Canopy dynamics of a tropical rain forest in French Guiana

De kronendak-dynamiek van een tropisch regenbos in Frans Guyana
(met een samenvatting in het Nederlands)

La dynamique de la canopée dans une forêt tropicale humide en Guyane française
(avec un résumé en français)

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Canopy dynamics of a tropical rain forest in French Guiana

Proefschrift
ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen
op gezag van de rector magnificus,
dr. C.M. Karssen,
in het openbaar te verdedigen
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ABSTRACT

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The canopy dynamics (i.e. the formation and closure of canopy gaps) of a tropical rain forest in French Guiana are described. The formation of canopy gaps is investigated. The difficulties with gap size measurements are studied, and causes and consequences of treefalls and branchfalls are examined. It is concluded that canopy gap location is not random. Soil factors may make some areas in the forest hot spots of disturbances, whereas other areas are less frequently disturbed. Furthermore, the closure of canopy gaps and tree seedling performance in gaps are discussed. Recruitment in gaps is largely determined by the fortuitous occurrence of seedlings and sapling that were present before the gap was formed. Specialisation of species is discussed and its concluded that detailed information on micro-habitat availability (in gaps) and on micro-habitat needs of species may indicate which individuals at which location have the highest chance of survival. Finally, the potential application of these findings for application in forest practices are examined.

CIP-DATA KONINKLIJKE BIBLIOTHEEK, DEN HAAG

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Stellingen behorende bij het proefschrift getiteld "Canopy dynamics of a tropical rain forest in French Guiana" van P.J. van der Meer, te verdedigen op 20 October 1995.

1. Open plekken zijn niet alleen voor planten maar ook voor onderzoekers de "hot spots" van tropisch regenbos.

2. Bij het vergelijken van het ontstaan van open plekken in tropische regenbossen wordt vaak onvoldoende rekening gehouden met (1) de invloed van de gehanteerde definitie van open plekken en (2) de onnauwkeurigheid van het meten (dit proefschrift).

3. Niet alle vallende bomen maken een open plek (dit proefschrift).

4. Niet alle open plekken zijn gevormd door gevallen bomen (dit proefschrift).

5. In het onderzochte bos in Nouragues ontstaan open plekken niet geheel willekeurig verspreid: hun locatie hangt samen met bodemfactoren (dit proefschrift).

6. Randen van grote open plekken worden regelmatiger verstoord door nieuwe vallende bomen en takken dan kleine open plekken (dit proefschrift).

7. Het bestuderen van de populatie-dynamiek van (boom-)soorten is essentieel voor het beter begrijpen van het functioneren van tropische bosecosystemen.

8. De snelheid en manier van het ontstaan en dichtgroeien van open plekken in natuurlijk regenbos moet als uitgangspunt dienen bij het ontwerpen van ecologisch verantwoorde uitkapsystemen.

9. Het aantal wetenschappelijke publicaties over tropisch regenbos is postitief gecorreleerd met de omvang waarmee tropisch regenbos verdwijnt.

10. Als het tropisch regenbos omschreven kan worden als de "groene hel", en het schrijven van een proefschrift als de "papieren hel", dan is het beter branden in de groene dan in de papieren hel.

11. Het sterk groeiende aantal AIO's leidt tot een steeds groter wordende probleemgroep op de arbeidsmarkt: de baanloze doctoren.

12. Voor bomen is het net zo belangrijk als voor mensen om op het juiste tijdstip op de juiste plaats te zijn.

voor pa en ma

Voorwoord

Mijmeringen van een jonge doctor in spé....

En daar zit je dan, het concept proefschrift naast je, klaar, af ! Al die jaren heb je hier naar uitgekeken en inderdaad, het kan dus niet anders dan een beetje tegenvallen nu. Wel een lekker gevoel dat het af is maar toch blijft er iets knagen omdat je het idee hebt dat het toch beter, anders, leuker had gekund. Maar goed, dat is het kruis dat je denk ik als perfectionist/twijfelaar met je mee moet dragen.

De basis voor dit proefschrift werd gelegd in November 1989, gedurende een "droomreis" naar Frans Guyana. Tijdens deze reis bestudeerden we met het kronendak-vlot de toppen van het regenbos. Vervolgens bezochten we het diep in het oerwoud verborgen onderzoeksstation Nouragues, waar je slechts per helikopter kon komen. Diep onder de indruk raakte ik daar van wat volgens mij één van de mooiste plekken op aarde is, en het was dan ook een perfecte plek voor een promotie-onderzoek. In de daarop volgende jaren heb ik met veel plezier in Nouragues gebivakkeerd: het leven midden in de natuur onder vrij primitieve omstandigheden was een zeer bijzondere ervaring: de grootsheid van het oerwoud, de schitterende planten en de onverwachte ontmoetingen met dieren hebben veel indruk op me gemaakt. Ik zal nooit het panorama vanaf de "inselberg" vergeten: zover het oog reikt onverstoord regenbos zonder ook maar een spoor van menselijke beschaving. De vele mede-onderzoekers in Nouragues, die een grote verscheidenheid aan onderwerpen onderzochten, maakten de veldwerk-perioden niet alleen leuk maar ook zeer leerzaam. Desondanks heb ik het verblijf in het bos ook weleens vervloekt: maandenlang opgesloten, levend in een klein kamp met continu dezelfde mensen om je heen kan af en toe heel benauwend worden. Ook de eentonigheid brak me soms weleens op: de komst van de helikopter was vaak de meest enerverende gebeurtenis van de maand, met als het meezat stapels post. En gelukkig zat het meestal mee, en blijft "Nouragues" een onvergetelijke ervaring.

