

Effect of microhabitat on seed fate and seedling performance in two rodent-dispersed tree species in rain forest in French Guiana

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Summary

1 The establishment probabilities, short-term survival, growth rates and biomass allocation patterns of seedlings in two large-seeded tree species, *Carapa procera* (Meliaceae) and *Vouacapoua americana* (Caesalpinaceae), were studied in contrasting microhabitats at Paracou, French Guiana.

2 Seeds (100 per habitat per species) were buried to simulate rodent caches into gap and understorey microhabitats ($n = 20$ of each) surrounding mature parent trees. The experiment was replicated in *Carapa procera* (in early March and May) to investigate the effect of temporal variation in seed dispersal on the establishment process.

3 Surviving seeds and sprouting seedlings were repeatedly censused during 2 years after establishment, and the causes of mortality determined. Growth and biomass parameters were calculated for surviving seedlings after 2.5 years.

4 A greater proportion of seeds and germinating seedlings were dug up but less seedlings suffered from damping-off in *C. procera* than in *V. americana*. For both species, short-term survival of seedlings was lower in the understorey where predation by mammals and damping-off occurred more frequently than in gaps.

5 Damping off killed more *Carapa procera* seedlings when buried in March than in May, whereas mammal predation caused more deaths in May planted seeds.

6 Although survival and growth were enhanced in gaps for both species, seeds and seedlings were much more intolerant to the understorey microhabitat in *Carapa procera* (almost 100% mortality in shaded habitat) than in *Vouacapoua americana*.

7 Seedling biomass allocation was consistent with previous data for large-seeded species but differed markedly between the two study species.

Keywords: biomass allocation, forest gap, rain forest, recruitment, seedling survivorship, seed dispersal, scatterhoarding

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Introduction

The terminology used to describe tree recruitment patterns varies between authors (Denslow 1980; Augspurger 1984b; Brokaw 1985; Swaine & Whitmore 1988; Alvarez-Buylla & Martinez-Ramos 1992; Popma, Bongers & Werger 1992; Kitajima 1994, 1996; Osunkoya *et al.* 1994). Using seed size and seedling attributes for classification, large-seeded species may be described as shade- or understorey-tolerant and small-seeded species as gap-tolerant (Sork 1987; De Steven 1988; Forget 1994; Osunkoya *et al.* 1994). The probability of a seed germinating and becoming established in the understorey may, however, be small if it is available to mammalian predators (De Steven &

Putz 1984; Sork 1985; Howe 1990; Forget 1992; Moloisky & Fisher 1993; Osunkoya *et al.* 1993; Osunkoya 1994). Several studies have shown that when isolated from adult specimens, seed–seedling survival depends on the microhabitat and mortality caused by terrestrial vertebrates is independent of distance from the parent tree (Schupp 1988a,b; Schupp & Frost 1989; Howe 1993; Notman *et al.* 1996; Hammond & Brown 1997).

Tree species with similar seed size may be segregated on either ecological or physiological features of seeds and seedlings (e.g. Kitajima 1994, 1996). Mode of dispersal may also be used, but species that are dispersed by birds and arboreal mammals illustrate contrasting patterns of recruitment that appear

to be correlated with seed-seedling ability to resist predators (vertebrates and invertebrates) and pathogens in shaded or sunny environments (Howe 1989). Water-dispersed species differ in the flooding tolerance of seedlings, which influence their spatial distribution along creeks (Ter Steege 1994). Survival and growth of seedlings of wind-dispersed species varies as a function of their tolerance to pathogens and drought stress in the understorey by comparison to gap microhabitats, especially during the wet-to-dry season transition (Augsburger 1984a; Veenendaal *et al.* 1996).

This paper compares the seedling ecology of two large-seeded tree species (*Carapa procera*, Meliaceae, and *Vouacapoua americana*, Caesalpiniaceae) that are exclusively dispersed by scatterhoarding rodents in Guianan forests (Forget 1990, 1996). I test the hypothesis that the recruitment pattern of these two rodent-dispersed species might differ because of different effects on seedling survival and growth of the microhabitat change, which follows seed-dispersal by animals into the understorey and into gaps away from the parent tree, i.e. outside the limit of the crown area. I also performed experiments in order to compare the short-term survival of seedlings from man-made seed caches in understorey and gaps, and to compare the seed dispersal effectiveness and subsequent growth throughout the seedling stage of seeds dispersed at different times within the natural range.

