


Tree seedling performance in canopy gaps in a

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Guiana

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ABSTRACT. The effect of natural canopy gaps on the performance of naturally occurring tree seedling populations was studied in a tropical rain forest in French Guiana. This was done at two levels of scale. Firstly, on a 20 m × 250 m forest transect intersecting four canopy gaps, it was investigated how patterns of recruitment, growth and survival of seedlings of *Cecropia obtusa*, *Dicorynia guianensis* and *Pourouma bicolor* differed between canopy gaps and closed forest. Secondly, for one large natural canopy gap, performance of seedling cohorts established before ('pre-gap' cohorts) and after ('post-gap' cohorts) gap formation was studied in relation to environmental heterogeneity. The direct site factor (DSF) was used as an indicator of light availability in the gap zone. *Cecropia* specialised in large gaps, and also in specific sites within the large gap: seedling performance was increased by light, and by dead wood. *Pourouma* mainly germinated under closed forest conditions, where it can survive for a long period until a canopy gap is formed nearby. *Pourouma* seedlings adjusted well to the new gap environment but they did not specialise in specific places within the gap. Seedling location of *Pourouma* seedlings was mainly determined by accidental positioning before gap formation. *Dicorynia* was able to germinate both in gaps and under closed forest conditions. Although the number of gaps studied in this study was low, the results show that seedling establishment, early growth and survival of the three tree species were affected by canopy gaps and by the environmental heterogeneity within a large gap.

KEY WORDS: Canopy gaps, *Cecropia obtusa*, *Dicorynia guianensis*, light availability, *Pourouma bicolor*, Seedling growth, Seedling dynamics, tropical rain forest.

INTRODUCTION

In tropical rain forests, canopy gaps are important for successful regeneration of many tree species (Hartshorn 1978, Whitmore 1978). In general, *c.* 1% of

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the canopy of tropical rain forests are opened up annually by falling trees or branches (e.g. Clark 1990). The micro-environments that are associated with canopy gaps are believed to have a major effect on the population dynamics of many tree species in the forest (Bazzaz & Wayne 1994, Bongers & Popma 1988, Brokaw 1985, Clark 1990, Denslow 1987). Pioneer or light-demanding species are highly specialised and can only germinate in canopy gaps. Non-pioneer or shade-tolerant species are able to germinate under a closed forest canopy but may need canopy gaps at a later stage during their life cycle to reach maturity (Swaine & Whitmore 1988). This is a broad generalisation, and many plant species are not unequivocally classified in either of these two categories. It is clear that the combination of (1) germination success, (2) growth rate, and (3) survival of tree seedlings (henceforth referred to as 'seedling performance') is affected by canopy gaps for most trees species in tropical rain forests.

In canopy gaps, the increased light availability is generally seen as one of the most important factors controlling seedling performance (Clark 1990, Welden *et al.* 1991). During the past decade, tree seedling performance in relation to canopy gaps in tropical rain forests has been studied extensively. Several methods have been used, including greenhouse experiments (Ashton & De Zoysa 1989, Augspurger 1984, Cornelissen *et al.* 1994, Kamaluddin & Grace 1993), and experiments with planted or placed seedlings in the field (Bongers *et al.* 1988, Denslow *et al.* 1990, De Steven 1988, Howe 1990, Osunkoya *et al.* 1993, Popma & Bongers 1988). Also, seedling performance in man-made gaps has been studied by Brown (1996), Brown & Whitmore (1992), Bongers *et al.* (1988), Kennedy & Swaine (1992), Newell *et al.* (1993) and Ter Steege *et al.* (1994). In general, these studies conclude that seedling performance is better in canopy gaps than below a closed canopy, and it is suggested that this occurs in natural tree populations too. However, only in a few cases has seedling performance been studied of naturally occurring tree seedling populations in naturally formed canopy gaps (Clark & Clark 1987, Nunez-Farfan & Dirzo 1988, Sork 1987; Turner 1990a, b).

Most of the latter studies do not distinguish between tree seedlings that were present before gap formation as advanced regeneration ('pre-gap' seedlings), and seedlings that established after the gap formation ('post-gap' seedlings). Studies on light acclimation of tree seedlings (Fetcher *et al.* 1987, Popma & Bongers 1991, Strauss-Debenedetti & Bazzaz 1991) indicate that pre-gap seedlings will respond differently to a new canopy gap than post-gap seedlings. So far, the difference in performance between pre- and post-gap seedlings has hardly been investigated for naturally occurring tree seedling populations.

The majority of studies relate seedling performance to gaps of different sizes (e.g. Denslow 1980, Whitmore 1978). However, light availability may vary considerably within gaps (Canham 1988, Chazdon & Fetcher 1984, Raich 1989, Rich *et al.* 1993). In some studies, tree seedling performance has been related

to different gap zones (Barton 1984, Brandani *et al.* 1988, Nunez-Farfan & Dirzo 1988, Orians 1982), but were not directly linked with (the variation in) light levels.

The objective of this study was to determine how the performance of naturally occurring tree seedling populations in a lowland tropical rain forest was affected by naturally formed canopy gaps. This was done at two levels of scale. Firstly, we investigated how patterns of germination, growth, mortality and density of seedlings of three tree species differed between canopy gaps and closed forest. Secondly, we compared the performance of pre-gap seedlings with that of post-gap seedlings in one large canopy gap, and investigated how seedling performance was affected by the variation in light availability within the gap.

METHODS

Site and species

The study was performed in the tropical rain forest at the Nouragues field station in central French Guiana (4°05'N; 52°40'W). Measurements were made in part of a 12-ha sample plot, which was established in 1991 to investigate natural treefalls and canopy dynamics (Van der Meer & Bongers 1996a,b). The 12-ha plot is situated on a plateau, ranging in elevation between 90–110 m above sea level. The forest is primary evergreen rain forest, with no traces of any recent human disturbance. The forest canopy height ranges between 30–40 m, with emergents up to 60 m tall. Annual rainfall averages *c.* 3000 mm, with a distinct dry season from September to November, and a drier period around February and March.

