive one (vine 3, F = 1.42, P > 0.05). Diurnal consumption was very low for vine 2.

SEED DISTRIBUTION

Among the 3,632 seeds recorded along the transects, 68.5 % were found empty ('dead') or infested by insects or fungi (Table III). The other seeds were

TABLE III

Number and distribution of seeds, germinations, and seedlings on three S. erichsonii, from two transects 30 m long per plant. Numbers in parentheses are percents of the total number of seeds.

Vine #	1	2	3	Total
# of seeds	1,109	468	2,055	3,632
# of intact seeds under the crown	321 (28.9)	141 (30.1)	602 (29.3)	1,064 (29.3)
# of dead/infested seeds under the crown	675 (60.9)	275 (58.8)	1,381 (67.2)	2,331 (64.2)
# of intact seeds beyond the crown	12 (1.1)	16 (3.4)	53 (2.6)	81 (2.2)
# of dead/infested seeds beyond the crown	101 (9.1)	36 (7.7)	19 (0.9)	156 (4.3)
# of germinations under the crown	9	1	1	11
# of germinations beyond the crown	2	1	0	3
# of seedlings under the crown	1	0	0	1
# of seedlings beyond the crown	0	0	1	1

found intact and presumed alive. The proportion of dead/infested vs intact seeds did not differ significantly between the three plants ($\chi^2 = 2.15$, 2 d.f., $P > 0.05$). However, the proportion of dead/infested vs intact seeds was significantly lower beyond than under the crown for vine 1 ($\chi^2 = 57.88$, 1 d.f., $P \ll 0.001$), and higher beyond the crown for vine 3 ($\chi^2 = 22.56$, 1 d.f., $P \ll 0.001$), whereas the proportion of dead/infested seeds did not differ beyond and under the crown for vine 2 ($\chi^2 = 0.20$, 1 d.f., $P > 0.05$).

Fourteen germinations and two seedlings were found along the three transects in 1991. Most germinations were located under the crowns of the three vines (Table III). The two seedlings were not retrieved in March 1993, but 16 new seedlings were censused (7 under the crown of the parent plants, 9 beyond the crown). Among these, respectively one and three were alive in November 1993, while 10 other seedlings (4 under the crowns, 6 beyond the crowns) were censused.

Seed density was higher on the first meters near the base of each plant, then decreased sharply until the edge or a few meters after the edge of the crown (Fig. 2). Seed density tended to zero after 10 to 15 m away from the base of the plant, except on one transect (transect 3 S) where seed density remained noticeable at at least 30 m (Fig. 2). However, the number of seeds, extrapolated to the whole area from transect censuses, was higher within a few (2 to 6) meters from the base of the parent plant. A second peak in seed number occurred at 22 m, and seed number remained noticeable at 30 m distance, both mainly due to vine 3 (Fig. 3).

Extrapolated to an area 30 m radius centered on the base of the parent plant, the proportion of seeds located beyond vs under the crown differed sharply between the three vines ($\chi^2 = 1133.23$, 2 d.f., $P \ll 0.001$), with a larger number of seeds beyond the crown for vine 3, under the crown for vine 1 and mainly for vine 2 (Table IV).