Material and methods

STUDY SITE AND SPECIES

Experiments were conducted at Paracou (5°18 N, 52°53 W) near Sinnamary, French Guiana, at a reference plot which supports a mature forest (Plot No. 6 in Schmitt & Bariteau 1990). This plot shows no sign of logging, and there is a predominance of small gap openings (Durrieu de Madron 1994), as observed in another mature Guianan forest (Van der Meer *et al.* 1994; Van der Meer & Bongers 1996). The mean annual rainfall at Paracou 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 pattern although, unusually, drier in May (451 mm) than in June (551 mm) (Forget 1996).

The two species studied, *Carapa procera* and *Vouacapoua americana*, share the same dispersal agents, i.e. the caviomorph rodents acouchi (*Myoprocta exilis*) and agouti (*Dasyprocta leporina*) (Dubost 1988), but most other ecological traits contrast widely (Table 1). Both are commercial timbers, categorized by foresters as being of secondary and primary interest, respectively, on the basis of wood density and tree growth.

C. procera is a sub-canopy tree with a narrow crown of several slender branches. It can produce from several to hundreds of multiple-seeded fruits, each of which is a globose capsule with five segments and contains, on average, nine quadrangular brown seeds weighing 15–25 g and measuring 3–4 cm in their greatest dimension. Some of the fallen seeds are removed by animals and, especially when the microclimate is humid, many of those that are left rot following moth infestation, which is responsible for pre-dispersal predation. Short-term survival of the remaining seeds that germinate and establish *in situ* in the drier months is unlikely but not impossible (Forget 1996). During the 1991 fruiting season, removal rate of *C. procera* seeds steadily increased from March to May, the proportion of seeds either consumed or hoarded was low in March but intense scatterhoarding in May coincided with low seed predation (Forget 1996).

V. americana is a large canopy tree with a wide crown that can bear 3000–4000 single-seeded fruits. Seeds weigh 25–35 g and measure 3–5 cm at their greatest length. During masting, many seeds remain under the parent and may be parasitized by several species of bruchid larvae (Forget 1990). As in *C. procera*, seeds may germinate underneath parent trees but because of the lower probability of long-term survival, this abiotic mode of recruitment is also generally unsuccessful for *V. americana* (Forget 1994, 1997) unless there is a canopy opening nearby (personal observation). Intense removal of *V. americana* seeds leads to high rates of seed dispersal compared with low predation throughout the season (Forget 1990; unpublished data).

SEEDFALL BACKGROUND PATTERN

Since fruit type and crop size contrasts widely between the study species (Table 1), the methods used to establish seedfall background pattern were different. The *C. procera* population in the study plot was visited weekly and checked for fruiting trees. The number of seeds produced was estimated from mid-March through early June 1991 by collecting fruit segments from the ground below parent trees and counting the number of prints left in there by seeds (Forget 1996). Such marks allow precise estimation of seed crop size. For *V. americana*, eight 50 × 50 cm areas were delimited with plastic stakes, around each of 20 trees with the closest base of each quadrat 2 m from the tree trunk, and oriented following cardinal points (N, NE, E, ES, S, ...). Each week, starting 8 April, I censused the number of *V. americana* pods (one pod equals one seed) falling in the delimited areas. After each census, the areas were cleared of seeds and pods. Figure 1 shows that in 1991 the fruitfall pattern for *C. procera* was bimodal (March & May), and fruiting in *V. americana* started in April and peaked by early May.

Table 1 Morphological and ecological traits of *Carapa procera* and *Vouacapoua americana*

	<i>Carapa procera</i>	<i>Vouacapoua americana</i>
Tree	Sub-canopy	Canopy
Crown	Small	Large
Height	< 20–25 m	> 30 m
Reproductive d.b.h.	> 17 cm	> 26 cm
Density (d.b.h. > 10 cm)	41 trees per 6.25 ha	89 trees per 6.25 ha
Wood density*	0.70 g m ⁻³	0.92 g m ⁻³
Annual diameter increment*	0.17 cm	0.06 cm
Flowering	October–December	February–March
Rhythmicity	Annual	Pluri-annual (masting)
Fruiting	February–June	April–May–June
Crop size	up to 1000 seeds	up to 4000 seeds
Fruit size	Multiple-seeded	Single-seeded
Seed weight	18.4 ± SD 5.2 g†	32.6 ± SD 1.8 g‡
Seed size	3–4 cm	3–5 cm
Parasitism	Moth (pre- and post-dispersal)	Moth (pre-) and bruchid
Seedling height (8 weeks)	c. 51.4 cm	c. 36.0 cm
Number of leaves (8 weeks)	4 entire	2 with 7 leaflets
Total leaf area (8 weeks)	316 cm ²	298 cm ²

*After Favrichon 1994.

†After Forget 1996.

‡After Forget 1990.

