Selbyana 18(1): 38–50

VEGETATION DEVELOPMENT IN CANOPY GAPS IN A TROPICAL RAIN FOREST IN FRENCH GUIANA

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ABSTRACT. Canopy gaps in tropical forests are important for regeneration of many species. Rates of gap formation are well studied, but data on rates of canopy gap closure are scarce. In this study I investigate how development of vegetation in recently created canopy gaps in a pristine tropical rain forest varies between three small and three large gaps.

The percentage of space occupied by vegetation ("vegetation occupation") was determined at one meter intervals through the expanded gap area (divided in a central and peripheral gap zone), and the first meters of the closed forest adjacent to gaps. Vegetation occupation above each inventory point was determined in three height ranges in different intervals: 0–>30 m (5 m intervals); 0–10 m (1 m intervals), and 0–2 m (0.25 m intervals). Inventories were done in October 1991 and November 1993.

In the central zone of small gaps, the net change in vegetation occupation was strongest in the 0–>30 m range, whereas in the central zone of large gaps, vegetation occupation increased mainly in the lower height ranges (0–2 and 0–10 m). Small gaps seem to fill mainly by means of lateral ingrowth of surrounding trees, and large gaps fill mainly through growth of gap floor regeneration (both advanced regeneration and new recruitment). I estimate that on average, small gaps "disappear" within 5 to 6 years after formation. In large gaps, it may take between 5 to 10 years before a canopy layer has been established which is at least 10 m high.

INTRODUCTION

Natural forests may be seen as a mosaic of forest patches in different developmental stages. Aubréville (1938) was one of the first to describe the cyclic nature of tropical rain forest regeneration, which was later called the mosaic theory of regeneration by Richards (1952). Watt (1947) recognized gap, building, mature, and degenerate phases in his studies on heather vegetation, which was later adapted to tropical forests by Oldeman (1978) and Whitmore (1978). Oldeman (1978, 1990) identified forest patches in reorganizing, aggrading, biostatic and degrading stages, calling them 'eco-units.' Whitmore (1975, 1978) adapted this concept to tropical rain forests in distinguishing three structural phases (gap, building, and mature) of forest, and named this the forest growth cycle. It is clear that canopy gaps, often created by the fall of one or several trees or branches, may be considered as the starting point of the forest growth cycle. Many studies demonstrate the ecological importance of canopy gaps on population dynamics of tropical tree species (for reviews see Denslow 1987, Denslow & Spies 1990, Platt & Strong 1989).

Regrowth in canopy gaps originates potentially from two sources: (1) regeneration from the gap floor (vertical growth); and (2) lateral ingrowth of branches from trees adjacent to the gap. Gap floor regeneration, either as plants established prior to gap creation, or as plants established after gap creation, is the focus of several studies. Brokaw (1985a, 1985b), and Brokaw & Scheiner (1989), studied gap regeneration over several years in 17 canopy gaps. In numerous other studies, seedling and sapling performance was monitored in and around gaps to obtain more information about species response to canopy gaps (e.g. Bongers *et al.* 1988, Brown 1993, de Steven 1988, Popma & Bongers 1988, Turner 1990a, 1990b, Uhl *et al.* 1988, Welden *et al.* 1991). In general, recruitment and growth of seedlings and saplings is enhanced in gaps. In comparison to gap floor regeneration, lateral ingrowth of branches from trees in the adjacent forest in canopy gaps has been less studied. Runkle & Yetter (1987) found the vertical increment of gap floor regeneration in canopy gaps in a temperate forest to be faster than lateral ingrowth. Young & Hubbell (1991) found that many crowns of trees adjacent to canopy gaps were asymmetrical, suggesting that these trees grew more rapidly into gaps than into the closed forest. It has been suggested that in general, large gaps close by vertical growth, and small gaps by lateral growth (e.g., Denslow 1987). Also, the speed of these processes may be affected by gap size. For instance, plant growth can be expected to be higher in large

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gaps than in small gaps, as fast-growing pioneer species only germinate in large gaps (e.g., Brokaw 1985a).

Within canopy gaps, vegetation structure (i.e. height and form) and micro-climate may vary greatly (Brown 1993, Canham *et al.* 1990, Chazdon & Fetcher 1984). Canopy gaps have been divided into different zones by several authors (e.g. Orians 1982, Nunez-Farfan & Dirzo 1985). Accordingly, processes of gap regeneration may differ across gap zones. Brandani *et al.* (1988) found differences in seedling germination between the root, bole, and crown zone of gaps, and Barton (1984) found higher pioneer densities in the center than in the edges of large gaps. Also, vertical growth of seedlings is expected to be an important way of gap filling in the central gap zone, whereas lateral ingrowth of branches may be more important in the peripheral zone of canopy gaps (Bazzaz 1984).

Canopy gaps not only stimulate vegetation growth, they may also increase mortality of the vegetation in their immediate environment. The sudden increase in light availability after gap formation can cause photoinhibition in the shade-grown seedlings and saplings, resulting in partial or complete mortality of the plant (e.g. Oberbauer & Strain 1985, Kamaluddin & Grace 1992, Lovelock *et al.* 1994). Also, branches of adjacent trees which were damaged by the gap creation may eventually die. Several studies mention that trees adjacent to canopy gaps are more likely to fall than trees farther away from gaps (Brokaw 1985a; Lang & Knight 1983; Putz & Milton 1982; Young & Hubbell 1991). However, Van der Meer & Bongers (1996) found that canopy gaps did not increase the chances of surrounding trees to initiate a tree- or branchfall.

The rate of gap formation in tropical forests has been studied extensively; about 1–2% of the forest canopy is annually opened up by falling trees or big branches (e.g. Clark 1990; Jans *et al.* 1993; Hartshorn 1990). In contrast, the process and rate of canopy gap closure is less well studied (e.g. Rebertus & Veblen 1993). Observations on both gap floor regeneration and lateral ingrowth into gaps are mostly on individual plants or on populations of plants, and can not easily be used for extrapolations to processes on the vegetation level. Published data on processes and rate of the development of a new vegetation layer in canopy gaps are scarce. Hubbell & Foster (1986) give some information on change in vegetation structure, but they do not reveal at what rate canopy gaps close.