We studied seedlings (individuals < 1 m tall) of three locally abundant tree species, which were chosen because they were expected to react differently to the formation of canopy gaps and the concomitant change in light availability: (1) *Dicorynia guianensis* Amsh. (Caesalpiniaceae), a shade-tolerant canopy tree, with an adult stature of 50 m, producing flat seeds, *c.* 1.6 cm × 1.4 cm × 0.4 cm, in winged pods; and anemochorous; (2) *Pourouma bicolor* Mart. spp. *digitata* Tréc. (Cecropiaceae), a shade-tolerant canopy tree, with an adult stature between 30–40 m, producing ovoid seeds, *c.* 2 cm × 1.4 cm; and endozoochorous; (3) *Cecropia obtusa* Tréc. (Cecropiaceae), a pioneer tree, with an adult stature between 30 and 40 m, with small seeds (0.2 cm long); and syn- and endo-zochorous (Schulz 1960, Van Roosmalen 1985). The species will be referred to by their generic names from hereon.

Closed forest versus canopy gaps

In a 0.5-ha transect (20 m × 250 m) in the central part of the 12-ha plot, seedlings of the three species were mapped to the nearest metre, tagged and measured (height) in November 1992. The transect intersected the extended gap zone (area bordered by the stembases of the adjacent canopy trees taller

than 20 m; after Runkle 1981) of four gaps. The canopy gaps were 2–3 y old, and they covered 750 m² of the transect. We determined whether a seedling was located in the extended gap zone of a canopy gap ('gap' seedling) or under a closed forest canopy ('forest' seedling). In November 1993, all tagged seedlings were measured again and newly established seedlings were recorded. Density, annual survival and annual relative height growth ($\ln(ht_1) - \ln(ht_0)$; cm cm⁻¹ y⁻¹) were determined for each species.

Large canopy gap

On 10 May 1991, a large canopy gap was formed in the 12-ha plot by the natural fall (a snap at 4 m) of a large (dbh of 84 cm) senescent tree (P. J. Van der Meer, *pers. obs.*). The tree fell and damaged several other trees, and created a large opening in the forest canopy. The central gap area measured 284 m² (i.e. the area delimited by the vertical projection of the adjacent canopy taller than 20 m; Van der Meer & Bongers 1996a), and the extended gap area was 965 m². The gap centre was located at some 80 m distance from the above-mentioned 0.5-ha transect. Seedling performance was measured on two (5-m wide) perpendicular transects through the extended gap area. These two perpendicular transects covered 400 m². Between September 1991 and November 1995 four inventories were carried out.

In September 1991, 4 mo after gap creation, the gap area was searched for seedlings of the three species. Seedlings were mapped to the nearest 10 cm, tagged and their height was measured. Seedling appearance (viz. presence of cotyledons, freshness of leaves), enabled distinction between pre-gap and post-gap (1991-cohort) *Dicorynia* seedlings. Adult trees of *Dicorynia* were close enough to the gap to cover the whole extended gap area with their seed dispersal range (P. J. Van der Meer, unpubl. data). *Dicorynia* sheds its anemochorous seeds usually within 30 m from the seed source (Loubry 1993). Fruit shedding generally peaks around June and germination is usually within 1 mo (Forget 1988). *Pourouma* trees generally fruit in February and March (D. Julien-Laferriere & B. Rièra, unpubl. data) and we assumed that all *Pourouma* seedlings present in September 1991 had germinated before the gap formation. *Cecropia* seedlings were not yet present during the first inventory.

In November 1992, 18 mo after gap creation, we determined the survival and height of tagged seedlings, and recorded establishment (location, height) of new seedlings (1992-cohort).

In November 1993 and 1995, 30 and 54 mo after gap creation respectively, we determined the survival and height of all seedling cohorts.

Large canopy gap: light availability

We placed a 5-m × 5-m grid system in and around the gap, covering the extended gap area and the first 5 m outside the extended gap area. The 67 grid-intersections were permanently marked with plastic pickets to facilitate

mapping of the seedlings and to monitor light availability. We made hemispherical photographs 1 m above each picket during the three inventories (September 1991, November 1992 and November 1993). In 1991, we took photographs using a Sigma Fisheye 8-mm lens. In 1992 and 1993, a Canon Fisheye 7.5-mm/5.6 lens was used. For each photograph the percentage of direct radiation which penetrates the forest canopy (DSF) was calculated using the program Hemiphot (Ter Steege 1993). A light climate map of the extended gap area was created by applying spatial interpolation (kriging) between the grid-points, using the (3-y) average DSF values. Interpolation was achieved using the SURFER Access System (Vers. 4.13). With the point and edit device of the program, we could derive values for the average DSF for every seedling in the extended gap area.

The DSF, rather than the TSF (percentage total radiation) or ISF (percentage indirect radiation), was used as the calculation of the DSF is more unequivocal than that of the ISF (and consequently TSF), where several approaches may be used (Mitchell & Whitmore 1993, Ter Steege 1993). In addition, the direct radiation (e.g. sun-flecks) contributes more than the indirect radiation to temporal and spatial variation in light availability at the forest floor (Mitchell & Whitmore 1993). For the whole gap, the average DSF, ISF and TSF over 3 y was 10.7, 7.6 and 10.3% respectively (option 'diffuse light = 15% direct light' model for high solar altitudes; Ter Steege 1993).

Statistical analysis

As the requirement of independence of data for both the transect study and the large gap study was not met, no conventional statistical methods could be used. Instead, randomisation tests were used to investigate whether seedling densities, survival and heights differed significantly between gaps and forest, and between seedling cohorts.