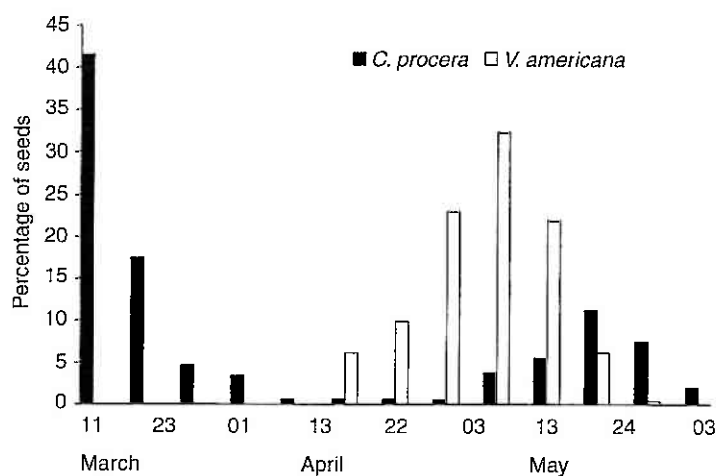


Fig. 1 Fruitfall pattern of *Carapa procera* and *Vouacapoua americana* at Paracou Plot number 6 in 1991. For *C. procera*, the first date (11 March) shows the percentage of seeds that had fallen before the study started.

SEEDLING ESTABLISHMENT AND FATE

Spatial distribution of the two species overlaps, as does the shadow of naturally rodent-dispersed seeds. The fate of buried seeds and seedlings was analysed after simulating natural seed dispersal in the understorey in the neighbourhood of the parent tree where the majority of rodent-dispersed seeds are likely to be found (Forget 1990; personal observation), and in gaps at various distances around. For each species, 20 fruiting trees were chosen and a transect established in a randomly selected direction, but avoiding those that crossed canopy gaps. Five seeds were planted along each transect at 2-m intervals, starting 5 m and 10 m from *C. procera* and *V. americana* tree base, respectively. All seeds were collected outside the study area. The closest seeds were approximately at the periphery of the crown-projected area within which seedfall is

concentrating and where seedlings may establish following seed dispersal by rodents (Forget 1994; personal observation). Each location was marked with a white plastic label planted into the ground. For *C. procera*, experiments were initiated on 12–22 March, as soon as seeds were available on the ground (Fig. 1), but due to a poor crop in April at Paracou, I was unable to find enough seeds to repeat the protocol 4 weeks later. The experiment was then replicated on 13–15 May 1991, seeds being buried along a transect at 1-m interval from those buried in March. *V. americana* seeds were set on 8–12 May 1991 during the fruit peak. In addition, five seeds of each species were buried along a transect 10 m long, at 2 m intervals, at the centre of each of 20 small gaps with open sky conditions that occurred either close to (between 5 and 10 m) or further (up to 50 m) from fruiting trees to which rodents are likely to disperse seeds. The under-

storey and gap treatments were close (> 10 m) in some instances but assumed to be independent: thus, the only visible difference was the absence or presence of a canopy opening, which was often associated with a mass of fallen debris on the ground. I was unable to measure the quantity of light at each burial sites, i.e. below opened and closed canopy, and I therefore assumed that the microhabitats were sufficiently different to show contrasting results, either between species or between habitats. Setting seeds at various distances mimics natural phenomena, where a seed can be transported and buried in a gap > 40 m away from the nearest potential parent tree (P.-M. Forget & P.A. Jansen, personal observation).

BIOMASS ALLOCATION

In October 1991, seedlings that established from buried seeds were censused and measured for height at stem tip and the number of leaves and leaflets were counted. The measurements and censuses were repeated in October 1991 and February and October 1993. Surviving seedlings were harvested in October 1993, and their biomass allocation analysed using the destructive procedure described in other studies (e.g. Oberbauer & Donnelly 1986; Popma & Bongers 1988; Popma *et al.* 1992; Osunkoya *et al.* 1993, 1994; Ter Steege 1994; Ter Steege *et al.* 1994). Samples were analysed at the Institut National de Recherche Agronomique (INRA) in Kourou on the same day of collection, and seedlings were separated into three parts: leaves and leaflets, petioles and stems, and root. There were no cotyledon reserves remaining in October 1993. Leaf area was measured with a portable leaf area meter (Licor Li3000), then leaves were oven dried at 80–100 °C for 24 h while woody parts were left drying for 5 days. Plant parts were weighed with a Sartorius balance with a precision of 0.01 g. From this data, I calculated the following parameters modified from Hunt (1978), as used by Ter Steege (1994), Ter Steege *et al.* (1994) and Kitajima (1994): leaf area ratio (LAR, leaf area per plant dry weight, cm² g⁻¹); specific leaf area (SLA, leaf area per leaf dry weight, cm² g⁻¹); leaf weight ratio (LWR, leaf dry weight per plant dry weight, g g⁻¹); stem weight ratio (StWR, stem dry weight per plant dry weight, g g⁻¹); shoot (stem + leaf) weight ratio (ShWR, shoot dry weight per plant dry weight, g g⁻¹); root weight ratio (RWR, root dry weight per plant dry weight, g g⁻¹); root–shoot ratio (R/S, root dry weight per shoot dry weight, g g⁻¹); and biomass relative growth rate (mg g⁻¹ day⁻¹) using the formula,

