

Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana

PIERRE-MICHEL FORGET

*Muséum national d'Histoire naturelle, Laboratoire d'Écologie Générale, CNRS URA 1183,
4 Avenue du Petit Château, F-91800 Brunoy, France
E-mail: forget@mnhn.fr*

ABSTRACT. Experiments were performed to investigate monthly variations in seed fate of *Carapa procera* (Meliaceae), a rodent-dispersed subcanopy tree species in French Guiana. A total of 600 thread-marked seeds were placed on the ground in mature forest under 20 adult trees during different months (March, April and May 1991) of the species' fruiting season. In 1991 the seed crop reached 1536 seeds in the study area, with a majority of seeds being produced in March and May. On average, seed removal rate steadily increased from March (23%) to May (96%). Of the seeds removed, the proportion cached almost doubled between March (28%)–April (25%) and May (48%), whereas the proportion eaten (gnawed) steadily declined between March (43%) and May (9%). Approximately 75–100% seed removal was therefore associated with intense scatterhoarding and low seed predation, especially in May. Greater seed dispersal rates occurred during the late wet season when fruit diversity decreased but when overall fruit biomass peaked because of fruiting occurrence of large-seeded species. The seasonal hoarding behaviour of rodents is discussed.

KEY WORDS: *Carapa procera*, French Guiana, rainforest, rodents, scatterhoarding, seed dispersal, seed predation.

INTRODUCTION

For decades, studies of frugivores and seed dispersers in the Neotropics focused on birds, bats, primates and larger terrestrial vertebrates that ingest and defecate or regurgitate seeds (see Howe 1986), while the role of fruit-eating rodents was less studied. Although the tendency of Neotropical rodents to hoard seeds was acknowledged (Morris 1962; Smythe 1970, 1978), it was rarely investigated in detail (Larson & Howe 1987, Meritt 1985, Smith 1974). Undeniably, when they consume or disperse seeds, rodents (Dasyproctidae) have a crucial effect on the recruitment of some plant species (Forget 1990, 1991a, 1994). This has great consequences for forest dynamics (Leigh *et al.* 1993, Terborgh 1992) and ultimately the maintenance of plant diversity (Janzen 1970, 1971). Hence, seed dispersal by Dasyproctidae, mainly agoutis (*Dasyprocta* spp.) and acouchies (*Myoprocta* spp.) (Emmons & Feer 1990), deserves more attention.

Seasonal changes in food removal and caching is commonly observed among animals, but the environmental and/or physiological factors that may regulate such changes are still unclear (Hurly & Robertson 1990, Vander Wall 1990). In temperate regions, many studies have independently documented the effects of the environmental and internal states of animals (often captive ones) on seasonal variation of food eating and hoarding; the former has been shown to have effects on the latter (reviewed by Vander Wall 1990). Large-seeded species that are strictly dependent on *Dasyproctidae* for dispersal tend to fruit seasonally and synchronously, either annually or every few years, generally in the wet season when the number of species fruiting in the community is decreasing (Foster 1982, Sabatier 1985, Smythe 1970). In theory, such animal-dispersed large-seeded species would be selected to fruit when rodents are more likely to scatterhoard seeds, in order to increase the chance of survival in comparison to unburied seeds (Sork 1987).

Janzen (1971) proposed that food abundance affects seasonal rate of caching, and therefore influences whether a rodent is a predator or a dispersal agent. On Barro Colorado Island, Panama, Smythe (1978) reported that *Dasyprocta punctata* hoarded considerably more seeds than they ate during the season of food abundance (May–August). I (Forget 1990) observed that removal of *Vouacapoua americana* (Caesalpiniaceae) seeds progressively increased during the fruiting season, from mid-April to the beginning of May, and that a large proportion of seeds removed had been cached by rodents in May. Scatterhoarding behaviour is certainly very complex, and many factors, such as rodent density, season, food abundance and sexual activity, may interact (Forget 1990, Hallwachs 1986, Rankin 1978, Vander Wall 1990). Consequently, throughout the wet season, seed dispersal may vary from month to month due to changes in internal state (e.g. hunger and deprivation) of the rodents (dispersers/predators) and/or environmental factors. Without preliminary reference data, it therefore appears misleading to make assumptions concerning the fate of removed seeds. Low seed removal rate could be just as effective in terms of the number of seeds cached as high seed removal rate if more seeds were consumed instead of being cached.