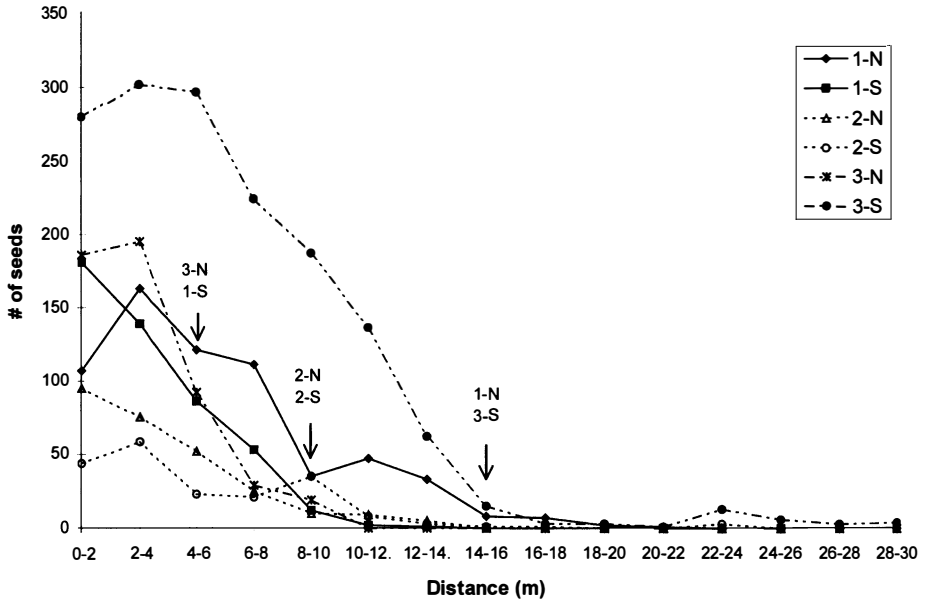


Figure 2. — Seed density (number per 2 m²) in three *S. erichsonii*, from two transects 30 × 1 m laid out from the base of each plant (one north, one south). Arrows point the edge of the crown along each transect.

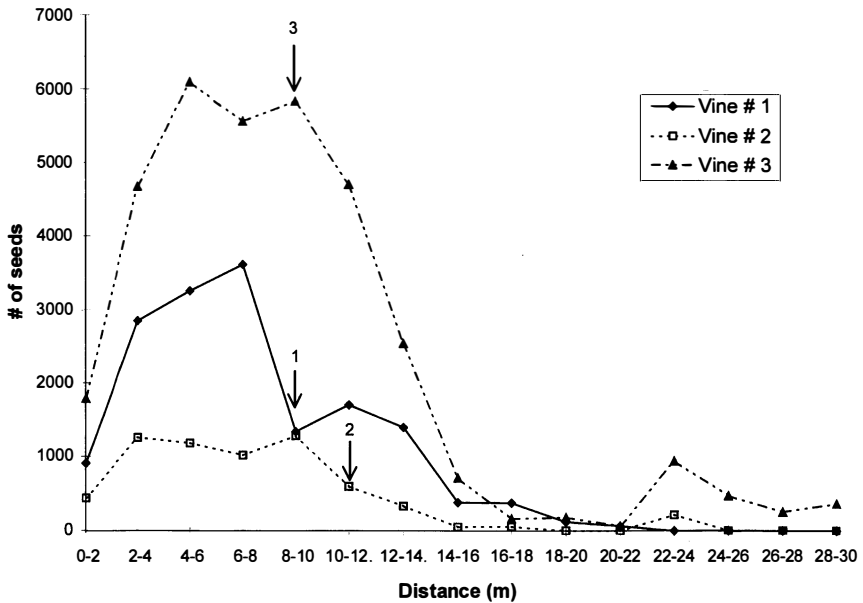


Figure 3. — Seed number as a function of distance in three *S. erichsonii*, extrapolated from two transects 30 × 1 m laid out from the base of each plant (one north, one south). Arrows point the mean position of the edge of the crown of each plant.

TABLE IV

Seed production and seed dispersal in three S. erichsonii, extrapolated from two transects 30 m long and 1 meter wide laid out from the base of each plant (one north, one south). Numbers are rounded to the nearest ten.

Vine #	1	2	3
Total # of seeds	15,960	6,390	34,330
# of seeds under the crown (%)	11,940 (74.8)	5,740 (89.8)	23,950 (69.8)
# of seeds beyond the crown (%)	4,020 (25.2)	650 (10.2)	10,380 (30.2)

DISCUSSION

The survey of frugivores feeding on three *S. erichsonii* revealed a lack of specialisation between the plant and a define taxon of fruit-eaters, and a large spectrum of potential consumers, both diurnal (gregarious monkey and parrot, solitary trogon) and nocturnal (arboreal procyonid and marsupial, terrestrial rodent, all solitary). The main nocturnal consumer, the Kinkajou, dispersed part of the seeds at long distance. Seeds are probably too large to be swallowed by Woolly Opossums (seeds dropped are more than 0.7 cm in diameter; Julien-Laferrière, 1989). One of the two mainly diurnal consumers, the Red-fan Parrot, was not a disperser of *S. erichsonii* seeds, but the parrots dropped the seeds after they had eaten the seed coat. Their handling technique was similar to that used by *Amazona farinosa* and *A. autumnalis* feeding on *Casearia corymbosa* fruits in Costa Rica (Howe, 1977). Visits by capuchin monkeys were scarce and short. Observations suggest, independently of the frequency and duration of visits, that capuchin monkeys have an impact on seed dispersal comparable to that of kinkajous. These peculiar both species drop part of the seeds but disperse the other part at long distance by endozoochory (Julien-Laferrière, 1993; Zhang, 1994).