$$\text{RGRw} = (\ln W_1 - \ln W_0) \times 1000 / (t_1 - t_0)$$

where W_0 is the average dry seed weight calculated from a random sample of 20 seeds (*C. procer*: 9.6 g; *V. americana*: 16.7 g), and W_1 is the final dry seedling weight in October 1993. Because there was no significant difference in total biomass between *C. procer*

seedlings arising from seeds planted 2 months apart ($P = 0.10$), I used the same standard time interval, i.e. between July 91 and October 93 (27 months), for comparison between species (pooled data in *C. procer*) and habitat.

DATA ANALYSIS

The experimental design conforms to a three-treatment split-plot design with two between-block treatments (microhabitat and fate) and one within-block treatment (species) (Kirk 1969: p. 283). Statistical analysis was performed using fully factorial ANOVAs after arcsin square root (percentage of seedlings surviving per transect) and log (biomass value) transformation of some data. The statistical package PCSM-Plus V6.3 (PCSM 1994) was used for all analyses. Because of the small number of seedlings surviving per transect per species in each habitat after 2 years, all data for a species within a given habitat were pooled and the percentage of seedling survival in 1993 was analysed with *G*-test of independence (Sokal & Rohlf 1981).

Results

SEED FATE AND SEEDLING SURVIVAL

Between March–May and October 1991, several causes of mortality were observed. Buried seeds may rot and fail to germinate because of undetected pre-dispersal infestation by moths, or because soil drought precluded sprouting (Forget 1997). During the cache and germination period, buried seeds, sprouts and established seedlings may be dug up by rodents, peccaries and possibly deer seeking edible cotyledons. Sprouting seedlings may also be damaged by rodents which cut sprouts without digging in the ground for cotyledons, or by grazing mammals such as deer. In moist conditions, i.e. mostly in the understory, newly established seedlings were observed dying because of damping-off after fungal infections developed on the stem and young achlorotic leaves in May–June, and exacerbated by drought during the wet-to-dry season transition in July–October. I therefore recognized four seed–seedling fate categories, i.e. rotten seeds, seedlings destroyed by mammals, seedlings killed by damping-off and seedlings that had become successfully established by October 1991.

Between blocks, the effect of fate (three-way ANOVA, $F_{3, 152} = 6.19$, $P < 0.001$) and of interaction of habitat and fate ($F_{3, 152} = 11.06$, $P < 0.001$) were significant. Within block, only the interaction of month and fate was significant ($F_{3, 152} = 18.49$, $P < 0.001$). *C. procer* seed–seedlings were more likely to be dug up in the understory (54.1% of potential sprouting seedlings, i.e. all seeds less those rotten) than in gaps (34.6%) after dispersal in May (Fig. 2). When buried earlier in March (data not

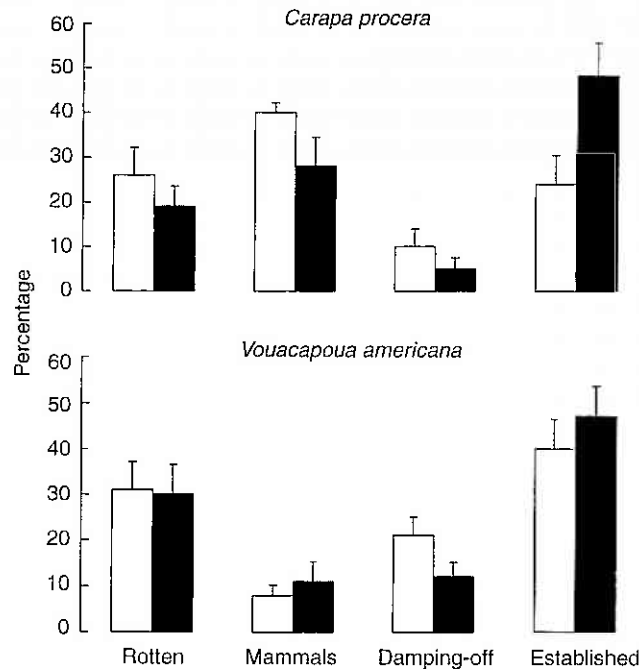


Fig. 2 Fate of *Carapa procera* and *Vouacapoua americana* seed-seedlings in the understory (□ + SEM, $n = 20$ transects) and in gaps (■ + SEM, $n = 20$ transects) in October 1991. See text for detail of fate categories.

shown), the proportion of seedlings dug up was much lower and the major fate of seedlings in the understory (48.3%) was damping-off, which was more common here than in gaps (26.8%) where it occurred later on during sprouting and establishment.