This study was designed to investigate short-term variation in harvesting, eating and hoarding rates of *Carapa procera* (Meliaceae) seeds by scatterhoarding rodents. The objectives of this study were to test the hypotheses: (1) that seed removal rates may widely change on a short-term scale throughout the fruiting season, and (2) that removed seeds in May are more likely to be cached than those in April or earlier in the wet season.

STUDY SITE AND SPECIES

Experiments were conducted at the experimental site of Paracou (5° 18' N, 52° 53' W) near Sinnamary, French Guiana, in a reference plot (No. 6) 6.26 ha in area which supports a mature forest (Durrieu de Madron 1994, Schmitt &

Bariteau 1990). The mean annual rainfall is $3040 \pm \text{SD } 627$ mm (unpublished data, CIRAD-Forêt Kourou). Rainfall is bimodal, with peaks in December–January and April–July separated by a short dry season in February and a longer dry season from September to November. Rainfall in 1991 was consistent with the general patterns though drier in May (451 mm) than in June (551 mm)

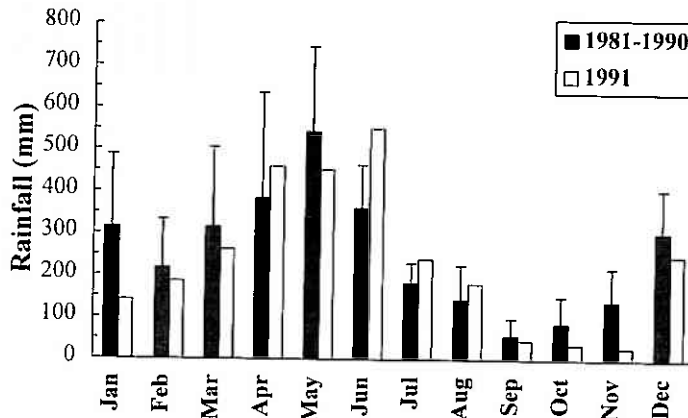


Figure 1. Mean (\pm SD) rainfall between 1981 and 1990, and the 1991 rainfall, at the Paracou Field Station, French Guiana (CIRAD-Forêt, pers. comm.).

(Figure 1). The vegetation at the study plot is characterized by a dense population of *Eperua falcata* and *E. grandiflora* (Caesalpinaceae) trees growing on blocked or poorly drained soil (Barthès 1991). Usually randomly-distributed in mature forest, *Carapa procera* occurs at a density of $c. 7 \text{ ha}^{-1}$ ($n = 41$ trees ≥ 10 cm at DBH in the study plot) in 1990 (CIRAD-Forêt; pers. comm.). *Vouacapoua americana*, another important food resource for rodents (Forget 1990, 1994) occurred at a density of 14 ha^{-1} ($n = 89$ trees); and it fruited in 1991.

C. procera is a non-pioneer subcanopy tree, up to 25 m tall in French Guiana. However, based on features other than the ability to germinate in shade such as tree growth and dynamics, *C. procera* might be considered a light-demanding species or so-called pioneer (Favrichon 1994). *C. procera* trees flower in October–December and fruit in February–June (Sabatier 1985). Enclosed in a dehiscent five-part capsule, seeds (mean number per fruit = 9) are attached to the fruit wall with no apparent organ such as a funicle or aril, which is commonly observed among other family-related genera dispersed by bats or birds and arboreal mammals in New World forests. Large brown quadrangular seeds, 2–5.5 cm in length and weighing on average $18.4 \pm \text{SD } 5.2$ g (range 8.5–30 g; $n = 10$ seeds \times 10 trees), are exposed after the pericarp has opened following primary dispersal on the ground (P.-M. Forget, pers. obs.).

Aside from predation-dispersal by agouti (*Dasyprocta leporina*) and acouchy (*Myoprocta exilis*), these species may also be consumed by other rodents such as spiny rats (*Proechimys* spp.) and squirrels (*Sciurus aestuans*) which eventually carry seeds to dens (see Forget 1991b) and trees (P.-M. Forget, pers. obs.). Also, deer

(*Mazama* spp.) and peccaries (*Tayassu* spp.) are known potential seed-eaters (G. Dubost, pers. comm.; P.-M. Forget, pers. obs.). While the cotyledons may be infested by a moth species when still on the tree, *C. procera* seeds also suffer from post-dispersal infestation by other unidentified moths, such as phyticid larvae on *C. guianensis* when it remains on the ground in the soaking rain (see also MacHargue & Hartshorn 1981, Rankin 1978).