For the forest transect study, four areas the same size as the four original gaps were randomly placed within the transect area at a minimum distance of 5 m. The seedling density in the gaps and in the forest area was determined using the original seedling locations. This was repeated 200 times. For each species it was tested whether the gap/forest seedling density ratio ($\log \{(\text{gap density} + 1)/(\text{forest density} + 1)\}$) for the observed gap locations differed significantly from the gap/forest seedling density ratio for randomly located gaps. The P-value (H_0 : no significant difference) was indicated by the percentage of the density ratios of the randomly located gaps which were greater than the density ratio of the observed gap location.

To investigate whether survival rates between gap and forest seedlings differed significantly, the observed ratio of gap/forest survivorship was compared with a random survivorship of gap and forest seedlings. For each species, the number of observed survivors (= number of survivors in gaps + number of survivors in the forest) was drawn at random out of the combined group of initial gap and forest seedlings, and the ratio of gap/forest survivorship was

determined. This was done 200 times. The P-value was indicated by the percentage of the random gap/forest survivorship ratios which were greater than the observed gap/forest survivorship ratios.

Likewise, to test whether density and survival differed between species, the observed density or survival ratio for species A and B was compared with the ratio after random relabeling of all seedlings of the two species involved. This was done 200 times, and P-values were determined as described above.

To test for significant differences in height growth between gap and forest seedlings, and between species, the observed height growth ratio (of species A and B, or cohorts A and B: $\{\text{Log}(\text{RGR}_A + 1)/(\text{RGR}_B + 1)\}$) was compared with 200 height growth ratios using randomly relabelled height values. Again, P-values were calculated as described above.

For the large canopy gap study no tests were done to investigate the statistical significance of the differences in seedling densities and survival between different cohorts. The number of observations in several cohorts was too low to allow for tests. Also, unobserved recruitment and early mortality between gap creation and the first inventory, and between the first and second inventory, may have affected the observed density and survival rates differently for the species, but also for the different cohorts. However, height growth was investigated using the randomisation tests as described above.

We tested how the frequency distribution of seedlings with respect to the light availability was affected by species or time of establishment. For the transect, the total area in each DSF class of 2% was calculated using the SURFER program. Accordingly, we made a frequency distribution in DSF classes (in steps of 2%) for the entire transect area. This frequency distribution was compared with frequency distributions of the DSF values above different groups of seedlings, and were tested for significant differences by the Kolmogorov-Smirnov test.

The relationships between DSF and height growth of the three species were investigated using linear regression analysis, after the data had been checked for normality. To test whether differences between DSF values above various locations were significant, a randomization test was applied. For statistical analyses, the statistical package SPSS for Windows (release 6) was used.

RESULTS

Closed forest versus canopy gaps

The three species showed a different pattern of seedling distribution (Figure 1). Seedlings of *Dicorynia* clustered around parent trees (trees > 50 cm dbh). The distribution of *Pourouma* seedlings did not seem to be related to the distribution of larger (dbh > 20 cm) *Pourouma* trees. *Cecropia* seedlings were clearly concentrated in and around canopy gaps. Exact patterns of clustering were not further analysed in this study.

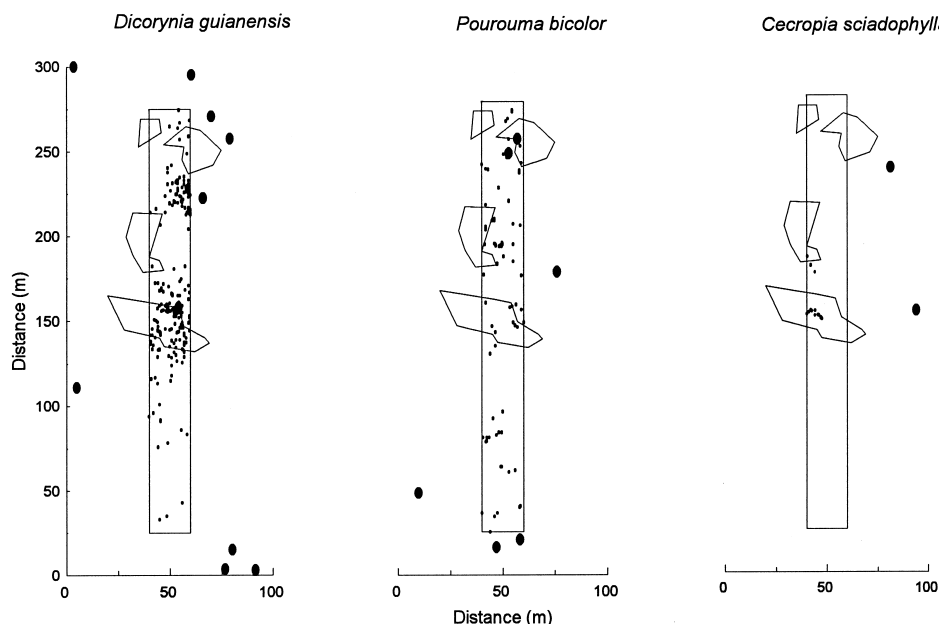


Figure 1. Distribution patterns of seedlings (.) of three tree species in a 20 m \times 250 m rain forest plot in French Guiana. Locations of large trees (●) with a potential to produce seeds are shown for the forest both within and around the transect (for *Dicorynia*, trees > 50 cm dbh, for *Pourouma* and *Cecropia*, trees > 20 cm dbh). Canopy gaps in the transect area are indicated by the polygons.