The fate of seed-seedlings also varies both between species and habitats within month. First, comparing species for seeds buried in May (Fig. 2), the interaction between species and fate categories was significant ($F_{3, 152} = 10.57$, $P < 0.001$). This result shows that a significantly greater proportion of seeds and germinating seedlings were dug up but less seedlings suffered from damping-off in *C. procera* than in *V. americana* between May and October 1991. Secondly, although there was no significant interaction ($P = 1.0$) between species and habitats, the interaction between habitats and fate was however, significant ($F_{3, 152} = 3.25$, $P = 0.02$). Considering each species individually, the interaction of habitat and fate was significant in *C. procera* ($F_{3, 152} = 3.80$, $P = 0.011$) whereas neither habitat ($P = 0.79$) nor the interaction with fate ($P = 0.52$) affected seedlings of *V. americana*, and only the proportion of each fate category differed significantly ($F_{3, 152} = 15.14$, $P < 0.001$). When the proportion of live seedlings in October 1991 is compared between species, then habitat had a significant effect on seedling establishment ($F_{1, 76} = 5.04$, $P < 0.025$) but neither species nor the interaction between species and habitat was significant (all $P \geq 0.23$). Thus, when comparing the overall effect of habitats for both species, a significantly greater proportion of seedlings established in gaps than in the understory. Overall establishment was greater in *V. americana* than in *C. procera* (Fig. 2).

When data from the two habitats are analysed separately, the interaction between species and seed-seedling fate is significant in the understory ($F_{2, 114} = 12.29$, $P < 0.001$). *C. procera* seed-seedlings here were predated by mammals more frequently (54.1%) than in *V. americana* (11.6%). Consequently, fewer establishing seedlings of *C. procera* survived in the shaded and humid conditions of the understory (32.4%) than in the sunny and drier environment of gaps (59.2%) while *V. americana* seedlings were equally successful in both habitats (understorey: 58.0%; gap: 67.1%).

Overall seed-seedling survival by October 1992 was significantly affected by species ($F_{1, 76} = 21.29$, $P < 0.001$) and habitat ($F_{1, 76} = 6.53$, $P = 0.012$). There was no interaction between the two factors ($P = 0.31$). In October 1993, this situation remained unchanged for the effect of species ($F_{1, 76} = 23.71$, $P < 0.001$), while the effect of habitat decreased to marginally no significant ($P = 0.053$) (Fig. 3). Within *C. procera*, habitat ($F_{1, 38} = 19.48$, $P < 0.001$) and the interaction between habitat and month ($F_{1, 38} = 6.86$, $P = 0.012$) significantly affected overall seed-seedling survival in October 1992 depending on whether they were buried in March or May.

One-year survival of established seedlings between October 1991 and October 1992 was significantly greater in *V. americana* (72.5% and 85.1% in the understory and in gaps, respectively, $P > 0.05$) than in *C. procera* (8.3% and 45.8%, respectively), the species which showed a more pronounced contrast between habitats ($G = 11.66$, $P < 0.001$) (between species: Understorey, $G = 27.8$, $P < 0.001$; Gap, $G = 16.9$, $P < 0.001$) (Fig. 3). By October 1993, *C.*

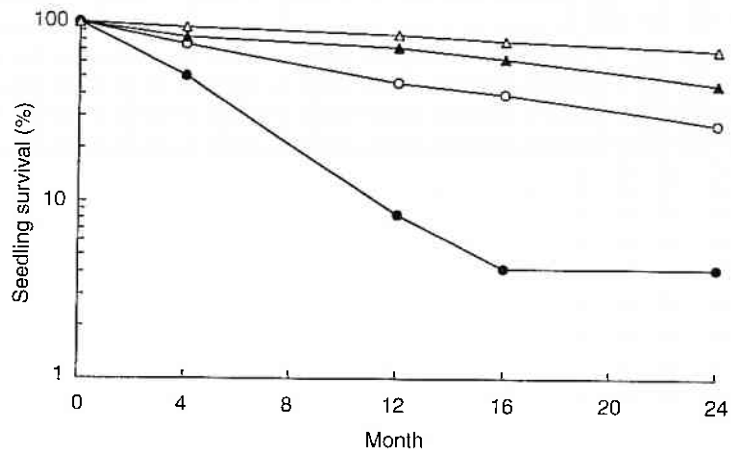


Fig. 3 Percentage of seedlings surviving between October 1991 and October 1993. *Carapa procera* (circle) – Understorey: $n = 24$; Gap $n = 48$. *Vouacapoua americana* (triangle) – Understorey: $n = 40$; Gap $n = 47$. Open and closed symbols are gap and understorey, respectively.