About one-third of the seeds checked within 30 m from the base of the parent plants were found intact and presumably alive. Nearly all intact seeds were located under the crown, while short dispersal distance (≤ 30 m from the base of the parent plant) did not exceed a few meters from the edge of the crown. The very low number of germinations and seedlings censused on the vicinity of the parents and the high turnover observed in this sample suggest a very high mortality at the first stage of recruitment under and near the parent plant, which is in favour of the Janzen-Connell model. Thus, recruitment in *S. erichsonii* could mainly if not completely be performed through a small part of the seeds being dispersed at long distance by a few species of frugivores such as the diurnal Capuchin Monkey or the nocturnal Kinkajou, which could be preferentially selected according to the size of the food patch.

Direct observations did not reveal obvious differences between the species assemblage using each of the three vines. However, after fruit trap collects, fruit consumption was higher during the night for the more productive plants (instantaneous productivity). This suggests that fruit productivity might be a prominent factor selecting for the 'frugivore assemblage' linked to a given fruiting plant, according to the richness of the feeding site. At a larger time scale, the size of the

food patch seems also to influence the seed dispersal pattern, as the proportion of seeds dispersed away from the crown was higher for the two more productive plants (overall productivity). The underlying process is unclear, but the preferentially selected consumers could have a different behaviour with regards to seed dispersal, which could lead to a different pattern of seed distribution. Moreover, the proportion of intact vs dead/infested seeds located beyond the crown was higher for the more productive vine (overall productivity), suggesting that predator satiation has occurred for this individual (Janzen, 1971; Kelly *et al.*, 1992; Greig, 1993).

The transition between the rainy and the dry season, with minimal production of fruits and nectar, may be a season of food shortage for many frugivores (Terborgh, 1986). At the time of this study, a critical level in fruit production is suggested by the fact that all *S. erichsonii* fruits collected in fruit traps were eaten, and that kinkajous frequently ate unripe fruits, which was never observed until now (Julien-Laferrière, 1989, 1993). A comparable shift was observed in the Long-tailed Manakin *Chiroxiphia linearis* during a season of unusual fruit scarcity in Costa Rica, leading to a considerable increase in ingestion of less nutritional unripe fruits by the birds (Foster, 1977). After extensive observations on several years (1991 and 1993: S.Y. Zhang, pers. comm.; 1992: Simmen & Sabatier, 1996; 1995: F. Bayart, pers. comm.), *S. erichsonii* regularly bears fruits at this season at the Nouragues site. Ripe fruits of *S. erichsonii* represent an important food resource for several frugivores at this season. This species was the sixth out of 134 more frequently used for fruits by a troop of capuchins observed during 19 months at the study site, and was used from June to August (Zhang, 1994). It was also the first ranking out of 8 species used for fruits by Spider Monkeys (*A. paniscus*) in June and July ('*Strychnos* sp. 2' of Simmen & Sabatier, 1996), and the first out of 5 species used for fruits by a kinkajou radio-tracked in the first half of August 1991 (Julien-Laferrière, 1993). In French Guiana, spider monkeys are mainly frugivorous year long (Guillotin *et al.*, 1994; Simmen & Sabatier, 1996). The same is true for kinkajous, except at the beginning of the dry season (August-September), when fruits are scarce and flowers abundant, and kinkajous shift their diet to feed on nectar (Charles-Dominique *et al.*, 1981; Julien-Laferrière, 1993; 1999). The diet of capuchin monkeys is more flexible and the part of insects and leaves may be high at some seasons, but fruits are constantly dominant or widely represented (Guillotin *et al.*, 1994; Zhang, 1995; Simmen & Sabatier, 1996). Spider monkeys, capuchin monkeys and kinkajous are mobile species that can move rapidly from one fruiting site to another on a large activity area (spider monkey: 80 ha [Simmen & Sabatier, 1996], capuchin monkey: 75 to 95 ha and 2 km/day, [Simmen & Sabatier, 1996; Zhang, 1995], kinkajou: 40 ha and 2.5 km/day [Julien-Laferrière, 1993]; data for the study site and the same or a comparable season). Because of its regular fruit production during the season of fruit scarcity and the importance of this food resource in the diet of several frugivorous mammals, *S. erichsonii* is probably an essential resource for these mammals during this season on the study site.