Seedling densities of *Dicorynia* and *Cecropia* were significantly higher in canopy gaps than under a closed forest canopy (Table 1). In gaps, seedling density of *Dicorynia* was higher than density of *Pourouma* and *Cecropia* seedlings. Under a closed forest canopy, seedling density was highest for *Dicorynia*, intermediate for *Pourouma*, and lowest for *Cecropia*. The preference of *Dicorynia* seedlings for canopy gaps could be the result of the accidental occurrence of a parent tree close to one of the four gaps (see Figure 1). To check this, we

Table 1. Seedling performance in relation to forest structure for three tree species on a 250-m \times 20-m (5000-m²) transect in a tropical rain forest in French Guyana. Total transect area as canopy gaps was 750 m². Randomisation tests were performed to determine whether differences were significant (see text for further explanation). Significant differences ($P \leq 0.05$) are indicated with different letters in superscript.

	<i>Dicorynia</i> (n)	<i>Pourouma</i> (n)	<i>Cecropia</i> (n)
Density in 1992 (n/100 m ²)			
Closed forest	3.4 ^c (145)	1.5 ^b (64)	0.02 ^a (2)
Canopy gap	10.9 ^d (82)	2.7 ^{bc} (20)	1.9 ^b (14)
Survival 1992–1993 (%)			
Closed forest	71.7 ^c (104)	57.8 ^b (37)	0.0 ^a (0)
Canopy gap	82.9 ^d (68)	95.0 ^d (19)	57.1 ^{ab} (8)
Relative height growth (cm cm ⁻¹ y ⁻¹)			
Closed forest	0.15 ^a (104)	0.07 ^a (37)	– (0)
Canopy gap	0.11 ^a (68)	0.28 ^b (19)	0.21 ^{ab} (8)

investigated seedling density within the seed dispersal range (30 m, after Loubry 1993) around one large *Dicorynia* tree (dbh=71 cm) which was situated at the edge of one of the canopy gaps. A randomisation test revealed a significantly higher seedling density in the canopy gap than under the closed forest canopy, being in accordance with the pattern found on the whole transect. We concluded that the higher *Dicorynia* seedling density in canopy gaps compared to the closed forest conditions was not caused by differences in the proximity of seed sources.

Between November 1992 and November 1993, *Dicorynia* seedling establishment was low, and did not differ significantly between canopy gaps (1.3 / 100m²) and closed forest (0.5/100 m²; randomisation test). Establishment of *Pourouma* seedlings was very low, and did not differ between closed forest conditions and canopy gaps (both 0.1/100 m²). *Cecropia* seedling establishment was not observed between November 1992 and November 1993.

Annual survival of *Pourouma* and *Dicorynia* seedlings was higher in gaps than in the forest (Table 1). The two closed forest individuals of *Cecropia* did not survive, while eight of the 14 individuals in canopy gaps did survive. Under a closed forest, *Dicorynia* survival was higher than *Pourouma* survival.

Pourouma seedlings grew significantly faster in gaps than in closed forest. Height growth of *Dicorynia* seedlings did not differ significantly between closed forest and gaps. In canopy gaps, *Pourouma* seedlings grew significantly faster than *Dicorynia* seedlings.

Large canopy gap

Density and survival of the different pre- and post-gap seedling cohorts are depicted in Figure 2. Of the post-gap seedlings, the *Dicorynia* 1991-cohort had a lower initial density than the *Dicorynia* 1992-cohort. However, the 1991-cohort seemed to survive better than the 1992-cohort. *Cecropia* seedlings recruited at a high density after gap formation but their number of survivors was low (Figure 2).

From 1991–1992 height growth of the post-gap *Dicorynia* 1991-cohort was significantly higher than that of the pre-gap *Dicorynia* seedlings (Table 2). From 1992–1993, there was no significant difference between height growth of the *Dicorynia* 1991- and 1992-cohorts, but from 1993–1995, the 1992-cohort grew faster than the 1991-cohort. Height increment of pre-gap *Pourouma* seedlings was lower in the first year than in the second year after gap formation, and lower between 1993–1995 than in the first year. Between species, pre-gap *Pourouma* seedlings grew faster than pre-gap *Dicorynia* seedlings. Height growth of post-gap *Cecropia* was higher height increment of post-gap *Pourouma* seedlings, and pre- and post-gap *Dicorynia* seedlings (Table 2). Height increment of all seedlings cohorts (apart from pre-gap *Dicorynia* seedlings) was lower during 1993–1995 than in the previous year.

Of the 61 (post-gap) seedlings of *Cecropia*, 50 had germinated on the gap floor, and 11 germinated on woody parts of the largest fallen tree. Annual