procera seedling survival in gaps was greater for seeds buried in March (50.9%) than in May (27.1%) ($G = 6.1$, $P < 0.025$) and the difference between habitats was very pronounced with only one seedling (not considered in biomass analysis) from a seed buried in May surviving in the understorey: 70.2% of *V. americana* seedlings survived under these conditions. Two-year survival of *V. americana* seedlings was different between habitats ($G = 5.7$, $P = 0.025$) and was much greater in gaps (45.0%). There, survival of *V. americana* seedlings was greater ($G = 18.28$, $P < 0.001$) than that of *C. procera* seedlings which established from seeds buried in May (Fig. 3).

SEEDLING GROWTH AND BIOMASS ALLOCATION

Because of low survival of *C. procera* seedlings in the understorey, comparison between seedling growth (weight, height increment, number of leaves and leaf area) and biomass allocation patterns and ratio were only possible between species for the gap habitat, and between habitats within *V. americana*. Except for a small significant difference in height in October 1993 ($F_{1,38} = 7.36$, $P = 0.009$) and a slight but not significant ($P = 0.056$) difference in leaf biomass between surviving seedlings from March and May cohorts (which is probably attributable to an initial difference in seedling height in October 1991) ($F_{1,38} = 4.27$, $P = 0.042$), there was no significant difference (all $P > 0.10$) in values for growth parameters and biomass allocation. Therefore, data for *C. procera* seedlings from both months were pooled in further analyses.

On the average, despite a smaller seed weight, seedlings which survived throughout the study period were taller in *C. procera* than in *V. americana* in October 1991. The contrast was still visible after 2 years of growth, i.e. in October 1993. Within *V. americana*, the initial difference in seedling height, possibly due to difference in seed weight, compensated for greater

height increments in gap vs. understorey seedlings (Table 2). No significant difference was observed between species for either percentage of seedlings which grew (*V. americana*: 85% of live seedlings; *C. procera*: 81%) or height increment in gaps (Tables 2 and 3). Allowing for damaged stems and resprouting, which would lead to loss in height, average 2-year height increment was identical in both species in gaps, i.e. c. 8–11 cm ($P = 0.88$). Among *V. americana* seedlings, height increment was 3-fold greater in gaps, i.e. 10.9 cm vs. 3.5 cm in the understorey.

C. procera seedlings allocate more biomass to both above- and below-ground organs, as well as producing more leaves and leaf area than *V. americana* seedlings in gaps (Table 2). In *V. americana*, non-photosynthetic organs (stem, roots) comprise more biomass in gaps than in understorey, but there was no significant difference in leaf characteristics (number, weight, area) between habitats, although there was a trend for greater biomass production in gap than in understorey.

SLA was significantly different between species and between habitat with a gradient of lowest values in *C. procera* (Gap) and highest in *V. americana* (Understorey). Although significant only between species for the gap habitat, the trend was similar for LAR. All other biomass ratios (LWR, StWR, ShWR, RWR and R/S) did not differ significantly between species within gap, and between habitats within *V. americana*. RGRw was greater in *C. procera* than in *V. americana*, and greater in the gap than in the understorey for the latter species.

Discussion

SEEDLING RECRUITMENT PATTERN

Carapa procera seedlings died more frequently due to pathogen and drought stress when buried in March than in May but fewer were subject to mammal predation. Overall, the seed-seedling survival prob-

Table 2 Architectural features (mean \pm SD) of 2-year-old *Carapa procera* and *Vouacapoua americana* seedlings in October 1993. Seeds planted in May 1991 in contrasting habitats (Gap and Understorey)