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REFERENCES

- ATRAMENTOWICZ, M. (1988). — La frugivorie opportuniste de trois marsupiaux didelphidés de Guyane. *Rev. Ecol. (Terre Vie)*, 43: 47-57.
- BORDENAVE, B. (in press). — The Loganiaceae Family. In: S. Mori (ed.), *Guide to the vascular plants of Central French Guiana*. Vol. 2. Memoirs of the New York Botanical Garden, New York.
- BURKEY, T.V. (1994). — Tropical tree species diversity: a test of the Janzen-Connell model. *Oecologia*, 97: 533-540.
- CHARLES-DOMINIQUE, P., ATRAMENTOWICZ, M., CHARLES-DOMINIQUE, M., GÉRARD, H., HLADIK, A., HLADIK, C.-M. & PRÉVOST, M.-F. (1981). — Les mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: inter-relations plantes - animaux. *Rev. Ecol. (Terre Vie)*, 35: 341-435.
- CLARK, D.A. & CLARK, D.B. (1984). — Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *Am. Nat.*, 124: 769-788.
- CONNELL, J.H. (1971). — On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pp. 298-310, in: P.J. Den Boer & G.R. Gradwell (eds), *Dynamics of population*. Centre for Agricultural Publishing and Documentation, Wageningen.
- FLEMING, T.H. & HEITHAUS, E.R. (1981). — Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica*, 13 (Suppl.): 45-53.
- FORGET, P.M. (1989). — La régénération naturelle d'une espèce autochore de la forêt guyanaise: *Eperua falcata* Aublet (Cesalpiniaceae). *Biotropica*, 21: 115-125.
- FORGET, P.M. (1991). — Comparative recruitment patterns of two non-pioneer canopy tree species in French Guiana. *Oecologia*, 85: 434-439.
- FOSTER, M.S. (1977). — Ecological and nutritional effects of food scarcity on a tropical frugivorous bird and its fruit source. *Ecology*, 58: 73-85.
- GREIG, N. (1993). — Predispersal seed predation on five *Piper* species in tropical rainforest. *Oecologia*, 93: 412-420.
- GUILLOTIN, M., DUBOST, G. & SABATIER, D. (1994). — Food choice and food competition among the three major primate species in French Guiana. *J. Zool. Lond.*, 233: 551-579.
- HEDGE, S.G., GANESHIAH, K.N. & UMA SHAANKER, R. (1991). — Fruit preference criteria by avian frugivores: their implications for the evolution of clutch size in *Solanum pubescens*. *Oikos*, 60: 20-26.
- HOULE, G. (1995). — Seed dispersal and seedling recruitment: the missing link. *Ecoscience*, 2: 238-244.
- HOWE, H.F. (1977). — Bird activity and seed dispersal of a tropical wet forest tree. *Ecology*, 58: 539-550.
- HOWE, H.F. & SMALLWOOD, J. (1982). — Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.*, 13: 201-228.
- HOWE, H.F. & VANDE KERCKOVE, G.A. (1979). — Fecundity and seed dispersal of a tropical tree. *Ecology*, 60: 180-189.
- HOWE, H.F. & VANDE KERCKOVE, G.A. (1980). — Nutmeg dispersal by tropical birds. *Science*, 210: 925-927.
- HUBBELL, S.P. (1980). — Seed predation and the coexistence of tree species in tropical forests. *Oikos*, 35: 214-229.
- JANSON, C.H., STILES, E.W. & WHITE, D.W. (1986). — Selection on plant fruiting traits by brown capuchin monkeys: a multivariate approach. Pp. 83-92, in: A. Estrada and T.H. Fleming (eds), *Frugivores and seed dispersal*. Dr W. Junk Publishers, Dordrecht.
- JANZEN, D.H. (1970). — Herbivores and the number of tree species in tropical forests. *Am. Nat.*, 104: 501-528.
- JANZEN, D.H. (1971). — Seed predation by animals. *Annu. Rev. Ecol. Syst.*, 2: 465-492.
- JORDANO, P. (1984). — Seed weight variation and differential avian dispersal in blackberries *Rubus ulmifolius*. *Oikos*, 43: 149-153.
- JORDANO, P. (1989). — Pre-dispersal biology of *Pistacia lentiscus* (Anacardiaceae): cumulative effects on seed removal by birds. *Oikos*, 55: 375-386.
- JULIEN-LAFERRIÈRE, D. (1989). — *Utilisation de l'espace et des ressources alimentaires chez Caluromys philander (Marsupialia, Didelphidae) en Guyane française. Comparaison avec Potos flavus (Eutheria, Procyonidae)*. Doctoral thesis. Paris 13 University. Villetaneuse.
- JULIEN-LAFERRIÈRE, D. (1993). — Radio-tracking observations on ranging and foraging patterns by kinkajous (*Potos flavus*) in French Guiana. *J. Trop. Ecol.*, 9: 19-32.
- JULIEN-LAFERRIÈRE, D. (1999). — Foraging strategies and food partitioning in the Neotropical mammals *Caluromys philander* and *Potos flavus*. *J. Zool., Lond.*, 247: 71-80.