The aim of this study was to reveal how the development of vegetation in canopy gaps varied between small and large gaps. I investigated how vegetation structure in different gap zones of small and large gaps changed during the first two years following gap formation. Also, I studied patterns of vegetation growth and mortality, and whether they differed between small and large gaps. Finally, I investigated how fast canopy gaps were filled by new vegetation.

METHODS

The study was conducted at the Nouragues field station, located in the pristine lowland rain forest of French Guiana (4°05′N; 52°40′W; FIGURE 1). The forest canopy height ranges between 20–40 m, with emergents to 60 m tall. Annual rainfall averages around 3000 mm, with a distinct dry season from September to November and a less conspicuous dry season around February. The hilly topography ranges between 60–120 m above sea level (a.s.l.), with some higher peaks between 300–450 m high. The area where this study was performed is on a relatively flat plateau, ranging in elevation between ca. 90–110 m a.s.l.. The plateau has well drained, clayey to sandy-clayey soils on weathered granite parent material. In the same area, a permanent sample plot of 12 ha was established in 1991 to investigate natural treefalls and canopy dynamics (Van der Meer & Bongers 1996).

In the study area, I selected three large and three small recent canopy gaps, which were not older than two years. Sizes of the large gaps were 965, 758 & 575 m^2, and of the small gaps 255, 232 & 187 m^2 (i.e. expanded gap size = area bordered by the stembases of canopy trees >20 m tall surrounding the canopy opening; after Runkle 1981). This is in accordance with Barton (1984), who used a breakpoint of 300 m^2 (expanded gap size) to divide 23 gaps in large and small gaps. The three large gaps had been created by the fall of several trees. Two small gaps had been created by the fall of a major branch, the third small gap by the fall of two trees (>20 cm dbh).

In and around the gaps I defined three gap zones (FIGURE 2). Firstly, within the expanded gap area, I distinguished the *central gap zone* (gap area with no vegetation over 20 m high; adjusted after Brokaw (1982) by Van der Meer & Bongers (1996), and the *peripheral gap zone* (gap area between the central gap border and the expanded gap border). Secondly, outside the expanded gap area, the first 1–5 meters in the adjacent forest were defined as the *adjacent forest zone.* In the following text, I shall refer to all three zones as "gap zones" (including the ad-

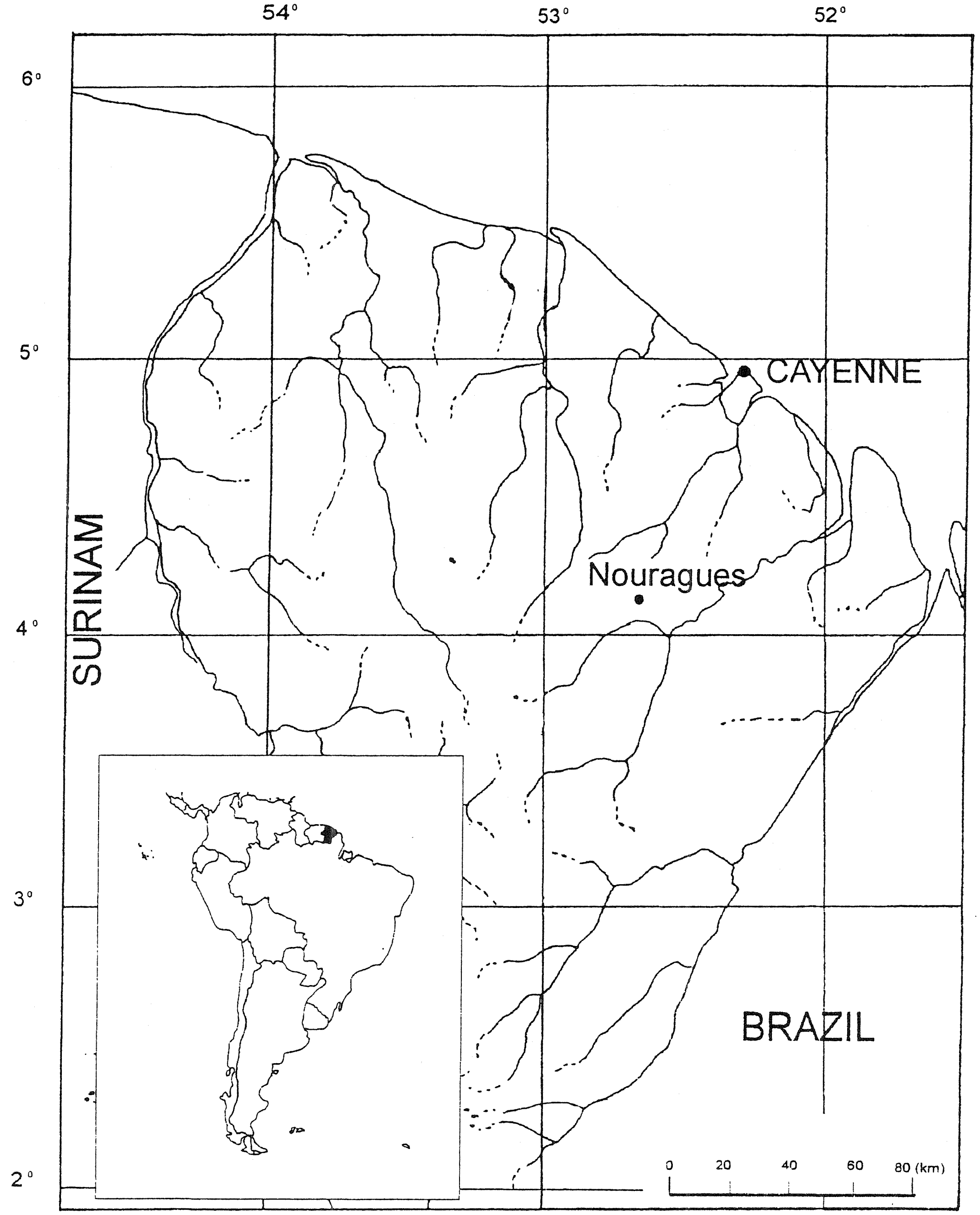

FIGURE 1. Location of biological research station "Nouragues," French Guiana.

jacent forest zone, which is strictly speaking not a gap zone).