	<i>Carapa procera</i> Gap*	<i>Vouacapoua americana</i>	
		Gap†	Understorey‡
Height '91 (cm)	42.0 (1.4)	30.5 (1.3)	36.5 (1.8)
Height '93 (cm)	50.5 (2.1)	38.7 (2.1)	37.5 (2.2)
Increment (cm)	11.6 (1.3)	10.9 (1.6)	3.50 (0.6)
Stem (g)	9.3 (0.8)	4.2 (0.4)	2.50 (0.2)
Leaf (g)	4.1 (0.5)	2.5 (0.3)	1.60 (0.2)
Shoot (g)	13.4 (1.2)	6.7 (0.7)	4.00 (0.4)
Root (g)	3.3 (0.3)	1.4 (0.1)	1.10 (0.1)
Number of leaves	6.3 (0.3)	4.3 (0.4)	3.40 (0.4)
Leaf area (cm ²)	739 (79)	519 (67)	366 (49)
LAR (cm ² g ⁻¹)	46 (2.9)	58.3 (3.8)	65.7 (6.9)
SLA (cm ² g ⁻¹)	185 (29)	219 (38)	242 (57)
LWR (g g ⁻¹)	0.25 (0.01)	0.27 (0.02)	0.28 (0.03)
StWR (g g ⁻¹)	0.56 (0.09)	0.52 (0.09)	0.50 (0.13)
ShWR (g)	0.8 (0.13)	0.8 (0.14)	0.78 (0.21)
RWR (g g ⁻¹)	0.2 (0.03)	0.2 (0.03)	0.22 (0.06)
R/S (g g ⁻¹)	0.26 (0.02)	0.3 (0.02)	0.30 (0.05)
RGRw (g g ⁻¹ day ⁻¹)§	0.61	-0.79	-1.31

* $n = 40$ except Increment with value > 0 cm ($n = 34$), and Root, LAR, LWR, StWR, SHWR, RWR and R/S ($n = 39$).

† $n = 33$ except Increment ($n = 27$).

‡ $n = 18$ except Increment ($n = 12$), and Root, LAR, LWR, StWR, SHWR, RWR and R/S ($n = 14$).

§Based on dry seed weight ($n = 20$) of 9.6 g for *Carapa procera* and 16.7 g for *Vouacapoua americana*, and a 27-month period between July 1991 and October 1993 for both species.

abilities appeared greater for the March cohort, although fewer seeds are usually dispersed by rodents during that month (Forget 1996). This result seems paradoxical, but one should not forget that because agouti and acouchi store food, the overall rodents' behaviour favours successful seedling establishment. If a seed dispersed in March does reach a gap it has a good chance of establishment and growth. The population of recruits surviving in a given year is therefore likely to be mixed, composed of individuals from different months of the fruiting period. This may have some consequences on genetic diversity and the trees' ability to flower and fruit in different months of the year, rather than having a restricted season as in *V. americana*.

The difference in early seedling survival between habitats for *C. procera* may be the consequence of differential foraging activity of rodents as well as differences in light regime between gap and understorey. This is consistent with the conflict occurring between the sites to which seeds are dispersed by animals and those to which seedlings successfully establish as summarized by Schupp (1995). Results are also consistent with other studies showing that seed-seedling survival is highly habitat-dependent, although habitat preferences differ between species (e.g. Schupp 1988a,b; Schupp & Frost 1989; Notman *et al.* 1996). First, seeds are unlikely to persist alive above ground level, either in the understorey or in gaps, since they will be eaten by mammals, infested

by moth or dispersed (scatter hoarded) by rodents. Secondly, only seedlings derived from buried seeds may survive during the first years in a gap. In *C. procera*, as in other species (see Forget 1991) but in contrast to *V. americana*, cotyledons are not exhausted by seedling establishment and remain edible for several further weeks depending on level of pre-dispersal predation (personal observation). The seed reserves are available to rodents throughout the wet-to-dry season transition when community-wide food availability is scarce. It is possible that seeds cached in May may have been retrieved and recached. However, because germination is rapid and because rodents regularly excise roots after digging up germinating seeds (personal observation), it is assumed that seeds cached a second or a third time will have a low chance of survival and establishment. Rodents also excise sprouts without excavating seeds, allowing them to exploit the reserve before exhaustion as the seedling grows. Basal sprouts are frequently observed after several occurrences of stem damage, even as late as November when seeds are empty. On the contrary, this type of exploitation of *V. americana* is low (c. 10%) and the main cause of seed-seedling mortality remains rotting, drought stress and fungus at our study site as at another site having a low population of ground-dwelling herbivores, especially peccaries (see also Forget 1994).

Seed dispersal effectiveness is a balance between arrival and survival of seeds at a given habitat

(Schupp *et al.* 1989). In this study, *C. procera* seed dispersal effectiveness varied between months, but it may also change between years depending on climate (Forget 1997), and between location depending on the terrestrial vertebrate community. Indeed, a rainy year and/or a stable population of peccaries would certainly lower the probabilities of seedling establishment despite intensive seed dispersal by rodents in May year after year. Thus, for both study species, it seems that the preferable period for seed dispersal and seedling establishment is the late wet season (Forget 1990, 1996, 1997) assuming that survival rate of seeds buried in April would be intermediate to the results presented in this study. Therefore, an increase in the frequency of seeds being cached during this period would lead to a greater number of seedlings emerging later on and surviving throughout the dry season.