- JULIEN-LAFERRIÈRE, D. & ATRAMENTOWICZ, M. (1990). — Feeding and reproduction of three didelphid marsupials in two neotropical forests (French Guiana). *Biotropica*, 22: 404-415.
- JULLIOT, C. (1996). — Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rainforest. *Am. J. Primat.*, 40: 261-282.
- KELLY, D., MCKONE, M.J., BATCHELOR, K.J. & SPENCE, J.R. (1992). — Mast seeding of *Chionocloa* (Poaceae) and pre-dispersal seed predation by a specialist fly (*Diptoxa*, Diptera: Chloropidae). *New Zeal. J. Bot.*, 30: 125-133.
- LEIGHTON, M. (1993). — Modeling dietary selectivity by Bornean orangutangs: evidence for integration of multiple criteria in fruit selection. *Int. J. Primat.*, 14: 257-313.
- MANASSE, R.S. & HOWE, H.F. (1983). — Competition for dispersal agents among tropical trees: influences of neighbors. *Oecologia*, 59: 185-190.
- MANZUR, M.I. & COURTNEY, S.P. (1984). — Influence of insect damage in fruits of hawthorn on bird foraging and seed dispersal. *Oikos*, 43: 265-270.
- MARTIN, T.E. (1985). — Resource selection by tropical frugivorous birds: integrating multiple interactions. *Oecologia*, 66: 563-573.
- SABATIER, D. (1985). — Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. *Rev. Ecol. (Terre Vie)*, 40: 289-320.
- SARGENT, S. (1990). — Neighborhood effects on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology*, 71: 1289-1298.
- SIMMEN, B. & SABATIER, D. (1996). — Diets of some French Guianan primates: food composition and food choice. *Int. J. Primat.*, 17: 661-693.
- SCHUPP, E.W. & FUENTES, M. (1995). — Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience*, 2: 267-275.
- TERBORGH, J.A. (1986). — Community aspects of frugivory in tropical forests. Pp. 371-384, in: A. Estrada and T.H. Fleming (eds). *Frugivores and seed dispersal*. Dr W. Junk Publishers. Dordrecht.
- ZHANG, S.Y. (1994). — *Utilisation de l'espace, stratégies alimentaires et rôle dans la dissémination des graines du singe capucin Cebus capucinus (Cebidae, Primate) en Guyane française*. Doctoral thesis, Paris 6 University. Paris.
- ZHANG, S.Y. (1995). — Activity and ranging patterns in relation to fruit utilization by brown capuchins (*Cebus apella*) in French Guiana. *Int. J. Primat.*, 16: 489-507.
- ZHANG, S.Y. & WANG, L.X. (1995). — Comparison of three fruit census methods in French Guiana. *J. Trop. Ecol.*, 11: 281-294.