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..en de bedankjes.

Tijdens en bij al dat wetenschappelijke gepuzzel heb ik heel wat hulp van anderen gehad. Ten eerste natuurlijk van Door. Van al die mensen die ik verder ga noemen is zij verreweg de belangrijkste geweest die ervoor gezorgd heeft dat dit boek hier nu zo voor U ligt. Zeker in de beginjaren waren de langdurige maar gelukkig tijdelijke "scheidingen" niet leuk, en voelden we ons vaak als een zeemans-paar. Ook de laatste maanden waren niet makkelijk, het leek er soms wel eens op dat ik met het proefschrift getrouwd was in plaats van met haar. Het is een cliché en het is dus echt waar: zonder haar steun had ik dit nooit kunnen doen.

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Wessel en Professor Werger wil ik beiden bedanken voor hun support en hun adequate en snelle commentaar op de vele manuscripten.

Tijdens het veldwerk in Frans Guyana werd ik geholpen door een aantal studenten: Lars Chatrou en Ad Koning; Job Engelage, Patrick Jansen en Lidewij van Katwijk; Andreas Hofmann; Yonke van Geloven, Jan Jansen en Kees Konings; Jan-Willem Gunnink, jullie wil ik graag hartelijk bedanken voor de samenwerking en gezelligheid. Ook Peter Leersnijder, Door, Joep en Marian wil ik bedanken dat ze het aangedurfd hebben mij te bezoeken in Frans Guyana en te helpen met het vaak saaie veldwerk. Daragh Little ben ik erkentelijk voor de analyse en interpretatie van een groot aantal fish-eye foto's.

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Peter van der Meer,
Wageningen, september 1995.

Contents

CHAPTER 1

General introduction

Canopy dynamics in a tropical rain forest in French Guiana:

General introduction.

Tropical rain forests

Tropical rain forests occur in the warm, ever-humid areas between the tropics of Cancer and Capricorn. They are found in areas where in general, the mean monthly temperature is never below 18° C, and annual rainfall exceeds 2000 mm (e.g. Jacobs 1981; Whitmore 1990). In this large globe-spanning zone of tropical rain forest potential, forests may show a marked variation: without considering azonal forests (e.g. mangroves, swamp forests, heath forests etc.), species composition and structure of rain forests vary between continents, and regionally.

Tropical rain forests have several characteristics in common, however. They all consist of woody, evergreen vegetation. Trees make up most of the biomass. Their crowns generally form a canopy between 30 - 50 metres above the ground, but emergent trees may reach up to about 70 metres. The overwhelming diversity of plant and animal species is one of the most noted features: tropical rain forests, which cover only seven percent of the earth's land area, are believed to contain more than half of all plant- and animal species (Wilson 1988).

In some areas, indigenous people still totally depend on forest resources for their daily living. On a much larger scale, tropical forests are being used by "urbanised" people; they provide wood, meat, fish, fruits, rattan, medicines, and many other kinds of products. Conversion of tropical rain forests into agricultural lands, and at a smaller scale logging of forests for wood, are two of the main causes of the rapid decline of tropical rain forests (e.g. Werger 1992; Whitmore & Sayer 1992). One way which may help to stop this deforestation is to develop alternative ways to use the forest in a "sustainable" way (Gomez-Pompa & Burley 1990). Also, it is important to know how to preserve the immense diversity of these forests, which can only be achieved through a proper understanding of the ecology of tropical rain forests (see reviews by Gomez-Pompa *et al.* 1990; Lieth & Werger 1989).

The canopy of tropical rain forests

The upper layer of the forest, "the canopy", is an important part of tropical rain forests. Most of the photosynthetically active foliage of tropical rain forests is found here: a large proportion (up to 99 %) of the daily sunlight is intercepted by the forest canopy (e.g. Canham *et al.* 1990; Kira & Yoda 1989). Another important feature of tropical rain forest canopies is that plant diversity is high, for instance through the diverse communities of vascular epiphytes (e.g. Nadkarni 1994). The forest canopy provide habitats for many animals species: Erwin (1982) estimated that insect communities in the canopies of tropical rain forests accommodated some 30 million species.

Since the early 1970's there has been a vast increase in the number of studies focusing on forest canopy structure (Nadkarni & Parker 1994). Several new access methods were developed or more intensively used (rope climbing, tree-top raft, aerial walkways, crane, spikes, etc.). Also, several international research groups have been formed which focus on different aspects of canopy biology (Stork & Best 1994).

Nadkarni & Parker (1994) define the canopy of a tropical rain forest as "the combination of all foliage, twigs, fine branches, epiphytes, as well as the interstices in a forest". In this thesis, "forest canopy" will be used as a rather loose term to address the uppermost vegetation layer of the forest, without specific details on for instance the depth of this layer. It is important to note that in most cases, the forest canopy is not a clear continuous layer of leaves and branches, but is rather an open, uneven layer with many interstices. Also, the vertical height of the uppermost part of this layer may vary between lower than one metre in canopy gaps (see below), and 50 metres or higher in closed forest.