Vegetation Occupation

Two perpendicular inventory lines (North–South and East–West) were located through the gap center, extending over the whole gap area and the first 1–5 meters of the adjacent forest (FIGURE 2). Inventory lines were between 20–65 m long, and were permanently marked with plastic pickets at 5 meter intervals. During both inventories, a measuring tape was placed along the inventory line, and vegetation structure was

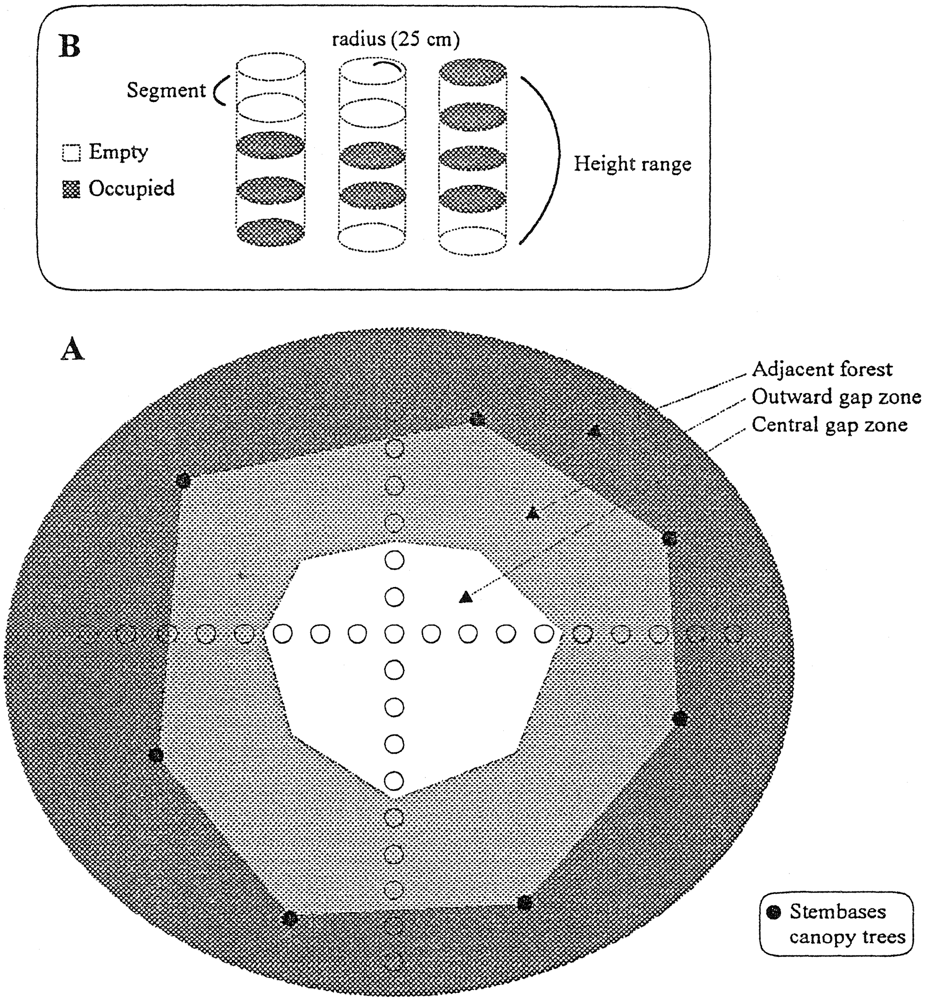

FIGURE 2. A. Schematic aerial view of a (small) imaginary canopy gap. The central gap zone is bordered as soon as vegetation is >20 m tall. The peripheral gap zone is bordered by the stembases of the canopy trees (>20 m tall) surrounding the canopy gap. Small circles indicate the line of inventory points (at one metre intervals) where vegetation occupation was determined (see **B**). **B**. Vegetation occupation above inventory points is determined in imaginary cylinders. Each cylinder has radius of 25 cm, and is divided in a certain number of segments, depending on the height range:
(1) whole range (0–>30 m): seven intervals (segments); each segment is five meter high; (2) range between 0–10 m, ten segments of one meter each; (3) range between 0–2 m, eight segments of 0.25 meter each. For each segment, presence ("occupied") of absence ("empty") of vegetation is determined. Vegetation occupation is determined as the percentage of the segments which is occupied. See text for further explanation.

determined above each meter (after Hubbell & Foster, 1986): presence or absence of vegetation was determined in imaginary vertical cylinders with a radius of 25 cm above each meter point. This was done in three height ranges, using different height intervals or levels of resolution: (1) whole range (0–>30 m), in five meter intervals; (2) range between 0–10 m, in one meter intervals; (3) range between 0–2 m, in 0.25 meter intervals.

Vegetation occupation (percentage of gap-space occupied by vegetation) was calculated as follows (FIGURE 2). When we would consider 10 inventory points, there are 10 cylinders in which the presence or absence of vegetation is determined. At a resolution of 5 meters, there are seven height intervals or "segments" per cylinder, so that in total 70 (10 × 7) segments are considered. When 35 segments contain vegetation, vegetation occupation is 50%. Obviously, this does not imply that 50% *of the volume* in the cylinders actually contains vegetation, but that 50% *of the segments* in the cylinders contain vegetation. Of the segments which contained vegetation, it proved not possible to determine the density of the vegetation. This implies that segments which contain one small branch, and segments which contain several dense leaf layers, both contribute equally to the vegetation occupation.

Vegetation occupation was determined in October 1991 and November 1993 in exactly the same manner. I checked whether the vegetation occupation in large gaps differed from vegetation occupation in small gaps. Also, I investigated whether in 1993 the vegetation occupation had changed significantly from the vegetation occupation in 1991 (=net vegetation change). Each gap was considered as one observation, so that for both large and small gaps there were three observations (per height range and per gap zone). A Student's t-test was used to test for differences in vegetation occupation.