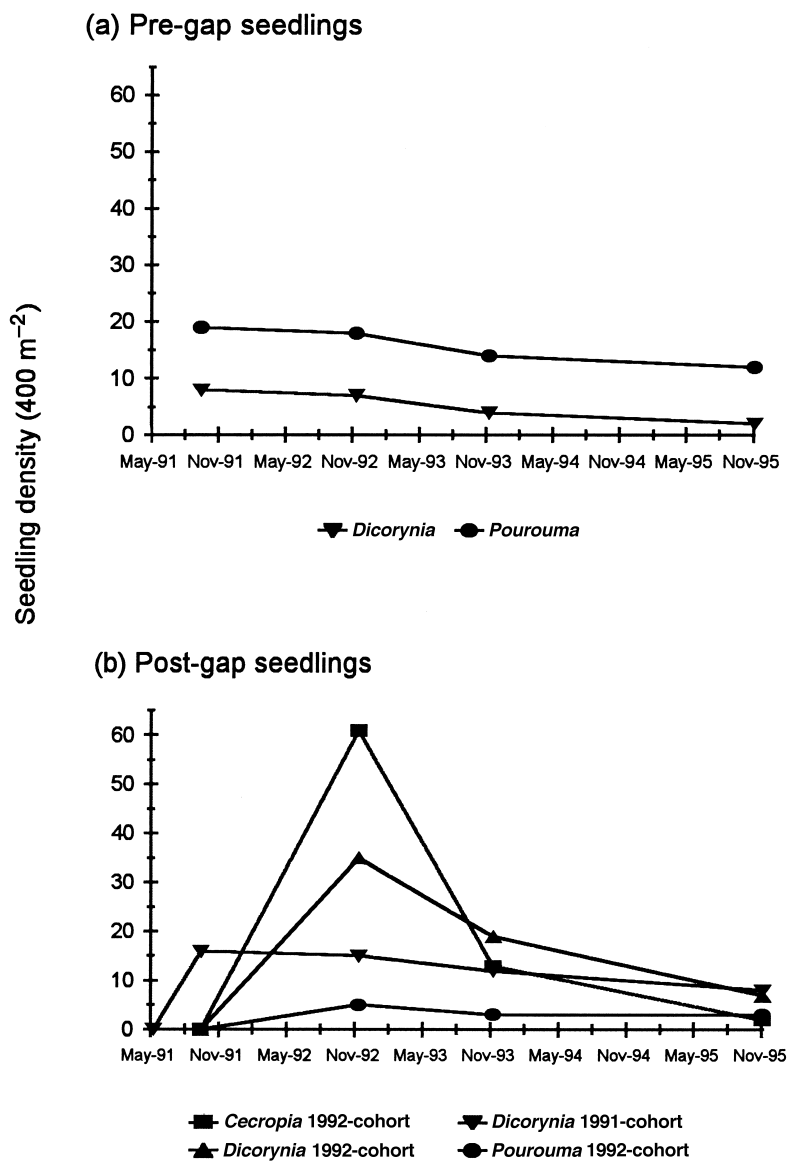


Figure 2. Densities and survival of (a) pre-gap and (b) post-gap seedling cohorts of three tree species in a large canopy gap in a tropical rain forest in French Guiana. Gap creation was in May 1991, and observations were made in September 1991 and in November 1992, 1993 and 1995.

survival during the first year was significantly higher for seedlings germinated on the fallen tree than for seedlings germinated on the gap floor (55 and 14% respectively; randomisation test, $P < 0.05$). After three years, the two sole survivors were seedlings which had established on dead wood. Also, relative height growth of the seedlings on dead wood was significantly higher than height growth of seedlings on the gap floor (randomisation test, $P < 0.05$).

Table 2. Relative height growth of seedlings of three tree species in a large canopy gap in tropical rain forest in French Guyana over three consecutive periods. Randomisation tests were used to investigate differences in relative height growth ($P \leq 0.05$) (see text for further explanation). Significant differences are indicated with different letters in superscript.

Species	Cohort	Relative height growth ($\text{cm cm}^{-1} \text{y}^{-1}$)					
		1991–1992		1992–1993		1993–1995	
			(n)		(n)		(n)
<i>Dicorynia</i>	pre-gap	0.12 ^{ab}	(7)	−0.09	(4)	0.11	(2)
	1991	0.29 ^{cd}	(15)	0.28 ^{bcd}	(12)	0.06 ^a	(8)
	1992			0.34 ^d	(19)	0.20 ^{bc}	(7)
<i>Pourouma</i>	pre-gap	0.28 ^{cd}	(18)	0.44 ^c	(14)	0.10 ^a	(12)
	1992			0.44	(3)	0.07	(3)
<i>Cecropia</i>	1992			0.71 ^f	(13)	0.18	(2)

Large canopy gap: variation in light availability

We constructed a light availability map using the 3-y average DSF values of the 67 grid-points (Figure 3). The average DSF in the extended gap area was 12.4% (range = 3.7–29.4%; $n = 42$), which was significantly higher than the average DSF in the first 5 m of the adjacent forest (7.9%, range = 3.0–15.1%, $n = 25$; randomisation test, $P < 0.05$). Within the extended gap area, we found a significant difference between the central gap zone (16.6%; $n = 15$), and the zone outside the central gap zone (‘outward gap zone’) (10.1%; $n = 27$; randomisation test, $P < 0.05$).

The (post-gap) *Dicorynia* 1991-cohort showed a clear preference for the darker places within the gap (Figure 4). In contrast, pre-gap *Dicorynia* seedlings and the 1992-cohort did not show a clear pattern with respect to the light availability. Pre-gap *Pourouma* seedlings were more abundant in darker than in lighter gap locations. Because of the low number of post-gap seedling establishment ($n = 5$), we could not investigate the relation between light and the location of *Pourouma* seedling establishment. Post-gap *Cecropia* seedlings have a distinct preference for the lighter places in the gap (Figure 4).

The average DSF above pre-gap *Pourouma* seedlings, and the post-gap *Dicorynia* 1991- and 1992-cohorts did not differ significantly from each other (randomisation test, $P > 0.05$). The DSF above post-gap *Cecropia* seedlings was significantly higher than the DSF above pre-gap *Pourouma* seedlings and both post-gap *Dicorynia* seedlings cohorts. The survival rate was not affected by the DSF for any of the three species in any group: we did not find significant differences between the DSF above surviving seedlings and above seedlings which had died (randomisation test, $P < 0.05$).

Height increment between 1992–1993 of *Cecropia*, *Dicorynia* 1992-cohort, and pre-gap *Pourouma* seedlings was significantly related to the DSF (Figure 5). No significant effect of DSF on height growth was detected for growth between 1991–92. Seedling growth between 1993–1995 was not investigated as light availability was only measured from 1991–1993.