Canopy dynamics in tropical rain forests

Major catastrophes such as landslides, volcanic eruptions, fire, and hurricanes or cyclones may severely disturb large parts of rain forest areas (e.g. Ashton 1993; Garwood *et al.* 1979, Walker *et al.* 1991a; Webb 1958; Whitmore 1990). Ashton (1993) suggests that on the long term these catastrophes may affect the physiognomy, structure and species composition of the forests. However, large scale disturbances do in general not affect the principles of forest dynamics (e.g. population dynamics of species, growth of individual plants, etc.) on a local, shorter time scale. Usually, large scale disturbances occur at relatively (human life) long time intervals, e.g. once every century or millennium. Hurricanes may occur more frequently, but are mostly confined to coastal areas (e.g. Walker *et al.* 1991b). In Amazonian rain forest, large blowdowns (> 30 ha) may also cause disturbance at a local scale, but are not believed to be an important mechanism of forest dynamics on a regional scale (Nelson *et al.* 1994).

On a smaller time- and spatial scale, tropical rain forests are dynamic. From many studies done in different rain forests all over the world it becomes clear that forest canopies are regularly opened up by the fall of trees or big branches. This creates gaps in the forest canopy, and there a new vegetation starts to develop which eventually closes the gap. Consequently, the forest canopy is a mosaic of patches of different canopy height and structure. The principles of this process were first described by Aubréville (1938) and Richards (1952), and were later elaborated by Hartshorn (1978), Oldeman (1978) and Whitmore (1978). This process of small scale canopy disturbance and the concomitant forest development ("patch dynamics"; White & Pickett 1985) plays an important role in the population dynamics (e.g. recruitment, growth, survival) of many species of tropical rain forests (for reviews see

Bongers & Popma 1988; Denslow 1987; Pickett & White 1985; Platt & Strong 1989). In this thesis, I will focus on these small scale canopy dynamics of tropical rain forests.

Formation of canopy gaps

In tropical rain forests, between 0.5 and 3.6 % of the trees (> 10 cm diameter) die per year (Phillips & Gentry 1994). A large proportion of these trees falls down, and may create canopy gaps ("hole in the forest canopy existing through all height levels", after Brokaw 1982). Estimates on the forest area which is annually affected by canopy gaps range in general between 1-2 % (using Brokaw's (1982) gap definition) (e.g. Clark 1990; Harthorn 1990; Jans *et al.* 1993).

Canopy gaps are easily detected in a tropical rain forest through the increased light levels on the forest floor. In contrast, it is very hard to determine borders of canopy gaps. In general, vegetation density decreases gradually from the undisturbed, closed forest, towards the gap centre, and there is no clear border between the gap area and the adjacent undisturbed forest. The height of the canopy is often used to determine gap borders: Brokaw (1982) for instance borders a gap where vegetation is taller than two metres. Several other gap definitions are used to measure gap sizes, and this is a major problem when comparing results between sites (Clark 1990).

In the neotropics, the rate of canopy gap formation has been investigated in less than ten sites (e.g. overview in Hartshorn 1990). Most of these studies were done in the relatively small rain forest area of Central-America. The rain forests of South America are proportionally very poorly investigated. Of the approximately 3 million km^2 of lowland rain forest in the Amazon Basin (dos Santos 1987), the rate of gap formation was studied on five sites with a total area of only 42.5 ha (0.425 km^2). Most of these 42.5 ha were investigated in French Guiana: 21.3 ha at Paracou by Durrieu de Madron (1994), and 18.8 ha at the Piste de St. Elie by Riera & Alexandre (1988). In Venezuela (Uhl & Murphy 1981) and in Ecuador (Kapos *et al.* 1990) relatively small areas were sampled (1 ha and 2 x 0.7 ha respectively). In French Guiana, between 1.1 - 1.3 % of the canopy was annually opened up by canopy gaps. Accordingly, the turnover time ("number of years it takes to cover a unit area of forest with gaps"; Hartshorn 1990) of these forests varies between 91 and 77 years. Uhl & Murphy (1981), assuming that gaps persist for five years, estimated that 1.0 % of the studied rain forest was annually disturbed by canopy gaps (turnover time = 100 years). Kapos *et al.* (1990) found that 1.4% and 5.1. % of the forest canopy was open in two sites of differing soil type and topography.

It has often been suggested that gaps are spatially clustered: once a canopy gap is formed, the chances increase that a new gap will be formed in its direct neighbourhood. This would be caused by increased turbulence around gaps (Brokaw 1985; Hubbel & Foster 1986a), variation in local topography (Poorter *et al.* 1994), or the asymmetrical crown shape of trees around gaps (Young & Hubbell 1991). This may have implications for the population dynamics of many species, and eventually also for the structure of the forest. For instance, species which can only germinate in gaps ("pioneer" species; see below) will, as a result of gap clustering, show a clustered spatial distribution.

Canopy gap environments

In canopy gaps, availability of plant resources is generally enhanced compared with the resource availability under closed forest. The nutrient availability might increase through the decomposition of fallen debris, although the rate at which this occurs might be marginal (Vitousek & Denslow 1986; Uhl *et al.* 1988). However, the increase in light availability, in gaps but also in the first metres of the adjacent forest, is generally thought to be the most important factor affecting forest regeneration (Clark 1990). In general, light availability beneath a closed canopy is some 1-2 % of the light availability above the canopy, whereas in canopy gaps light availability may increase to 30 % or more (Canham *et al.* 1990; Chazdon & Fetcher 1984).