Gain & Loss in Vegetation Occupation

The net change in vegetation occupation is the result of vegetation growth and vegetation mortality. The *gain in vegetation occupation* was defined as the gap segments which had been empty in 1991, and were filled by new vegetation in 1993. Similarly, the segments which had been occupied by vegetation in 1991, and were empty in 1993, were marked as the *loss in vegetation occupation.* As this study focuses on processes of gap filling, both gain and loss are expressed in terms of percentage of the gap volume (in reality: percentage of the segments) which was newly occupied or was lost. I checked whether percentages gain and loss differed between large and small gaps (Student's t-test). Also, I investigated whether the average vertical height of the "gain segments" and "loss segments" differed significantly between large and small gaps.

Central Gap Zones: Vegetation Occupation & Canopy Layer

For the central gap zone only, I investigated whether the vertical height of the net change in vegetation occupation between 1991–1993 differed between large and small gaps. This was done for all three height ranges. For each gap, the average percentage vegetation occupation was determined per height class. Accordingly, for both large and small gaps, I had three values per height class. With these values I determined the average occupation per height class for large and small gaps. The distribution of the vegetation occupation percentages over height classes was compared between large and small gaps (Kolmogorov-Smirnov test).

Also for the central gap zones only, the average vertical height of the "canopy layer" was investigated. Per gap, the vertical height of the highest segment which was occupied by vegetation was determined above each inventory point (in 0–>30 m range). By averaging these values, I obtained the average vertical height of the canopy layer per gap. Increase in the lower canopy layer (between 0–10 m) was determined above those inventory points where the canopy layer was lower than 10 m in 1991. I checked whether between 1991–1993 the vertical height of the canopy layer had changed significantly (Student's t-test).

A telescopic measuring pole (SENSHIN PAT. Prod.; max. height 8.25 m) with a small leveller was used to determine the exact horizontal and vertical position above each point. A pentagon prism was used to determine the presence of vegetation above the point higher than 8 m; an optical range finder (Ranging Optimeter 120; range 2–30 m) was used to determine the height of this vegetation. Statistical analyses were done using the SPSS package version 6.

RESULTS

Vegetation structure was determined above 218 points in large gaps and 133 points in small gaps (TABLE 1). Average diameter of the central gap zone was 17 m for large, and 6 m for small gaps. The expanded gap zone (central and peripheral gap zone; see FIGURE 2) of large gaps and small gaps had an average diameter of 32 m and 15.5 m respectively.

Vegetation Occupation in 1991 and 1993

The percentage vegetation occupation in both 1991 and 1993 is generally higher in large gaps than in small gaps, but differences were not always significant (TABLE 2). Also, as expected, vegetation occupation is generally lower in the central gap zone than in peripheral and adjacent forest zone in both small and large gaps.

Net vegetation change between 1991 and 1993 in the 0–>30 m height range seems to be more substantial in small gaps than in large gaps (but n.s.; FIGURE 3). In contrast, in the lower height ranges (at higher levels of resolution), net vegetation change seems to be more important in large gaps than in small gaps. In small gaps,

TABLE 1. Number of inventory points per gap zone, for three large and three small gaps. Above each point, vegetation abundance was determined in 3 height ranges at different levels of resolution (see text for further explanation). Expanded gap size (after Runkle 1981) is given behind gap number. The average width of the central and expanded gap zone are given.

	Number of inventory points in gap zones				Width of gap zone (m)	
	Central	Peripheral	Adjacent forests	Total	Central	Peripheral
Large gaps						
Gap 1 (965 m^2)	39	45	12	96	19.5	42.0
Gap 2 (758 m^2)	34	19	8	61	17.0	26.5
Gap 3 (575 m^2)	30	24	7	61	15.0	27.0
All	103	88	27	218	17.0	32.0
Small gaps						
Gap 4 (255 m^2)	12	20	14	46	6.0	16.0
Gap 5 (232 m^2)	13	20	13	46	6.5	16.5
Gap 6 (187 m^2)	11	17	13	41	5.5	14.0
All	36	57	40	133	6.0	15.5

net vegetation change decreases from the gap center toward the adjacent forest, especially in the 0–>30 m height range. In large gaps, trends between gap zones are less clear.

Gain & Loss in Vegetation Occupation

In the 0–>30 m range of central gap zones, the gain in vegetation occupation is significantly faster in small gaps than in large gaps (TABLE 3). In contrast with this, gain in vegetation occupation is faster in large gaps than in small gaps in the lower height ranges (0–10 m & 0–2 m). Also, the gain in vegetation occupation differs between gap zones: in general, gain decreases from the gap center toward the adjacent forest. Only in large gaps, the gain seemed to increase from the gap center toward the adjacent forest. Differences between vegetation loss in large gaps and loss in small gaps, or between gap zones, did not show clear trends (TABLE 3).

The average vertical height of the gain was significantly larger in small gaps than in large gaps in the 0–>30 m range of the central and the peripheral gap zone (Student's t-test; $p < 0.05$). In the 0–10 m and 0–2 m height range I did not encounter such clear differences in the vertical height of vegetation gain of large and small gaps. The vertical height of vegetation loss did not differ significantly between large and small gaps.

Central Gap Zones: Vegetation Occupation & Canopy Layer

In the central gap zone of small gaps, vegetation occupation between 0–>30 m seemed to change more and at larger vertical heights than

TABLE 2. Vegetation occupation in three large and three small canopy gaps in 1991 and 1993. Occupation of vegetation is calculated as the percentage of the gap where vegetation was present (see text for further explanation). Occupation was determined in 3 different height ranges (from 0–>30 m; between 0–10 m; and between 0–2 m), and in three different gap zones. Significant differences between large and small gaps are indicated beween the rows with an "x" (Student's *t*-test; $P < 0.05$).