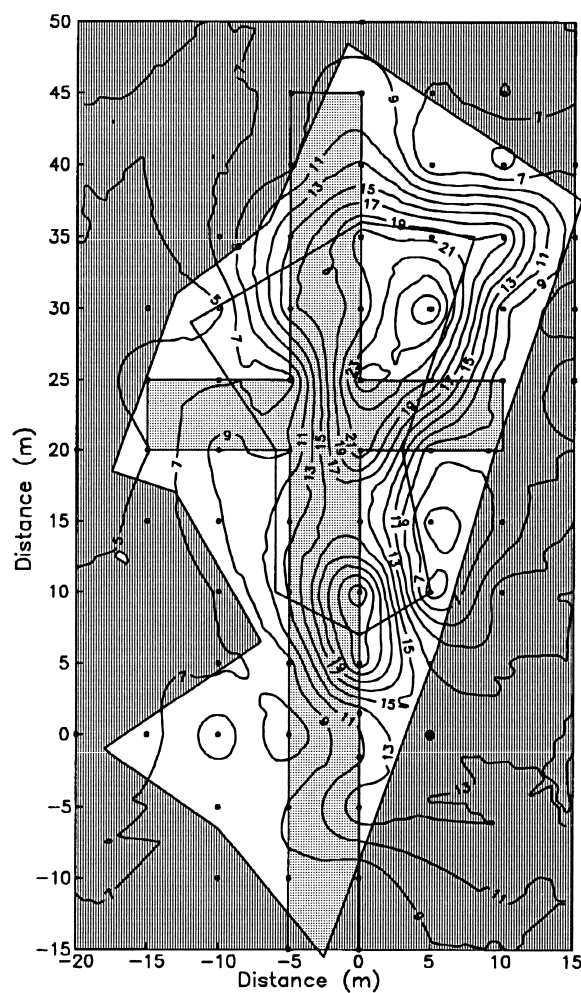


Figure 3. Light distribution in a large canopy gap (white area marks the extended gap area = 965 m², *sensu* Runkle 1981) in a tropical rain forest in French Guiana. Isolines represent 2% intervals of the average direct site factor between 1991 and 1993. Black dots indicate the location of the grid-points where hemispherical photographs were made. The forest adjacent to the extended gap area is shaded; the central gap area is indicated by the inner polygon. Transects where seedling performance was monitored are indicated by the shaded cross.

DISCUSSION

It is well known that *Cecropia* spp. only recruits in large, young (1–2-y-old) canopy gaps (e.g. Brokaw 1987, Schulz 1960, Vazquez-Yanes & Orozco-Segovia 1987). High levels of light availability may be related to high variations in temperature and other micro-environmental factors (e.g. Bazzaz & Wayne 1994), which may trigger germination of *Cecropia* spp. (Vazquez-Yanes & Orozco-Segovia 1987). In the studied forest transect, *Cecropia* was only found in the largest canopy gap, and no *Cecropia* seedlings established in the canopy gaps between 1992 and 1993 when the gaps were older than 2 y.

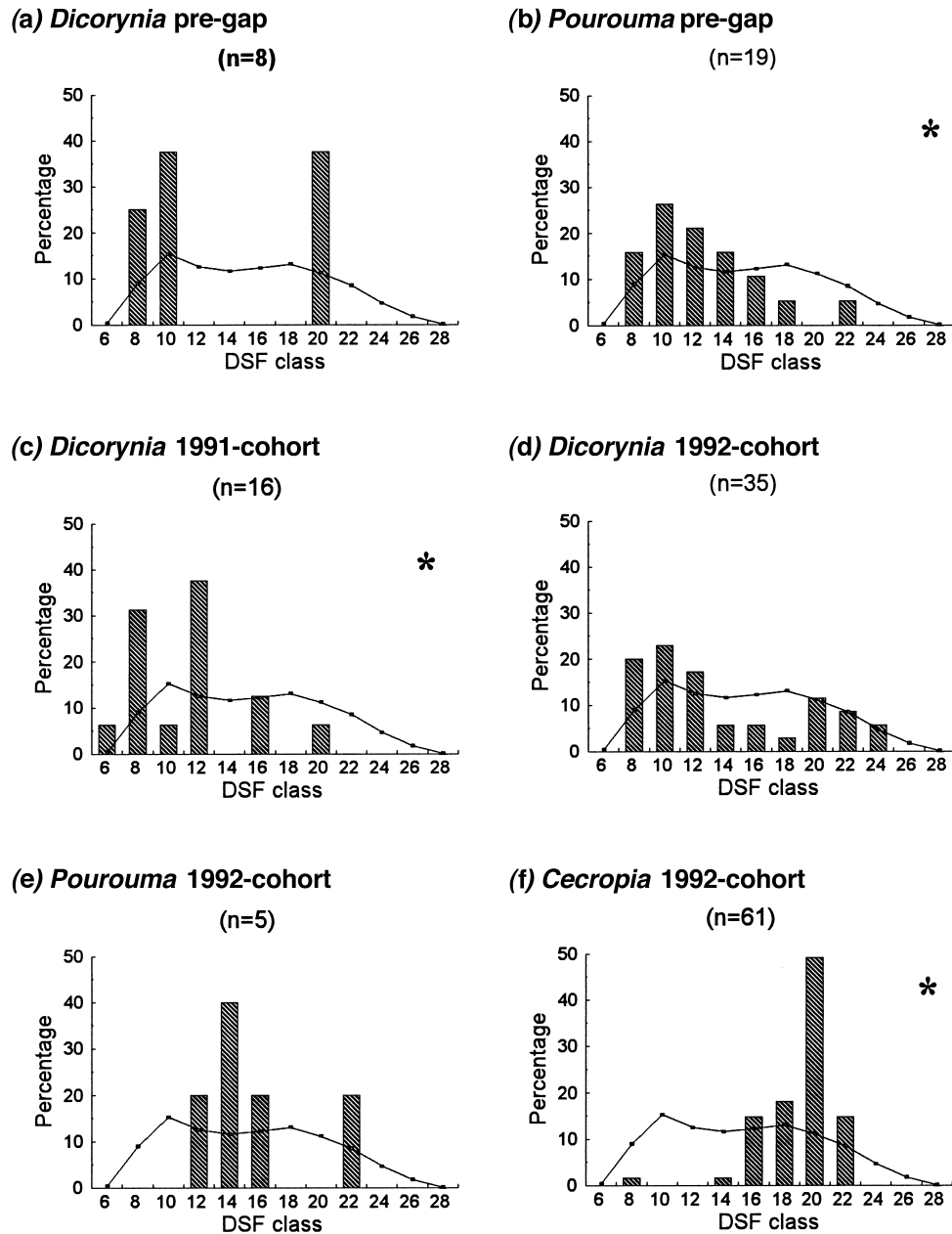


Figure 4. Frequency distribution of the light availability (the average direct site factor between 1991 and 1993) above the transect area in a large canopy gap (line), and above tree seedlings on that transect of three species (bars). Tree seedling cohorts were assigned in two groups: seedlings established before gap formation ('pre-gap' seedlings), and seedling cohorts which established after gap formation. An * indicates a significant difference between the two frequency distributions (seedlings vs. studied transect area) (Kolmogorov-Smirnov test, $P \leq 0.05$).