TO BE, OR NOT TO BE, A (NON-)PIONEER TREE SPECIES

C. procera and *V. americana* do not require canopy gaps for germination, and thus can be defined as non-pioneer species (*sensu* Swaine & Whitmore 1988) although classifications based on seedling and juvenile life-cycles mean that pioneer species may also be defined as shade-tolerant (Alvarez-Buylla & Martinez-Ramos 1992). The successional status of *C. procera* and *V. americana*, however, is entirely consistent with data on biomass allocation, which confirms their rank at one extreme of a spectrum of recruitment pattern for species with increasing seed size in Guianan forests (Ter Steege 1994; Ter Steege *et al.* 1994) and in other tropical forests, whereby the large-seeded species tend to have the lowest LAR and SLA values (Osunkoya *et al.* 1993, 1994; Oberbauer & Donnelly 1986; Popma *et al.* 1992). Seed size in *C. procera* and *V. americana* is of the same magnitude, i.e. more than 10 g, and the difference in seedling recruitment between the two species is more dependent on the seedling's ability to establish and maintain in understorey habitats than on seed size and/or on light requirement for leaf, stem and root production alone. The understorey-tolerance shown by *V. americana* seedlings is result of (i) greater resistance to abiotic causes of mortality, such as moisture (fungal pathogens are often associated with the wet season, e.g. Augspurger 1984a,b); (ii) better adaptation to drought stress (e.g. Veenendaal *et al.* 1996) in the wet-to-dry season transition; and (iii) less susceptibility to biotic factors (such as the grazing activities of seed-seedling herbivores) than *C. procera*.

The tall *C. procera* seedlings are indeed more susceptible to grazing than *V. americana* seedlings, since their cotyledons, as well as young sprouts, can be attacked by animals as late as 2–3 months following establishment. As suggested by Stapanian (1986) for temperate tree species, it is possible that such contrast relates to the nature of seed nutrients (lipid in *C.*

procera, cf. results on related species, *C. guianensis*, Rankin 1978; carbohydrate content in *V. americana*) and, to the rapid germination and exhaustion of reserves in the latter. The faster the seed reserves are consumed by seedlings, the earlier damage to digging by rodents and peccaries will become less likely. Differences in defences (Coley 1983; Coley & Aide 1989) between species need to be emphasized, and young whitish *C. procera* leaves seems to be less protected from herbivory than young red *V. americana* leaves (personal observation). Leaf gas exchange in *C. procera* seedlings may be more sensitive to drought in the upper soil layer during the wet-to-dry season transition than in *V. americana* seedlings (see Huc & Guchl 1989) and a deeper root system (Alexandre 1991; see Table 3, personal observation), as well as greater leaf area, may compensate for such sensitivity in gaps. After 1 or 2 years, *C. procera* seedlings survived only in gaps whereas *V. americana* seedlings were present and grew both in the understorey and in gaps, although they grew better in the gaps. Finally, although, once buried, both species can establish in shade as well as in gap, the differences in seed-seedling survival and growth between habitats separate the two species in their regeneration niche (Grubb 1977).

Seedling performance of the two species, measured as height increment, is comparable in gaps but biomass allocation differs. Based on potential size (maximum diameter) and sensitivity of annual girth increment to light in trees of d.b.h. > 10 cm, Favrichon (1994) classified mature *C. procera* as a light-demanding species and *V. americana* as a (shade-?)tolerant species. Huc *et al.* (1994) showed that the eco-physiology of *C. procera* (misnamed as *C. guianensis*, personal observation) was intermediate between that of pioneer and climax species, although its leaves are more like those of pioneer species. No data are currently available for *V. americana* but, given the behaviour of seedlings in the understorey, and LAR and SLA values close to that of the non-pioneer *Eperua falcata*, Caesalpiniaceae (Ter Steege 1994), it is probable that its leaves are of the non-pioneer type. *C. procera* germinates in shade and is therefore not an obligate gap species according to Popma *et al.* (1992)'s classification into three recruitment patterns. On this scheme, *V. americana* was previously classified as an understorey-tolerant species (Forget 1994) as it is not gap-independent. *C. procera* and *V. americana* may therefore both be defined as gap-dependent species on the basis of seedling dynamics. However, *C. procera* seedlings are understorey-intolerant whereas those of *V. americana* are understorey-tolerant.

Traditional classification of recruitment patterns often underestimates the impact of the understorey habitat activities via biotic and abiotic factors to limit recruitment of seedlings. *C. procera* is characteristic of species with a short seedling half-life (several months to less than a year) in the understorey, that allocate more biomass to root and stem (lower LAR