METHODS

Seed production

In March–June 1989 and 1991 the *C. procera* population ($n = 41$) in the study plot was surveyed for reproductive trees. Depending on rainfall regime, trees were visited every two or three days in 1989, and weekly in 1991. The number of seeds produced was estimated from mid-March to late May 1989 and in early June 1991. Fibrous fruit husks do not decompose rapidly and each mature seed leaves a mark in the fruit part. Therefore, counting the number of imprints in fruit parts that were found on the ground below parent trees allowed for an easy and precise estimation of the seed crop. Trees were also visited in early July 1990 and their crop estimated (G. Dubost, pers. comm.). Twenty trees with DBH >17 cm (minimum DBH for fruiting in 1989–1991, see Table 1) and scattered over the entire study plot were then selected as potentially mature trees for the experiment in 1991. Of them, 11 and 18 had been previously observed fruiting in 1989 and 1990, respectively. No seeds were removed from below the parent trees during the experiment.

Seed fate experiment

Before each experiment, *C. procera* seeds were collected outside the study areas, several hundred metres away, and after inspection those obviously infested by moth larvae were rejected. However, it cannot be sure that all seeds were 100% free from insect infestation. On 9 March, 6 April and 7 May 1991, piles of 10 *C. procera* seeds each were placed below the 20 monitored adult trees. The experimental method of marking and analysing seed fate used here conforms to that of a study on another large-seeded species dispersed by rodents (Forget 1992). Fine white nylon thread was passed through each seed leaving a line 50–60 cm long that was easy to retrieve above ground once the seed had been buried or eaten by rodents (Forget 1990). Seed fate was determined by searching for thread-marked seeds that were removed by animals and were retrievable within 10 m from their origin. Seeds were censused weekly for four weeks. The effect of time of dispersal on the mean number of seeds removed per tree after four weeks was tested by one-way repeated-measures analysis of variance. The effect of month on the mean number of seeds found cached, eaten or lost (i.e. not relocated, fate unknown) within four weeks was tested by repeated-measures analysis of covariance taking the number of seeds removed after four weeks as a covariate of each measure of seed fate (cached, eaten or

lost) (Sokal & Rohlf 1981). This approach assumes a linear function between the number of seeds removed and seed fate; the greater the number of seeds removed the greater the number of seeds cached or eaten. Data were square-root transformed. Statistics were performed using the PCSM-plus statistical package V6.3 (PCSM 1994). The low number of marked seeds surviving in caches precluded any long-term survey of fate of naturally buried seeds.

RESULTS

Compared to previous years, 1991 was a poor year for crop production with approximately half of the number of seeds produced in 1989 and 1990 (Table

Table 1. Total seed production in *Carapa procera* at Paracou experimental plot No. 6 in 1989, 1990 and 1991. Trees are ordered by increasing diameter at breast height (DBH). n = Total number of seeds; % expressed as percentage of total seed production per year.

No. Tree	DBH (cm)	1989		1990		1991	
		n	%	n	%	n	%
1	17	0		14	0.4	0	
2	18	0		5	0.1	82	5.3
3	21	0		19	0.5	0	
4	22	0		6	0.2	104	6.8
5	24	0		0		0	
6	26	388	10.9	377	10.2	28	1.8
7	26	0		430	11.6	197	12.8
8	26	0		559	15.1	7	0.5
9	29	0		33	0.9	16	1.0
10	30	1041	29.3	284	7.7	78	5.1
11	30	89	2.5	9	0.2	193	12.6
12	31	326	9.2	358	9.7	0	
13	33	120	3.4	6	0.2	50	3.3
14	33	96	2.7	827	22.3	0	
15	33	0		0		0	
16	34	664	18.7	105	2.8	195	12.7
17	39	118	3.3	13	0.4	107	7.0
18	40	600	16.9	357	9.6	465	30.3
19	40	69	1.9	27	0.7	14	0.9
20	40	43	1.2	277	7.5	0	
Total		3554		3706		1536	

1). Crops were very variable between years among trees ranging, for instance, from <100 to >1000 seeds for tree No. 10. Of the 18 *C. procera* trees previously observed fruiting in 1989–1990, 13 fruited in 1991 (Table 1), mostly in March (67%) and May (30%) whereas in 1989 a majority of seeds fell in April and May (data not shown). The prevalence of seeds falling in March 1991 was essentially due to four trees (Nos 7, 11, 16 and 18 in Table 1), which altogether produced 68% (n = 1050) of all seeds counted.