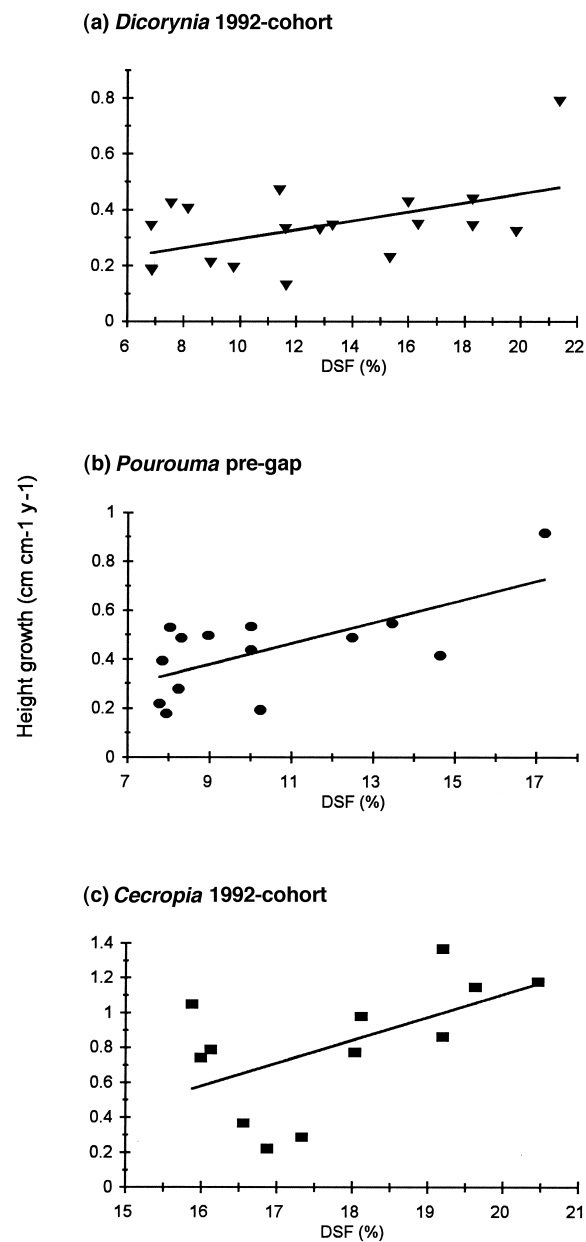


Figure 5. Relationships between relative height growth and light availability (direct site factor, DSF) for seedlings of three tree species in a large canopy gap in a tropical rain forest in French Guiana. Only significant ($P \leq 0.05$) linear regressions are shown. Equations are: (a) *Dicorynia*: $RGR = 0.14 + 0.02 * DSF$; $r^2 = 0.26$, $P = 0.02$; (b) *Pourouma*: $RGR = -0.003 + 0.043 * DSF$; $r^2 = 0.44$, $P = 0.01$; (c) *Cecropia*: $RGR = -1.52 + 0.13 * DSF$; $r^2 = 0.32$, $P = 0.05$.

The high gap density of *Dicorynia* may have been caused by a relatively higher input of *Dicorynia* seeds (anemochorous) into canopy gaps than in closed forest sites, as was observed for other wind-dispersed seeds by Augspurger & Franson (1988). Between 1992–1993, we did not find a significant difference between the number of new recruitment in the ageing (2–3-old) gaps and under the closed forest canopy which indicates that *Dicorynia* recruits mainly in young gaps.

Pourouma spp. seedlings are most likely to establish under a closed forest canopy, and are able to survive without much growth for long periods of time (F. Bongers, unpubl. data; King 1993). The relatively large *Pourouma* seeds are abundantly consumed by kinkajous (*Potos flavus*), red howler monkeys (*Alouatta seniculus*), and other arboreal animals (D. Julien-Laferriere, unpubl. data). Accordingly, seeds may be mainly dispersed under a closed forest canopy, as arboreal animals are unlikely to defecate in canopy gaps (Schupp *et al.* 1989). Concentrations of seeds and seedlings may appear at places where animals frequently defecate (e.g. under sleeping sites and large trees where animals frequently sleep), which explains the observed clustering in small groups of most seedlings. The density of *Pourouma* seedlings was higher (but not significantly so) in gaps than under a closed forest canopy, which is likely to have been caused by the significantly higher survival and growth rate of (pre-gap) seedlings in canopy gaps.

Orians (1982) suggested that the internal heterogeneity of (large) gaps affects the location of seedling establishment and the growth rate of species. Indeed, Barton (1984), Brandani *et al.* (1988) and Popma *et al.* (1988) found evidence that, within gaps, seedling performance may differ between gap zones. Nunez-Farfan & Dirzo (1988) discovered that of two dominant tree species in gaps, *Cecropia obtusifolia* seedlings survived better in the crown zone (cf. Orians 1982) than in the root zone, and that *Heliocarpus appendicularis* showed the opposite response. However, in these studies, seedling performance was not directly linked to the variation in micro-environmental factors within the gap zone.