		Vegetation occupation 1991 (%)			Vegetation occupation 1993 (%)		
Height range	Gap size	Central	Peripheral	Adjacent forest	Central	Peripheral	Adjacent forest
0–>30 m	Large (*N* = 3)	32.2	69.2	72.0	35.5	70.5	75.8
			x				x
	Small (*N* = 3)	28.8	59.0	67.1	39.0	65.3	64.8
0–10 m	Large (*N* = 3)	34.2	57.0	50.6	45.3	62.9	62.8
			x		x	x	
	Small (*N* = 3)	24.4	33.8	39.5	28.6	38.0	41.3
0–2 m	Large (*N* = 3)	43.4	57.1	47.4	56.8	66.6	54.2
	Small (*N* = 3)	45.2	55.1	49.7	55.2	64.4	58.7

TABLE 3. Gain and loss in vegetation occupation in three large and three small canopy gaps during two years. Gain is calculated as the % of the gap which was open in 1991 and occupied by new vegetation in 1993. Loss is calculated as the % of the gap which was occupied by vegetation in 1991 and was empty in 1993. Gain & loss were determined in 3 different height ranges (from 0–>30 m; between 0–10 m; and between 0–2 m) and in three different gap zones (see text for further explanation). Significant differences between large and small gaps are indicated beween the rows with an "x" (Student's *t*-test; $P < 0.05$).

		Gain in occupation (%)			Loss in occupation (%)		
Height range	Gap size	Central	Peripheral	Adjacent forest	Central	Peripheral	Adjacent forest
0–>30 m	Large ($N = 3$)	7.6	9.5	10.0	4.3	8.1	6.3
		x					
	Small ($N = 3$)	17.4	11.3	7.6	6.6	5.1	9.9
0–10 m	Large ($N = 3$)	16.4	14.0	15.2	5.3	8.1	3.0
			x	x		x	
	Small ($N = 3$)	9.6	9.3	7.5	5.4	5.0	5.7
0–2 m	Large ($N = 3$)	22.2	19.2	13.1	8.8	9.7	6.3
		x					
	Small ($N = 3$)	16.3	15.0	15.2	6.3	5.6	6.3

in the central zone of large gaps (FIGURE 4). In contrast, at the lower height ranges (0–10 m & 0–2 m) in the central zones, changes in small gaps were less important than in large gaps. The average vertical height of the canopy layer in the 0–>30 m range increased faster in small gaps than in large gaps (TABLE 4). The increase in vertical height of the lower canopy layer (0–10 m) was slightly faster in large gaps than in small gaps. However, in neither case, were differences significant (Student's t-test).

To visualize the process of gap filling between 0–>30 m, the canopy heights above each point in the central zones of large gaps (103 points) and small gaps (36 points) were "symmetrically" ordered. The lowest canopy height was placed in the center of the gap, and increasing heights were placed (at both sides of the center) at increasing distance of the center. This was done for both 1991 and 1993 (FIGURE 5). These transformed canopy layer diagrams do not represent the exact situation as observed in the field for two reasons. First, each diagram is the sum of the canopy layer of three gaps. Secondly, canopy heights in 1991 and 1993 above each point in the diagram are most likely to be values above different points. For instance, point A might have the highest canopy value in 1991, but the third-highest in 1993. Consequently, point A will have a different position on the x-axis in 1991 and 1993. Despite this simplification, the diagrams illustrate clearly the different patterns of increment in the average canopy layer height in the central gap zones of large and small gaps. Also, they indicate the rate at which processes take place.

DISCUSSION

Origin of Gap Regrowth: Gap Floor Regeneration Versus Lateral Ingrowth

Regrowth in gaps originates from gap floor regeneration, from lateral ingrowth of branches, or from both. The patterns of gap floor regeneration are best described by the changes in vegetation occupation in the lower height ranges (0–2 and 0–10 m), whereas the vegetation occupation at the 0–>30 m range is more appropriate to study the lateral ingrowth of branches. As the central gap zone is the zone where the larger changes will occur, we focus here on the processes in the central gap zones.

Light availability in canopy gaps is generally higher in large than in small gaps (e.g. Whitmore *et al.* 1993). Consequently, colonisation and growth of seedlings and saplings is generally enhanced with an increase in gap size (e.g. Brokaw 1985a, Popma & Bongers 1988, de Steven 1988, Kennedy & Swaine 1992, Popma & Bongers 1991, Runkle & Yetter 1987). Also, lateral expansion of saplings may increase in larger gaps (e.g. Ogden *et al.* 1991). In this study, gap floor regeneration seems to be more important in large gaps than in small gaps too: the net change in vegetation occupation between 0–2 and 0–10 m is larger in the central zone of large gaps than of small gaps (FIGURES 3 & 4). Vegetation gain rather than vegetation loss is responsible for these differences (TABLE 3).

The net change in vegetation occupation in the 0–>30 m range is larger in small gaps than in large gaps (FIGURES 3 & 4), which may indicate that the lateral ingrowth of branches is