The number of *C. procera* seeds removed progressively increased from the March to May cohorts, being significantly greater for the May than for the

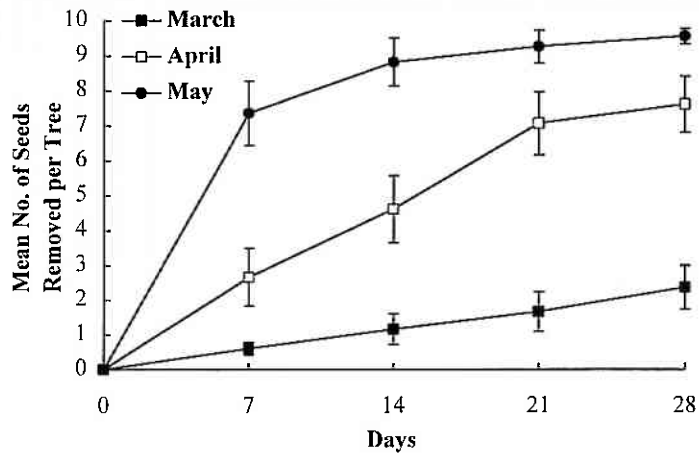


Figure 2. Mean number (\pm SE) of thread-marked *Carapa procera* seeds removed (of 10 seeds deposited per tree each month) within four weeks after seed placement at 20 trees ($n = 200$ seeds per month) in March, April and May 1991 at Paracou Plot No. 6, French Guiana.

April or March cohorts ($F_{2,38} = 45.28$, $P < 0.0001$; Figure 2). The number of seeds removed per tree was significantly correlated with the number of seeds either cached ($r = 0.65$, $df = 1,59$, $P < 0.001$), eaten ($r = 0.38$, $P < 0.005$) or lost ($r = 0.67$, $df = 1,59$, $P < 0.001$). Controlling for the mean number of seeds removed after four weeks, there was a significant effect of the interaction between the mean number of seeds per seed fate category and month (two-way repeated measured ANCOVA: $F_{4,113} = 11.09$, $P = 0.001$). The mean number of retrieved seeds that had been cached or eaten varied between months (Figure 3); and the mean number of cached seeds in the May cohort was significantly greater (one-way repeated measures ANCOVA: $F_{2,37} = 8.99$, $P < 0.0001$) than

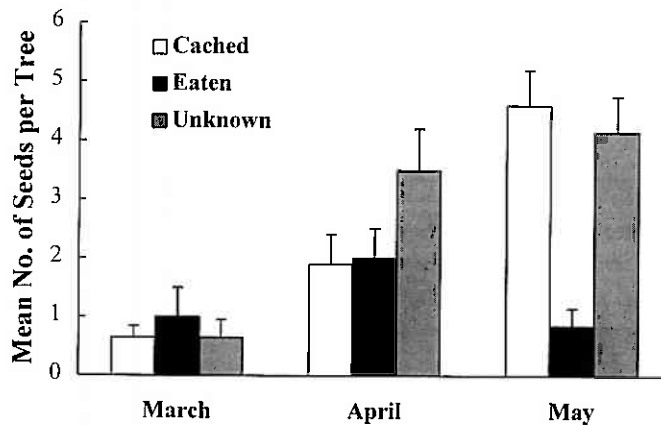


Figure 3. Mean number (\pm SE) of thread-marked *Carapa procera* seeds removed by animals (of 10 seeds deposited per tree each month) and retrieved cached or eaten (within 10 m of the origin), or for which the fate was unknown (i.e. not retrieved <10 m) within four weeks at Paracou Plot No. 6, French Guiana.

those of March or April, while the opposite trend was observed for seeds eaten ($F_{2,37} = 9.03$, $P < 0.0001$). The pair-wise comparisons (*a posteriori* Newman-Keuls test) for the mean adjusted number of seeds cached and eaten show that there was no significant difference between March and April cohorts ($P > 0.05$). Using total seeds removed after four weeks as a covariate, the mean number of seeds whose fates were unknown did not change significantly between months ($F_{2,57} = 0.92$, $P = 0.59$), suggesting that the greater number of seeds lost in April and May (Figure 3) was due to a greater number of seeds removed and most likely cached more than 10 m away (see Forget 1990). On average, seed removal steadily increased from March (23%) to May (96%). Of the seeds removed, the proportion cached almost doubled between March (28%)–April (25%) and May (48%), whereas the proportion eaten (gnawed) steadily declined between March (43%) and May (9%).