The spatial and temporal variation in light availability may be considerable in tropical rain forests. The spatial variation in light availability is caused by the differences between gaps (e.g. difference in gap size, gap shape etc.), and also by the internal variation in vegetation structure within gaps (Bazzaz & Wayne 1994; Brown 1993; Canham 1988; Chazdon 1992; Raich 1989; Rich *et al.* 1993; Smith *et al.* 1992; Whitmore *et al.* 1993). Temporal variation in the light-environment of gaps may also be large, for instance through the ingrowth of crowns of surrounding trees (Denslow & Hartshorn 1994).

Stochastically occuring events like tree- and branchfall, create environmental heterogeneity on a micro-scale. According to the gap partitioning and niche differentiation theory, this environmental heterogeneity can be exploited by many different species (e.g. Grubb 1977, Denslow 1980; Orians 1982; Ricklefs 1977). In contrast with the gap partitioning and specialisation concept, it has been proposed that most species are generalists, which is promoted by biotic uncertainty (Hubbell 1979; Hubbell & Foster 1986b). In this view, gap filling is largely determined by the growth of seedlings or saplings which were present before the gap was created.

Vegetation development in canopy gaps

When a gap is formed, the remnant vegetation typically forms a low, uneven canopy layer, which is usually not higher than several metres. At some places in gaps, a vegetation layer may be absent, for instance where large stacks of fallen debris have destroyed and covered all pre-existing vegetation. In newly created canopy gaps, a new patch of forest starts to regrow. This forest patch will form a more or less closed vegetation cover, which gradually grows up to the original canopy stature. Whitmore (1978) identified gap, building, and mature forest patches, and Oldeman (1990) distinguished reorganising, aggrading, biostatic and degrading "eco-units" or "regeneration units" ("*every surface on which at one moment in time a vegetation development has begun, of which the architecture, eco-physiological functioning and species composition are ordained by one set of trees until the end*"). Torquebiau (1987) described a dipterocarp rain forest in Indonesia in terms of a mosaic of eco-units, using tree size and tree architecture to distinguish between different types of eco-units. In three investigated sites, between 14.7 - 17.9 % of the forest surface was in young eco-units (reorganising & aggrading), between 77.4 - 84.2 % in mature (biostatic) forest, and between 1.2 - 4.7 % in senescent (degrading) forest.

Gap regeneration originates from different sources. Small gaps usually fill by lateral branch growth from adjacent trees (Bazzaz 1984; Denslow 1987). With an increase in gap size, gap regeneration originates relatively more from saplings (advanced regeneration) and sprouting of damaged plants. Finally, very large gaps are mainly filled by new colonisers, germinating from seeds which either (1) were present before or (2) arrived after the moment of gap creation (Bazzaz 1984). Despite this knowledge about the general pathways of gap filling, the exact processes and rates of canopy gap closure in tropical rain forests are still poorly understood.

Tree seedling responses to formation of canopy gaps

Plants which have a similar life strategy have been classified in functional groups (Simberloff & Dayan 1991). Some species only germinate in canopy gaps ("pioneers species"), whereas others can successfully recruit beneath a closed canopy, but need gaps for advance growth ("non-pioneer species") (Swaine & Whitmore 1988). This is of course a very broad generalisation, and is based on the ideas of Van Steenis (1958) ("nomad" and "dryads"), and MacArthur & Wilson (1967) ("r" and "K" strategies). Oldeman & van Dijk (1990) not only used the plant's strategy during germination and seedling phase, but also during later phases of its life, to classify trees into six "tree temperaments". The temperaments range from plants which are shade-tolerant during their entire life cycle ("hard strugglers"), via plants that change during their life cycle from shade tolerant to light demanding ("strugglers", "struggling gamblers") or vice versa ("gamblers", "gambling strugglers"), to plants which require light throughout their entire life cycle ("hard gamblers").

The recruitment, growth and survival of seedlings are critical limiting stages in the population structure of tree species (Clark 1986). The effects of canopy gaps on recruitment, growth and/or survival of tree-seedlings have been extensively studied during the last decades. Most of the studies are performed under controlled or manipulated conditions. Several approaches are used: (1) exposing seedlings to different, controlled light levels (e.g. Augspurger 1984; Ashton & De Zoysa 1989; Cornelissen *et al.* 1994; Kamaluddin & Grace 1993; Turner 1989); (2) placing or planting seedlings in gaps and understorey conditions (e.g. Bongers *et al.* 1988; Denslow *et al.* 1990; De Steven 1988; Howe 1990; Osunkoya *et al.* 1993; Popma & Bongers 1988; Schupp 1988); (3) creation of artificial gaps, and studying patterns of recruitment, growth and/or mortality of (established) seedlings therein (Brown & Whitmore 1992; Kennedy & Swaine 1992; Newell *et al.* 1993; Raich & Khoon 1990; ter Steege *et al.* 1994). Despite the range of methodologies used and the different species studied, most studies conclude that light gaps enhance seedling growth, although in some cases seedling growth decreased in very large gaps.