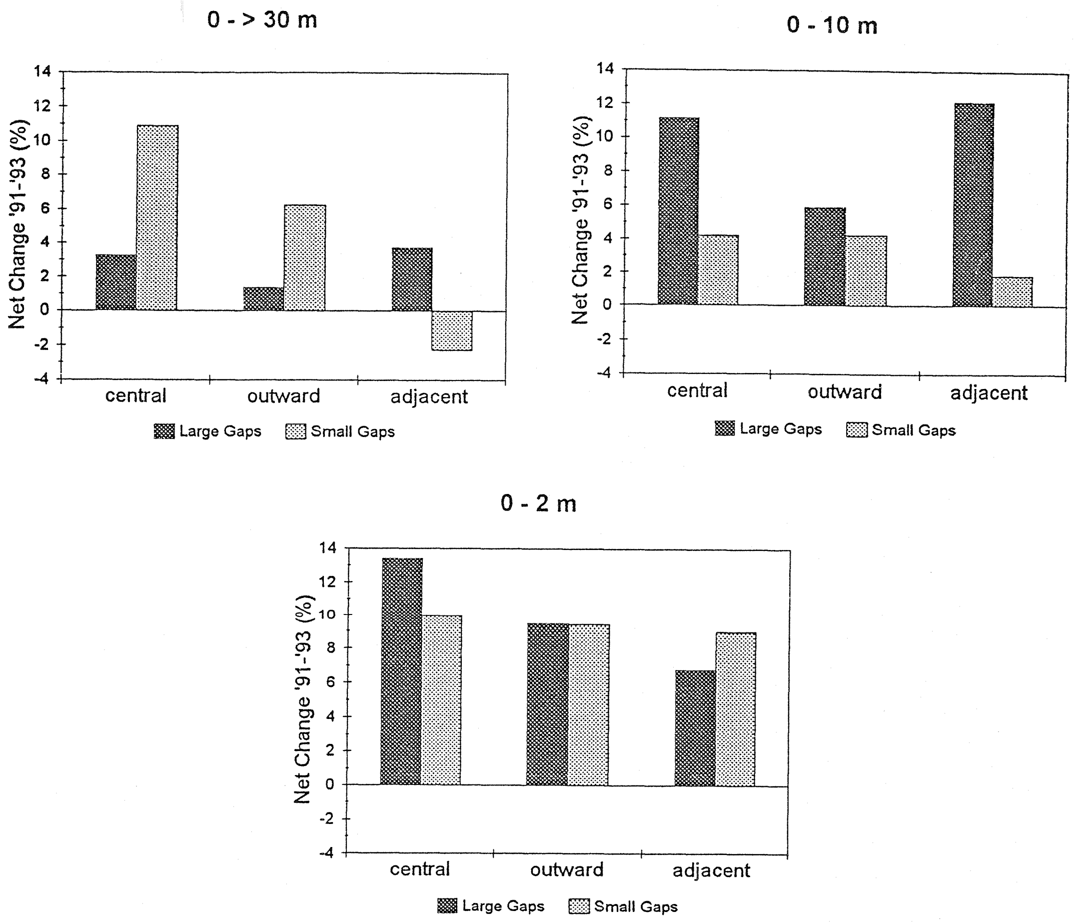

FIGURE 3. Net change in vegetation occupation between 1991 and 1993 in three large and three small gaps. For each height interval, net change was measured in central, peripheral, and adjacent forest gap zone. Differences between large gaps and small gaps were not significant (Student's t-test).

especially important in small gaps. The gain of vegetation is more substantial in the central zone of small gaps than of large gaps, whereas vegetation loss does not differ between large and small gaps (TABLE 3). Also, vegetation gain in small gaps takes place at larger vertical heights than vegetation gain in large gaps. Although I did not directly measure the origin of the vegetation gain, I believe that most gain in the central zones of small gaps originated from lateral crown expansion of trees adjacent to the canopy gap (Van der Meer, personal observation). The vertical expansion of vegetation in small gaps was in most cases not large enough to be measured in the 5 meter resolution.

Vegetation occupation and change in occupation are calculated in terms of the percentage of gap volume, which might have consequences when comparing large and small gaps: one meter lateral ingrowth has a relative larger effect in small gaps than in large gaps. From this it could be derived that absolute rates of lateral branch growth may not differ between large and small gaps. However, calculations on the rate of gap filling suggest that also in absolute terms, lateral growth in small gaps is faster than in large gaps (see below: speed of initial gap filling). Also, it remains undisputed that lateral branch growth is relatively more important in small gaps than in large gaps.

There are at least two arguments which might explain the possible lower lateral growth rates of branches around large gaps. First, a significant higher proportion of the trees adjacent to large gaps has a damaged crown (by the gap creating event) than of the trees surrounding small gaps. This was found in another study in the Nouragues forest, where 55.6% of the trees