Carapa procera seeds that remained undispersed on the ground were subject to heavy insect (moth) infestation and were not subsequently removed by mammals. Of the 96 seeds undispersed in the March cohort and remaining after eight weeks, 13 germinated despite moth infestation of the cotyledons. By October 1991, only five germinating unburied seeds successfully established and survived as seedlings. Despite the germination of 17 out of 46 seeds from the early April cohort, none survived by late May. All undispersed seeds ($n = 9$) from the May replicates were rapidly infected and did not germinate, rotting and drying within four weeks of placement on the floor.

DISCUSSION

The peak fruiting period in the forest of Paracou is March–April (Henry 1994b). This study demonstrated that when food was abundant on the ground, especially in March, freshly fallen seeds often remained undispersed beneath the parent trees. It is possible that, during that period, animals were satiated presumably due to the abundance of fruit produced in that period (see also Sabatier 1985, Zhang & Wang 1995). *Carapa procera* usually fruits between February and June but appeared variable in intensity between trees and months with a peak during the late wet season of April to May, when other large-seeded species are likely to fruit (Sabatier 1985). Nevertheless, in the study plot as well as in pristine forests at the Nouragues (study site of Forget 1990), I observed that hundreds of *C. procera* seeds may be produced by some trees as early as February or March, with their undispersed seeds being easy prey to vertebrates such as peccaries and invertebrate seed-eaters. Given the low seed removal and hoarding rates within this period, March is apparently an inopportune month for intense seed dispersal. Despite the low production of *C. procera* seeds in April 1991, the number of seeds disappearing was largest in April–May at Paracou, just before the onset of a period of food scarcity during June and July in French Guiana (Henry 1994a, Sabatier 1985). Similar rainfall in April (459 mm) and May (451 mm) cannot account for this difference and is not consistent with the

rainfall hypothesis of Hallwachs (1986) to explain the observed increase in seed removal and hoarding rates. The fact that a greater proportion of seeds were removed and cached during the peak of mature fruit production showed that the usual phenological pattern (Sabatier 1985; this study) of *C. procera* fitted well with the period during which a large proportion of seeds would be likely to escape other vertebrate and insect predators due to satiation. The fate of those few seeds that are removed and buried as early as March in comparison to those cached in late April to early May remains unknown.

The high rate of seed removal and hoarding in *C. procera* in May at Paracou is comparable to that observed in *Gustavia superba* (Meliaceae) in June–July on Barro Colorado Island (Panama). Rapid seed disappearance in *C. procera* in French Guiana also agrees with that of *Carapa guianensis* in Trinidad in the late wet season (Rankin 1978). Given the low occurrence of seeds gnawed at the seed piles at both sites, the results of these studies are therefore consistent with Rankin's (1978) hypothesis that seed removal in rodent-dispersed species is not a good estimator of seed predation, rather of seed dispersal. For other large-seeded species harvested and buried by rodents in Central America, hoarding may not be limited to the period of food abundance and may also occur in August–September (late wet season) and in March–April (late dry season) when food is scarce (Forget 1993, Forget *et al.* 1994; Smythe 1970, 1978; P.-M. Forget, pers. obs.). During those transitional periods between seasons, however, high rates of seed removal were often associated with either high predation (Panama) or great hoarding (French Guiana, Trinidad) rates. The results therefore suggest a continuum of seed dispersal rates from 0% to 100% throughout the year at these sites. Effectiveness of seed dispersal by rodents is also likely to be affected by within-year variations.