In contrast, only a small proportion of "canopy gap - seedling" studies were performed *in situ*, i.e. investigating the effect of natural gap formation on actual rates of recruitment, growth and survival of naturally occurring seedlings. For instance, Clark & Clark (1987) found that gaps were not necessary for germination and establishment of *Dipteryx panamensis*, but that seedling growth was enhanced by gaps. Nunez-Farfan & Dirzo (1988) found differences in seedling performance between gap zones: for instance, *Cecropia obtusifolia* survived better in the crown than in the root zone (cf. Orians 1982) of gaps. Turner (1990a) found that seedling growth was enhanced in gaps, but that survival rates of seedlings in gaps did not differ from survival rates under closed canopies. In another study, Turner (1991b) found seedlings to germinate more readily under canopy shade than in canopy gaps, but seedling survival and growth was higher in gaps.

Experimental studies are well suited and needed to answer particular questions (e.g. effect of light) about specific aspects (e.g. growth of species) of the forest regeneration process and the role of canopy gaps therein. However, to understand the population dynamics of tree species in tropical rain forests, and how they are affected by the formation of canopy gaps, *in situ* studies of recruitment, growth and survival of seedlings are essential. Of course, this should be followed by studies on subsequent sapling growth and survival (Barton 1984; Brokaw 1985; Clark *et al.* 1993; Uhl *et al.* 1988; Welden *et al.* 1991), and by studies focusing on later stages in the tree's life cycle (Ashton & Hall 1993; Kornig & Balslev 1994a & 1994b; Lieberman & Lieberman 1987; Milton *et al.* 1994).

Aim and outline of this thesis

The principal subject of study in this thesis concerns the canopy dynamics of a tropical rain forest in relation to natural tree- and branchfalls: the canopy dynamics (here defined as "all changes in the structure of a forest canopy") in a tropical rain forest are mainly caused by the formation and closure of canopy gaps. As mentioned before, major catastrophes are not considered here. In this study, I want to reveal (1) how, and how often canopy gaps are formed by means of treefalls and branchfalls ; (2) how, and how fast canopy gaps close; and (3) how canopy gaps affect the population dynamics of tree seedlings.

Chapter 2 investigates how three different gap definitions result in different gap size estimates, and how this affects the calculation of the turnover time. The significance, accuracy, and the practical workability of gap definitions are discussed.

In Chapter 3, I study the annual number and spatial distribution of fallen and damaged trees in Nouragues. Also, some of the causes of the tree- and branch-falls are revealed. Furthermore, the spatial relation between treefalls and/or branchfalls, and existing canopy gaps is investigated. Finally, consequences of tree- and branchfalls in terms of canopy gaps are explored.

In Chapter 4, the formation and closure rates of canopy gaps in the Nouragues forest is investigated. The number, size, and total area covered by canopy gaps is described for a three year period. I investigate whether old gaps increase the chances of the formation of a new gap nearby. Furthermore, the change in canopy openness during three consecutive years is studied.

Chapter 5 focuses on vegetation development in canopy gaps, and how this varies between large and small gaps. Vegetation structure was determined in six recently created canopy gaps, and was determined again two years later. Patterns of vegetation growth and mortality are studied, and differences between large and small gaps are analysed. I try to estimate how fast a new canopy will form in small and large gaps.

In Chapter 6, recruitment, height growth, and mortality of seedlings of three tree species is monitored in relation to canopy gaps, with a special focus on light availability. First, I investigate whether height growth and mortality of seedlings differs between canopy gaps and closed forest. Secondly, within one large gap, spatial distribution of the light availability was monitored during two years. I check how the patterns of seedling recruitment, growth and mortality within this gap are related to the variation in light availability.

Finally, in chapter 7 I discuss the major findings of this study, guided by the three questions mentioned at the start of this paragraph. The potential of these findings for practical applications are briefly discussed.

French Guiana: research station "Les Nouragues"

French Guiana is a relatively small country (83.500 km^2) in the north-eastern part of South America, between 2° and 6° northern latitude, and 52° and 54° western longitude (Figure 1). It is situated on the Pre-Cambium Guiana Shield, which extends to Surinam, Guyana, and

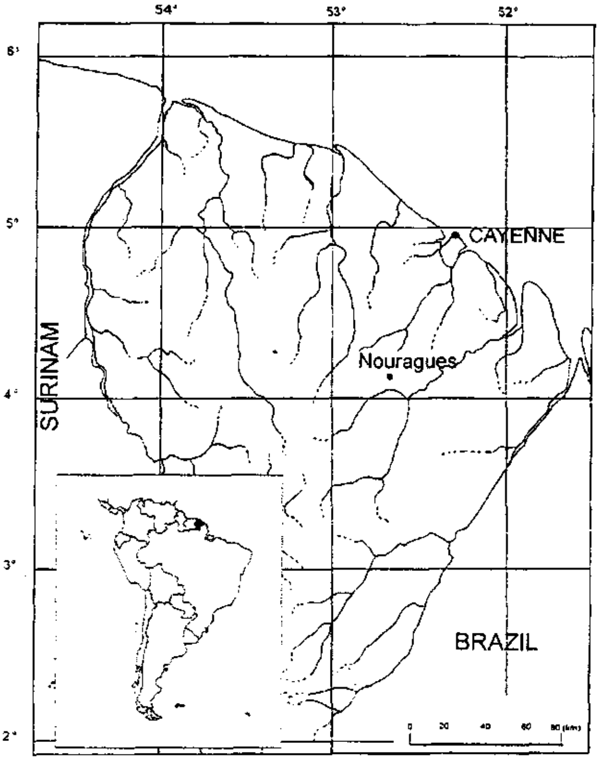

Figure 1. *Location of French Guiana and the biological research station "Les Nouragues"*

Venezuela, totalling an area of some 1.000.000 km^2 (Lindeman & Mori 1989). Mean annual rainfall in coastal areas of French Guiana amounts to 4000 mm and more, and gradually decreases inland to less than 2000 mm in the southern part of French Guiana (De Granville 1982). Rainfall is seasonal, with drier periods from September to November, and around February- March. Mean daily temperatures do not vary much through the year, and normally fluctuate around 26° C.