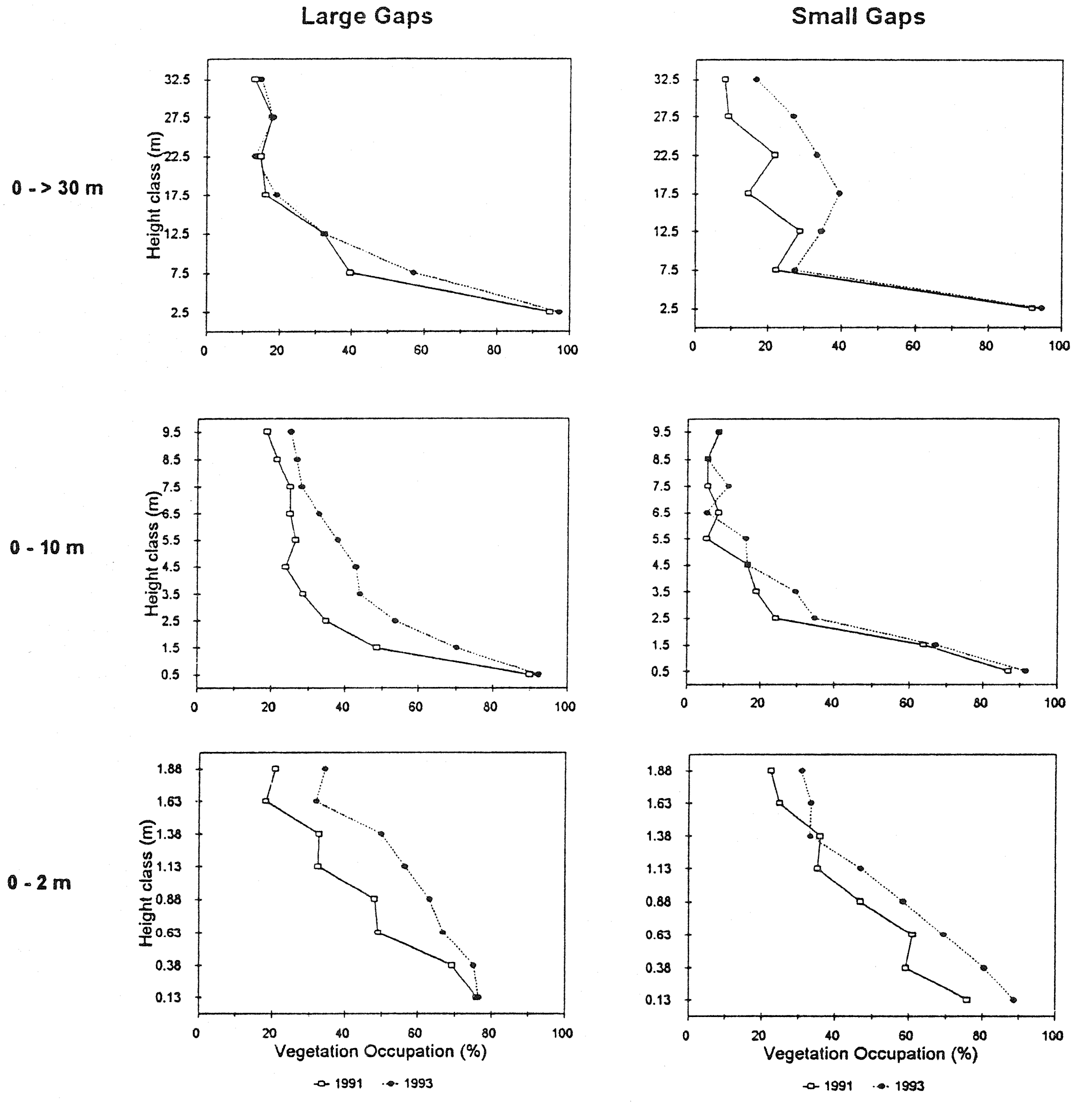

FIGURE 4. Vegetation occupation per height interval in 1991 and 1993 in the central gap zones: averages of three large and three small gaps. Vegetation occupation is expressed as the percentage of the gap where vegetation was present, and was determined in three height ranges (see text for further explanation).

adjacent to large gaps were damaged, against 31.6% of the trees adjacent to small gaps (van der Meer, unpublished data). Damaged trees may have higher rates of mortality than undamaged trees (e.g. Clark & Clark 1991, Putz & Chan 1986), and may not be able to respond as readily to the increased light levels around canopy gaps as non-damaged trees. A second possible explanation might be that a higher percentage of the leaves of trees around large gaps experience photoinhibition (e.g. Lovelock *et al.* 1994, Mulkey & Pearcy 1992) than around small gaps, due to the higher light levels in large gaps.

It is important to note that the patterns described in this study are based on processes of initial gap filling. Ultimately, it is likely that also trees adjacent to large gaps will expand their crown more readily into the gap area than into the forest. For instance, Young & Hubbell (1991) found that many trees adjacent to large gaps had asymmetrical crowns into their adjoining gap.

TABLE 4. Height of the canopy in the central gap zones in 1991 and 1993 for two height intervals. For the canopy layer between 0–>30 m, all inventory points were used. For the canopy layer between 0–10 m, only those inventory points were considered which had no vegetation above 10 m in 1991 (51 of the 103 points in large gaps, and 17 of the 36 points in small gaps). Mean height increment (between 1991 and 1993) of the canopy layer in large gaps did not differ significantly from increment in small gaps (Student's *t*-test).

	Canopy layer height (m)			
	(0–>30 m)		(0–10 m)	
	1991	1993	1991	1993
Large gaps				
Gap 1	16.0	14.0	2.3	3.5
Gap 2	12.1	14.3	5.7	5.9
Gap 3	9.8	11.1	2.2	5.3
Mean	12.6	13.1	3.3	4.9
Small gaps				
Gap 4	15.4	19.6	4.8	6.0
Gap 5	7.9	18.3	1.9	3.5
Gap 6	15.7	21.1	1.5	1.8
Mean	12.8	16.4	2.7	3.8

Vegetation Occupation: Differences Between Gap Zones

For both large and small gaps, differences in vegetation occupation between gap zones is largest in the 0–>30 m range, and diminishes in the lower height ranges (TABLE 2). After two years, the differences between gap zones in vegetation occupation in the 0–2 m height range has largely disappeared in both large and small gaps. Eventually, when vegetation starts to fill in gaps, differences between gap zones will disappear in all height ranges. However, local differences in vegetation occupation may persist, for instance due to species composition.

For most height ranges, the vegetation occupation in the adjacent forest increased between 1991 and 1993, which is most likely the effect of the increased light levels and consequent higher rates of plant growth. Especially between 0–10 m, vegetation occupation increased markedly in the forest surrounding large gaps (FIGURE 3). This indicates that canopy gaps also may affect vegetation dynamics at larger distances from the gap center, as was stressed already by others (e.g. Popma *et al.* 1988).

Vegetation occupation might continue to increase during the years following 1993, but is expected to reach eventually similar values as were found for vegetation occupation in 1991 in the adjacent forest area (TABLE 1). The vegetation occupation does not seem to reach 100% coverage in any of the height ranges, which is understandable as it is unlikely that the complete forest volume would contain foliage and branches.

Speed of Initial Gap Filling

In comparison with the numerous studies on canopy gap formation, only a few studies deal with actual processes of natural vegetation regrowth in canopy gaps. Brokaw (1982, 1985a, 1985b) was one of the first to monitor regrowth in canopy gaps, and focused mainly on seedling or sapling performance of some species. Runkle (1982), and Runkle & Yetter (1987) investigated rates of height growth and lateral expansion of saplings in canopy gaps in the Smoky Mountains. In the same forest, Barden (1989) mentions closure rates for canopy gaps ranging between 5–12% annually. Ogden *et al.* (1991) estimated that median sized gaps in subalpine and montane forest in New Zealand were filled in by lateral branch expansion in some 31–44 years.

Mature forest in Nouragues is characterised by a more or less continuous canopy layer, ranging in height between 20 and 40 m, with occasional emergents to 50 or 60 m. On average, 85% of the forest adjacent to the six gaps had a canopy layer of at least 25 m in 1991 (92.3% in 1993). The average canopy height for the forest adjacent to gaps was 28.6 m in 1991 (29.6 m in 1993). Accordingly, I assume that gaps have filled in and returned to the closed forest situation when the gap zone has a continuous canopy layer between at least 25–30 m height.