Why do rodents remove and hoard more seeds of *C. procera* than eating them, during April to May in French Guiana? Recent studies in May 1995 at Nouragues confirmed the results obtained at Paracou for *C. procera*, i.e. 100% seed removal within four weeks correlated with intense hoarding activity and low seed predation by rodents contrasted with high seed consumption by peccaries at the study site (P.-M. Forget, P. Jansen & L. Van der Voort, pers. obs.). Other large-seeded species such as *Vouacapoua americana* (Forget 1990), *Moronobea coccinea* (Clusiaceae) (Forget 1991a) and *Astrocaryum sciophyllum* (Arecaceae) (Sist 1989) have their seeds produced and dispersed by large terrestrial scatterhoarding rodents in April–May in French Guiana. Maybe the key to understanding such a temporal pattern partially lies in the spatial distribution and local density of the community-wide large-seeded species, as well as the spatial foraging pattern and density of rodents over the rodents' home ranges. Depending on food abundance, the level of hunger and/or the hormonal state of the animals may also influence rate of hoarding (see Vander Wall 1990). Furthermore, it is possible that the rodent hoarding behaviour was well marked in April–May because they competed with other ground-dwelling frugivorous vertebrates during a transition period in overall food quantity available between the wet and dry seasons (Smythe 1986).

In natural Guianan field conditions, rodents are unlikely to be nutritionally stressed from March to May. Otherwise, a greater proportion of seeds should have been removed and gnawed in this study. Henry (1994a) found that there were no significant differences in the amount of food ingested by agoutis over time in French Guiana, the greatest quantity being ingested, paradoxically, in August–September when fruit/seed production was lowest. During this latter period, Henry (1994a) also observed that the seed/cotyledon fractions accounted for 70% of dry stomach contents. These results show that when crops of large-seeded species become depleted, agoutis as well as acouchies usually subsist on their buried hoards, supplementing them with other resources available, such as leaves, flowers and animal matter (Dubost 1988, Forget 1992, 1993; Henry 1994a; Smythe 1970, 1978; Smythe *et al.* 1982; P.-M. Forget, pers. obs.).

In the forest, the ratio of the amount of food that can be eaten or cached to the overall food biomass over a rodent's home range is not constant with time (among months) in contrast to conditions under which they are kept in captivity. This changing ratio may influence the level of seed removal and hoarding between March and May in French Guiana. Spatial variation in food abundance also occurs and might possibly affect the level of seed removal and dispersal between trees. This effect was not analysed during this study because it would have required, in addition to the studied tree crop, the measurements of the overall fruit availability during each month from the neighbouring (within *c.* 30 m) *C. procera* trees. More studies are needed to test the hypothesis of the effect of a changing ratio on the level of seed removal and dispersal.

Monthly variation in seed dispersal could also be related, directly or indirectly, to the hormonal state regulating monthly sexual activity and agonistic behaviour (see Vander Wall 1990). Henry (1994b) found that the presence of spermatozoids in seminiferous tubes was lowest in April and May, and that fewer agouti females were pregnant in those months of intermediate food abundance. It is during that period that I observed the greatest seed dispersal rate in *C. procera* (this study) and *Vouacapoua americana* (Forget 1990). Therefore, it is possible to postulate that when rodents do not mate and breed, and when aggression is lowest (Smythe 1978), both male and female agoutis would be hormonal determined to bury seeds over their home range before the season of food scarcity, i.e. starting in June in French Guiana and in August in Panama. Trends are likely to be similar among acouchis (G. Dubost, pers. comm.). The relationship between seed hoarding and rodent reproduction thus requires further investigation on captive animals at both the physiological and behavioural levels.

ACKNOWLEDGEMENTS

This research was supported by a CORDET grant number 88-126 from the Ministère des DOM-TOM to Gérard Dubost (Muséum National d'Histoire Naturelle, MNHN) for a study on food and reproduction of terrestrial game

mammals. Thanks are extended to all staff members at CIRAD-Forêt and INRA in Kourou for their logistic support in the field and for providing us with worthwhile tree maps. I also thank G. Dubost for his valuable help while censusing *C. procera* seeds in 1989, and for communication of the 1990 data. G. Houle, E. G. Leigh, Jr, E. W. Schupp, S. B. Vander Wall and three anonymous reviewers kindly corrected and gave comments and advice on a previous version of the manuscript: many thanks to them.