In the large canopy gap, we found a smooth continuum of decreasing light availability from central gap locations to the adjacent closed forest. Similar to the observation of Brown (1993, 1996), this resulted from a gradual increase in over-topping tree crowns and other vegetation towards the adjacent forest. Light availability was highest in the crown zone of a canopy gap. However, we found a second local maximum in light availability (Figure 2), associated with the former location in the canopy of the crown of the tree which initiated the gap. The smooth changes in light availability from gap centres to adjacent forest provides for different habitats which may be exploited by different species.

We did not observe *Cecropia* seedling establishment during the first inventory (4 mo after gap formation). Also, some 20% of the seedlings had germinated on top of dead wood, which shows that at least some new seeds were dispersed

into the gap area. In the surrounding 12-ha plot, and also outside this plot, several fruiting *Cecropia* trees were observed during the field work periods (P. J. Van der Meer, *pers. obs.*). Fruiting of *Cecropia* species may be almost continuous, and seeds may be dispersed at least 86 m from parent trees, for instance by birds or bats (Alvarez-Buylla & Martinez-Ramos 1990, Charles-Dominique 1986, Estrada *et al.* 1984). Thus, for at least the wood-occupying seedlings we assume that they originate from fruiting trees and not from dormant seeds in the soil. In Mexico, dormant seeds in the seedbank of the closely related species *Cecropia obtusifolia* contribute less to new seedling establishment in gaps than freshly arrived seeds (Alvarez-Buylla & Martinez-Ramos 1990, Martinez-Ramos & Alvarez-Buylla 1986). They expected no seeds to survive more than 2 y after they reached the soil. However, Holthuijzen & Boerboom (1982) found that *Cecropia* seeds buried for long periods in ceramic pots (and thus excluded from pathogens and predators) were still able to germinate.

Germination on top of dead wood was highly advantageous for *Cecropia*. Riera (1985) also observed the importance of treefall mounds for successful germination and survival of *Cecropia obtusa*, and suggested that this was related to microclimatic factors. However, light availability (calculated from hemispherical photographs made at 25 cm height) did not differ significantly between 'gap floor' sites and 'dead wood' sites (randomisation test, $P < 0.05$). This suggests that 'dead wood'-*Cecropia*'s may profit from a reduced competition for other resources (e.g. space), or may profit from an enhanced level of inputs (nutrients, water) from the dead wood. Individuals germinating on dead wood may have higher chances on future growth and survival than those on soil substrate as they have already achieved some height gain at the time of germination and may outgrow those on the forest soil. Also, *Cecropia* seedlings growing on dead wood may be less likely to be shaded out by falling litter than soil individuals.

Pre-gap *Pourouma* seedlings were more abundant in darker places than lighter places in the gap which is probably the effect of the destruction of seedlings in the central zones by falling branches and foliage. Locations in gap edges may be advantageous as environmental stress (water, temperature) may cause a higher mortality in gap centres than in gap edges (e.g. Brown 1993, 1996). In this way, seedlings have the time to adjust to the new micro-environment, which may take more than 6 mo (Popma & Bongers 1991). The pre-gap *Pourouma* seedlings seem to require at least 1 y to adjust to the new light environment as the relative height growth rate of pre-gap *Pourouma* seedlings was significantly affected by the DSF during the second year, but not during the first year following gap creation. Also, the growth rate was higher in the second year than in the first year. This time lag between the gap creation and growth responses of seedlings is larger than the time lag found by others (Bongers *et al.* 1988, Fetcher *et al.* 1987, Newell *et al.* 1993, Popma & Bongers 1991). An explanation for this discrepancy may be that the seedlings in our

study suffered from drought stress due to the increased light levels whereas seedlings in the acclimation experiments of others may have been watered to prevent them from drought stress. Another reason may be that younger seedlings (in the experiments) react faster than the older seedlings in this study.

The post-gap *Dicorynia* 1991-cohort seedlings had a preference for the darker sites of the canopy gap. In contrast, the post-gap 1992-cohort did not show a preference for a particular light environment. This may be explained by the large amount of fresh leaves and branches in the central (lightest) gap zones following the gap creation, preventing successful germination and/or establishment of the 1991 cohort in those zones. In the subsequent year, with the gradual decomposition of this organic material, these zones may have become more receptive for *Dicorynia* germination and establishment. The higher growth rates (1993–95) of the 1992-cohort indicate that these seedlings were in a better competitive position. The DSF above the 1992-cohort survivors in 1995 was 15.1% (n=7), whereas the DSF above 1991-cohort survivors in 1995 was 10.8% (n=8), although this difference was not found to be significant (randomisation test, $P > 0.05$).

Most seedling cohorts of the three species seem to have had a lower annual growth rate between 1993–95 than in the previous years. This may have been caused by the increasing competition for light, nutrients and water from surrounding vegetation and other gap regeneration, and points to the fact that light availability not only varies in space but also in time.

Although the number of gaps studied here was low, and for a generalisation of the results further studies are needed, this study shows that seedling establishment, early growth and survival of the three tree species were affected by canopy gaps, and by the environmental heterogeneity in a large gap.

Cecropia not only specialises in large gaps, but also for specific sites in the large gap: seedling performance is increased by light and by dead wood. *Pourouma* mainly germinates under closed forest conditions, where it can survive for a long period until a canopy gap is formed nearby. Once a gap is formed, survival and growth of *Pourouma* seedlings is enhanced, but they do not specialise for specific places in the gap. Seedling location is mainly determined by the accidental positioning before gap formation, and by the position of the fallen stems and branches. *Dicorynia* is able to germinate and grow successfully in gaps and under closed forest conditions. Seedlings of this species have higher chances on survival and grow faster in gaps compared to closed forest.

In general these data support the idea that seedlings of species perform differently in relation to closed forest versus gaps and also in relation to the spatial heterogeneity within gaps.

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