In the central zone of large gaps, the average height of the canopy layer between 0–>30 m did not increase between 1991 and 1993 (FIGURE 5). However, in small gaps, the canopy layer between 0–>30 m increased by some seven meters. If average canopy height continues to increase at the same rate (3.5 m annually), the small gaps will have a closed canopy layer (between 25–30 m) some five to six years after gap creation. This will mainly be by means of lateral ingrowth of branches. The speed at which this happens seems to decrease with an increase in height (FIGURE 5). This may be related to a more severe midday depression of photosynthesis higher in the canopy (as a result of lowered air humidity higher in the canopy) (e.g. Roy & Salager 1990). However, more data are needed to be able to corroborate this.

Annual height increment of the canopy layer between 0–10 m was on average 0.8 m in large gaps (TABLE 4). This height increment is caused by both height increment and lateral expansion of (fast-growing) saplings. In large gaps, some fast-growing pioneers (like *Cecropia spp.*, *Mi-*

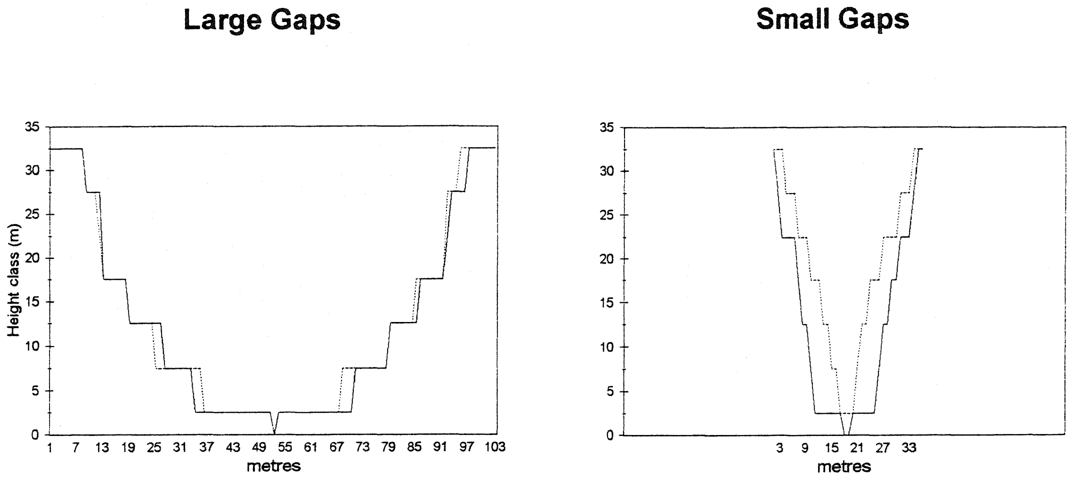

FIGURE 5. Idealized canopy layer in the central gap zones in '91 and '93 between 0–>30 m. Canopy height (maximum height of observed vegetation) above each point in the central zones of large gaps (103 points or cylinders) and small gaps (36 points or cylinders) were "symmetrically" ordered. The lowest canopy value was placed in the centre of the gap, and increasing heights were placed (at both sides of the centre) at increasing distance of the centre (see text for further explanation). Diagrams do not represent actual field situations, but visualise the general trend of the rate and the height at which large and small gaps fill in.

conia spp., etc.) established between 1991 and 1993 (Van der Meer personal observation), eventually may have growth rates of several meters per year (e.g. Brokaw 1985b). Considering that large gaps had an average canopy height of 3.3 m in 1991, I estimate that between 5–10 years after gap formation, vegetation in large gaps will have formed a canopy layer of at least 10 meters height. In the same time, a considerable but unknown part of the canopy layer is likely be higher than 10 meters.

In the central zones of small gaps, height increment of the canopy layer between 0–10 m was slightly less fast (0.6 m annually) than in large gaps, and is believed to be caused mainly be lateral expansion of crowns of saplings. In small gaps however, the vegetation layer between 0–10 m will after several years be overtopped by a canopy layer at higher vertical heights, and growth rates may drop accordingly.

The average height of the canopy layer in 1991 varied considerably within both large gaps and small gaps (TABLE 4). This may be caused by differences in the amount of advanced regeneration which survived the gap formation, or by the differences in gap age. This was however not further analysed.

CONCLUSIONS

Vegetation occupation in gaps changed considerably during two years. As expected, vegetation growth in small gaps originates mainly from lateral growth of branches of trees adjacent to gaps. In large gaps, initial vegetation growth originates mainly from growth of gap floor regeneration. Vegetation grew fastest in gap centers, and decreased toward the gap edges. However, also in the forest adjacent to gaps, vegetation occupation increased in the two years following gap formation.

Most of the vegetation gain (open space in 1991 which was occupied by new vegetation in 1993) was situated in the central gap zones. In the peripheral gap zone and the adjacent forest, vegetation gain was less important. In small gaps, vegetation gain in the central gap zone (between 0–>30 m) was more important and took place at larger vertical height than in large gaps. Loss of vegetation in and around canopy gaps was not affected by either gap zone or gap size.

On average, small gaps will persist five to six years after formation. In large gaps, it may take between five to ten years before the vegetation has formed a canopy layer of at least 10 meters high. I found few significant differences in vegetation occupation between large and small gaps, or between 1991 and 1993. This suggest that it is preferable to study more gaps, and/or to extend the period of observation. In this way it is possible to further investigate rates of gap closure, which are needed for a better understanding of the role canopy gaps play in providing resources for plant species in tropical rain forests.

ACKNOWLEDGMENTS

I want to thank the following persons: Frans Bongers, Jan den Ouden, Lourens Poorter, Marinus Werger and Marius Wessel for comments on earlier drafts of the paper. Pierre Charles-Dominique for permission to stay in Nouragues. Ed de Bruin for assistance with making some of the figures. Yonke van Geloven, Dorothé Jacobs, Jan Jansen, Kees Konings, Joep and Marian Van der Meer for field assistance. I am grateful to foundation "Het Kronendak" for financial support.

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