LITERATURE CITED

- BARTHÈS, B. 1991. Influence des caractères pédologiques sur la répartition spatiale de deux espèces du genre *Eperua* (Caesalpiniaceae) en forêt guyanaise. *Revue d'Écologie (Terre et Vie)* 46:303-320.
- DUBOST, G. 1988. Ecology and social life of the red acouchy, *Myoprocta exilis*; comparisons with the orange-rumped agouti, *Dasyprocta leporina*. *Journal of Zoology (London)* 214:107-123.
- DURRIEU DE MADRON, L. 1994. Mortalité des arbres en forêt primaire de Guyane française. *Bois et Forêts des Tropiques* 239:43-57.
- EMMONS, L. H. & FEER, F. 1990. *Neotropical rainforest mammals. A field guide*. University of Chicago Press, Chicago, USA.
- FAVRICHON, V. 1994. Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplements en forêt guyanaise. *Revue d'Écologie (Terre et Vie)* 49:379-403.
- FORGET, P.-M. 1990. Seed dispersal of *Youacapoua americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana. *Journal of Tropical Ecology* 6:459-468.
- FORGET, P.-M. 1991a. Comparative recruitment patterns of two non-pioneer canopy tree species in French Guiana. *Oecologia* 85:434-439.
- FORGET, P.-M. 1991b. Scatterhoarding of *Astrocaryum paramaca* by *Proechimys* in French Guiana: comparison with *Myoprocta exilis*. *Tropical Ecology* 32:155-167.
- FORGET, P.-M. 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). *Biotropica* 24:408-414.
- FORGET, P.-M. 1993. Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. *Oecologia* 94:255-261.
- FORGET, P.-M. 1994. Recruitment pattern of *Youacapoua americana* (Caesalpiniaceae), a rodent-dispersed tree species in French Guiana. *Biotropica* 26:408-419.
- FORGET, P.-M., MUNOZ, E. & LEIGH, E. G., Jr. 1994. Predation by rodents and bruchid beetles on seeds of *Scheelea* palms on Barro Colorado Island, Panama. *Biotropica* 26:420-426.
- FOSTER, R. B. 1982. The seasonal rhythm of fruitfall on Barro Colorado Island. Pp. 151-172 in Leigh, E. G., Jr, Rand, A. S. & Windsor, D. M. (eds). *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C.
- HALLWACHS, W. 1986. Agoutis *Dasyprocta punctata*: the inheritors of guapinol *Hymenaea courbaril* (Leguminosae). Pp. 119-135 in Estrada, A. & Fleming, T. H. (eds). *Frugivores and seed dispersal*. Dr Junk Publishers, The Hague. 392 pp.
- HENRY, O. 1994a. Caractéristiques et variations saisonnières de la reproduction de quatre mammifères forestiers terrestres de Guyane française: *Oryzomys capito velutinus* (Rodentia, Cricetidae), *Proechimys cuvieri* (Rodentia, Echimyidae), *Dasyprocta leporina* (Rodentia, Dasyproctidae) and *Tayassu tajacu* (Artiodactyle, Tayassuidae). Influence de l'âge, des facteurs environnementaux et de l'alimentation. Thèse de l'Université Paris 7, Paris.
- HENRY, O. 1994b. Saisons de reproduction chez trois Rongeurs et un Artiodactyle en Guyane Française, en fonction des facteurs du milieu et de l'alimentation. *Mammalia* 58:183-200.
- HOWE, H. F. 1986. Seed dispersal by fruit-eating birds and mammals. Pp. 123-189 in Murray, D. R. (ed.). *Seed dispersal*. Academic Press Australia, Sydney.
- HURLY T. A. & ROBERTSON, R. J. 1990. Variation in the food hoarding behaviour of red squirrels. *Behavioral Ecology and Sociobiology* 26:91-97.
- JANZEN, D. H. 1970. Herbivores and the number of species in tropical forests. *American Naturalist* 104:501-528.
- JANZEN, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematic* 2:465-492.
- LARSON, D. & HOWE, H. F. 1987. Dispersal and destruction of *Virola surinamensis* seeds by agoutis: appearance and reality. *Journal of Mammalogy* 68:859-860.