Most of French Guiana (97.7 %) is covered by evergreen tropical rain forest (Groene 1989), and relatively little is disturbed by human activity. Species diversity is high: Sabatier & Prévost (1989) found 1050 tree species attaining a diameter of at least 10 cm. The total number of vascular plants in French Guianan rain forests is estimated at between 6.000 and 8.000 (De Granville 1982). Also, a high proportion of the vascular species may be endemic (Lindeman & Mori 1989).

In general, the forest grows on poor, well drained, clayey soils. Topography of French Guiana is flat, with most of its area between 0 - 200 m a.s.l.; its highest peak reaches 851 m

(Mount Inini). Inselbergs (granitic outcrops which project above the forest) occur occasionally in the inland areas of French Guiana (Sastre & de Granville 1975).

The biological research station "Les Nouragues" is located at approximately 100 km from the coast (4°05' northern latitude and 52°40' western longitude). The station was established in 1986 by the French research group Ecotrop-Centre National de Recherche Scientifique (C.N.R.S.). The evergreen rain forest surrounding the station has been free of human disturbance since early 1700, when the last local Indians left the region. The topography is determined by a low mountain ridge ("Montagne Balenfois"), with a maximum elevation of some 460 m, including an inselberg of some 400 m. The area has well-drained, clayey to sandy-clayey ferralitic soils on weathered granite parent material. No long term data on rainfall are available, but between 1990 and 1994, the mean annual rainfall was 2920 mm (Figure 2). This corresponds with estimates of Hoff *et al.* (1992), who indicate that the annual rainfall at the (currently abandoned) Arataye research station (7 km south of Nouragues) varies between 3000 and 3250 mm. There is a distinct dry season around September - October, and a slight dip in the amount of rainfall around February-March. The average daily minimum temperature fluctuates around 21° C, and the daily average maximum around 32° C.

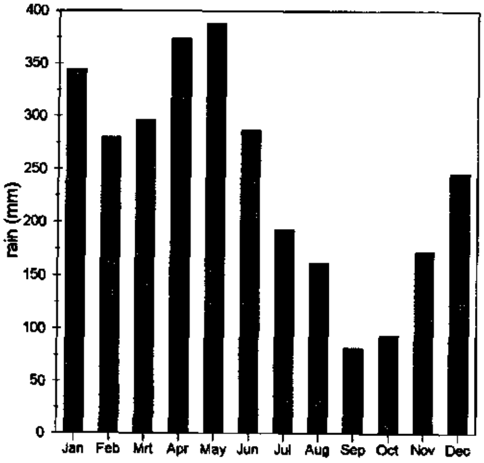

Figure 2. *Mean monthly rainfall in Nouragues, based on observations in 46 months between January 1990 and December 1994. Mean annual precepitation is 2920 mm.*

The Nouragues forest is dominated by tree species in the plant families *Lecythidaceae*, *Sapotaceae*, *Caesalpiniaceae*, *Chrysobalanaceae* and *Burseraceae* (Sabatier and Prévost, 1990). The number of individuals of woody plants > 10 cm diameter per ha varies between around 470 (around creeks, valley bottoms) and 700 (on crests), and the basal area between 31 and 46 m^2/ha. Trees are generally not very large, and do seldom exceed one metre in diameter. The canopy height varies between 20 and 40 metres, with occasional emergent trees up to 60 metres or more. For trees and lianas > 10 cm dbh, species diversity varies between 148 and 182 species per ha (Sabatier & Prévost 1990).

Most of the research done at Nouragues focuses on processes of forest regeneration, and the role of animals therein (e.g. Charles- Dominique 1993; Julien-Laferriere 1993; Théry & Larpin 1993). Accessibility of the forest is facilitated by a 100 x 100 m trail system (Figure 3). Most of the research presented in this thesis was performed on the 12 ha of forest on a plateau.

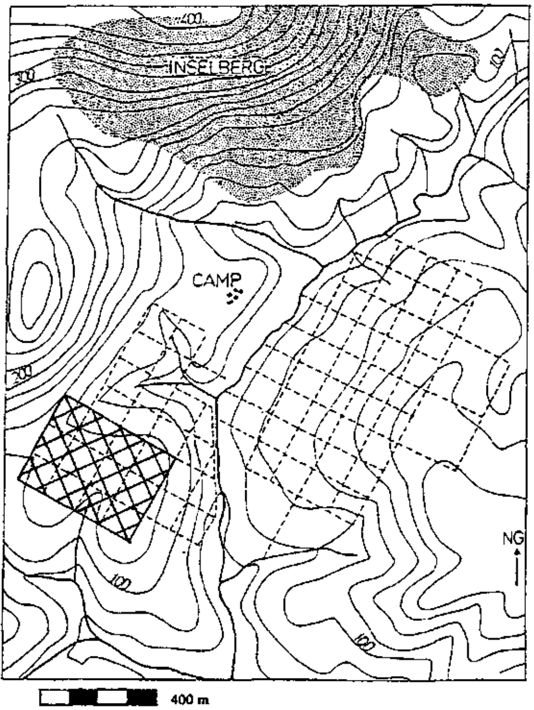

Figure 3. *Surroundings of the research station "Les Nouragues", indicating the 12 ha plot were most of the research took place (after Théry 1990).*

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CHAPTER 2

Defining gaps in tropical rain forests

Defining canopy gaps in a tropical rain forest: effects on gap size and turnover time.