- LEIGH, E. G., Jr, WRIGHT, S. J., HERRE, E. A. & PUTZ, F. E. 1993. The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. *Evolutionary Ecology* 7:76-102.
- MacHARGUE, L. A. & HARTSHORN, G. S. 1981. Seed and seedling ecology of *Carapa guianensis*. *Turrialba* 33:399-404.
- MERITT, D. A. 1985. Palm fruit as a food for central American agoutis, *Dasyprocta punctata*, in the Republic of Panama. *Zoologische Garten* 55:166-168.
- MORRIS, D. 1962. The behaviour of the green acouchi (*Myoprocta pratti*) with special reference to scatter hoarding. *Zoological Society of London Proceedings* 139:701-733.
- PCSM. 1994. Programme conversationnel de statistiques pour les sciences et le marketing. Deltasoftware, Meylan.
- RANKIN, J. M. 1978. *The influence of seed predation and plant competition on tree species abundances in two adjacent tropical rain forest*. PhD thesis, University of Michigan, Michigan.
- SABATIER, D. 1985. Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. *Revue d'Écologie (Terre et Vie)* 40:289-320.
- SCHMITT, L. & BARITEAU, M. 1990. Gestion de l'écosystème forestier guyanais. Étude de la croissance et de la régénération naturelle. Dispositif de Paracou. *Bois et Forêts des Tropiques* (Spécial Guyane) 220:3-24.
- SIST, P. 1989. Peuplement et phénologie des palmiers en Guyane française (Piste de Saint-Elie). *Revue d'Écologie (Terre et Vie)* 4:113-151.
- SMITH, N. J. 1974. Agouti and babassu. *Oryx* 12:581-582.
- SMYTHE, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *American Naturalist* 104:25-35.
- SMYTHE, N. 1978. The natural history of the Central American agouti (*Dasyprocta punctata*). *Smithsonian Contribution to Zoology* 257:1-52.
- SMYTHE, N. 1986. Competition and resource partitioning in the guild of neotropical terrestrial frugivorous mammals. *Annual Review of Ecology and Systematics* 17:169-188.
- SMYTHE, N., GLANZ, W. E. & LEIGH, E. G., Jr. 1982. Population regulation in some terrestrial frugivores. Pp. 227-238 in Leigh, E. G., Jr, Rand, A. S. & Windsor, D. M. (eds). *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C.
- SOKAL, R. R. & ROHLF, F. J. 1981. *Biometry* (2nd edition). W. E. Freeman, New York.
- SORK, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. *Ecology* 68:1341-1350.
- TERBORGH, J. 1992. Maintenance of diversity in tropical forests. *Biotropica* (Supplement) 24:283-292.
- VANDER WALL, S. B. 1990. *Food hoarding in animals*. University of Chicago Press, Chicago.
- ZHANG, S. & WANG, L. 1995. Comparison of three fruit census methods in French Guiana. *Journal of Tropical Ecology* 11:281-294.

Accepted 22 January 1996

Book review

READING, A. J., THOMPSON, R. D. & MILLINGTON, A.C. 1995. *Humid tropical environments*. Blackwells, Oxford, UK. 429 pages. ISBN 0-631-19174-7. Price: £19.95 (paperback)

This is a source book that has been needed for some time. As the Preface notes, potentially useful 'tropical' texts have turned out to be either not really about the humid tropics (e.g. Thomas' (1974) focus on savanna environments) or to concern only one aspect of the tropical environment (e.g. Jackson's (1989) climatological / hydrological approach). From the authors' working definition of environments characterised by the 'consistently high receipt of solar radiation, heat and moisture' – beautifully illustrated, incidentally, by a cover image of dripping tree ferns in a Costa Rican cloud forest – here, at least, is a text with a definite humid tropical focus.

Humid tropical environments begins with chapters on the tropical atmosphere and tropical climates; these are then followed by sections on soils and vegetation. These chapters cover a tremendous spread of material. Sometimes there is only a regurgitation of a few published sources and a striving for comprehensiveness which leads to a dry classificatory approach and superficial treatments of complex material. But at its best, and this is often, the authors provide an up-to-date synthesis of a disparate literature. And Chapter 6, "humid tropical landscapes", and Chapter 7, "humid tropical hydrosphere", are more 'holistic' and more innovative. The book finishes with chapters on environmental resources and hazards and on environmental issues in the humid tropics.

This text is primarily aimed at a Geography and Environmental Science undergraduate market. Nevertheless, it has value at a research level in repeatedly drawing attention to the variability and diversity of processes and landscapes in the humid tropics. For the tropical ecologist, it offers a starting point to a wider knowledge of low latitudes and a way of locating the geographical context of more specialised research. A recommended addition to the bookshelves.

T. Spencer

Department of Geography, University of Cambridge, UK.

THOMAS, M. F. 1974. *Tropical geomorphology*. Macmillan, London, UK.

JACKSON, I. J. 1989. *Climate, water and agriculture in the tropics* 2nd edition. Longman, Harlow, UK.