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Abstract

The effects of different gap definitions on gap size and concomitant changes in turnover time were investigated. In a tropical rain forest in French Guiana, 18 canopy gaps were measured using 3 different gap definitions. Gap size measures differed significantly between the three gap definitions. Strong positive correlations were found between gap sizes according to the different definitions. Effects of gap definitions on turnover time calculations were evaluated. It was found that in the studied forest, the turnover time at the forest floor is much lower (some 4 to 8 times) than the turnover time at the forest canopy. It is concluded that it is doubtful whether it is valid to compare gap- and turnover time studies which have been carried out so far. To be able to make valid comparisons between different studies on forest dynamics in the future, it is important to reach consensus on the choice and application of one or more clearly defined gap definitions.

Key words: *canopy gap - disturbance regime - gap definition - gap size - treefall - tropical rain forest - turnover time*

Introduction

Small scale disturbance of tropical rain forests by gap producing canopy destruction is being investigated extensively. Watt (1947) was one of the first to theorise on gap formation in vegetation. This eventually resulted in the development of the concept of small scale disturbance in (tropical) forests, where canopy gap creation leads to local forest regeneration (Hartshorn 1978; Oldeman 1974, 1978; Whitmore 1975, 1978). Since then, an ever increasing number of studies focuses on gaps and vegetation dynamics of tropical forests (for reviews see e.g. Clark 1990; Denslow 1987; Hartshorn 1990; Oldeman 1989; Pickett & White 1985; Platt & Strong 1989).

Natural treefalls are the major small scale disturbance in many tropical rain forests. Gaps created in the forest canopy by falling trees or limbs are generally considered to be an important factor in maintaining the high species diversity of tropical rain forests (e.g. Brokaw & Scheiner 1989; Clark 1990; Connell 1978; Denslow 1987; Hartshorn 1989; Orians 1982). Differences in the area affected by canopy gaps as well as the temporal variability in the creation of gaps cause environmental heterogeneity between gaps. This is assumed to have important consequences for the nature of the gap regeneration (e.g. Platt & Strong 1989). Thus, the disturbance regime of a forest is an important deterministic factor for species abundance and forest structure.

To study how the disturbance regime affects the species abundance and the forest structure, we must know how many gaps are annually created and how large they are. Here, we can distinguish between studies focusing on quantifying the disturbance regime of a forest (e.g. Hartshorn 1978), and studies focusing on the effects of gaps on the population dynamics of plants (seedlings) (e.g. Popma & Bongers 1988; Brown 1993). Accordingly, a distinction can be made between measuring the *direct consequences* and the *indirect consequences* of gap creation. A direct result of the creation of a gap is the destruction of a certain volume of vegetation in the *forest canopy*. This may be quantified as the area covered by the vertical projection of the hole in the forest canopy (e.g. Brokaw 1982a). The indirect result of a gap creation can be quantified by the area at the *forest floor* where environmental conditions were affected by the gap formation and thus population dynamics of seedlings might be affected (e.g. Popma *et al.* 1988).

To determine either the direct or the indirect consequences of the gap creation, defining a canopy gap in a tropical rain forest and measuring its size is not an easy task. As Brokaw (1982a) put it, behind one's desk it is easy to imagine how a treefall gap would look like. In the forest however, one will never find such an ideal gap. Canopy gaps are often very irregularly shaped openings in the forest canopy, and the border between gap area and closed forest is usually not very clear (Oldeman 1978). During the last decade, at least four different gap definitions have been proposed (Brokaw 1982a; Popma *et al.* 1988; Riéra 1982; Runkle 1981). Using different gap definitions in gap studies may well result in differences in gap size and gap density. Popma et al. (1988) for instance found that Brokaw's definition underestimated the area colonised by pioneer plants around gaps by 44 to 515%. Consequently, their average gap size was 3.4 times larger than the gap size according to Brokaw. Both the availability of several gap definitions, as well as the irregular and often vague border between gaps and forest, makes the measurement of gap size complicated.

Recently, in other studies on gaps and forest regeneration, gaps are defined in terms of canopy openness, based on the analysis of hemispherical photographs taken in the centre of a canopy gap (e.g. Brown & Whitmore 1992; Brown 1993; Whitmore *et al.* 1993). Canopy openness seemed to be highly correlated with the gap micro climate (Whitmore *et al.* 1993). However, they did not succeed in relating the canopy openness to a measure of gap size at the forest floor.

The "turnover rate" or "turnover time" is generally used to quantify the disturbance regime of forests (Hartshorn 1978, 1980, 1990; Brokaw 1982a; Lieberman *et al.* 1985). The stand turnover time is defined as the number of years it takes to cover a unit area of forest with gaps, using the average area annually affected by gaps (Hartshorn 1990). However, there are some problems with using the stand turnover time. First, in different studies, different gap definitions might be used, so that turnover times can not readily be compared (e.g. Clark 1990). Second, the absolute value of stand turnover time is of limited value. For instance, a stand turnover time of 100 year would imply that each spot in the forest would be affected by a gap once in every 100 years. In reality this is often not true; some spots may be affected by gaps twice or three times in a hundred years, other spots may be affected by gaps once in 200 years or more. The reason for this is that a new gap may be (partly) superpositioned onto an older one (Riéra & Alexandre 1988). Thirdly, as gap formation rate may vary from year to year, turnover time calculations which are based on one-time gap surveys might not correspond with the real turnover time on the longer term. Finally, differences in minimum size of smallest gap category might account for differences in the calculation of the turnover time (Clark 1990).

In this study we investigate how the use of different gap definitions affects gap size, and how gap sizes according to different methods relate to each other. It is checked how estimates of the turnover time are affected by the use of different gap definitions. Also, the relation between the turnover time at the forest floor and the turnover time in the forest canopy is evaluated. The significance, accuracy and practical workability of the gap definitions are discussed.

Study Area

Data were obtained from the mixed evergreen rain forest surrounding the Nouragues field-research station, French Guiana (4°05'N and 52°40'W). The station was established in 1986 by the French research group Ecotrop-CNRS. The forest has been free of human disturbance since the beginning of the 18th century, when the last local Indians left the region. The physiography is determined by a low mountain ridge (460 m), including an inselberg of some 400 m. The studied forest site has well-drained, clayey to sandy-clayey ferrelitic soils on weathered granite parent material. The forest canopy height varies from 20 to 60 m; stem densities of trees and lianas over 10 cm diameter average some 535 stems per hectare (van der Meer, unpubl.). On 5 transects in the forest surrounding the station (covering 4.8 ha.), some 180 woody species have been identified so far, the dominant plant families being *Lecythidaceae*, *Sapotaceae*, *Caesalpiniaceae*, *Chrysobalanaceae* and *Burseraceae* (Sabatier and Prévost 1990). Average annual rainfall at the nearest meteorological stations is circa 3800 mm in Regina (65 km NE from the study site) and circa 3500 mm in St. George (100 km E from the study site). There is a distinct dry season from September-November and a less conspicuous dry period around February. Average temperature is almost constant all year long with a daily averages minimum of circa 21° C and a daily average maximum of circa 32° C.

Methods

Some 20 hectares of forest were partly (at 15 meter on either sites of a 100 x 100 meter trail system) searched for recently created gaps. All encountered gaps in the forest canopy, created by the fall of either one or more trees, were included. Gaps had to be bigger than 4 m^2 (according to Brokaw) to be considered. Gap size was determined using the gap definitions of Brokaw (1982a), Runkle (1981, 1982) and Riéra (1982). The gap definition of Popma *et al.* (1988) proved too difficult to apply, amongst other things because of insufficient knowledge about the pioneer species at the study site. As the method proposed by Whitmore *et al.* (1993) does not give a measure of how large the gap area is, this method was also not considered here. The 3 gap definitions used are defined and applied as described below. Whilst applying all three methods, an optical range finder (Ranging Optimeter 120; range 2-30 meters) was used to measure distances. This facilitated the application of all three methods considerably. Figure 1 shows a profile diagram of an imaginary treefall gap, visualising how in general the gap was bordered according to the 3 gap definitions.

Brokaw (1982a) defines a gap as "*a hole in the canopy extending through all levels down to an average height of 2 m above ground. The sides of forest openings are irregular in profile, but, for a workable definition, the sides of that space defined as a gap are vertical.*

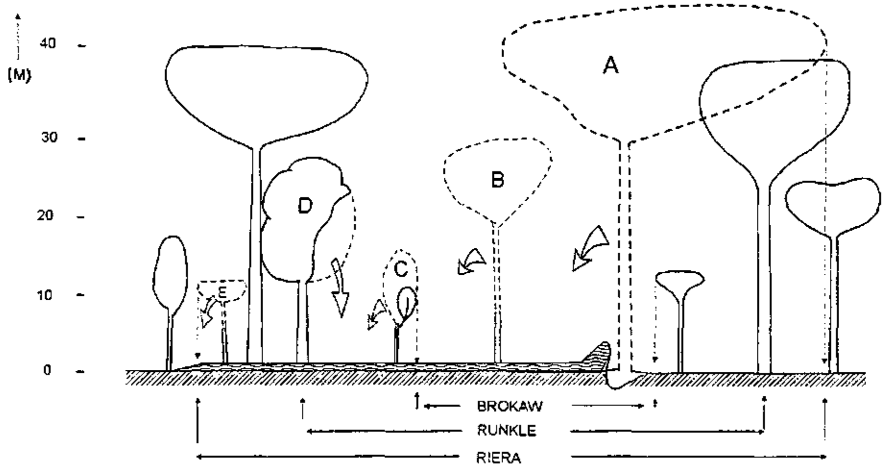

Figure 1. *Profile diagram of an imaginary treefall gap, indicating the overall situation encountered in the field while applying different gap definitions. Trees **A** and **B** fell down, damaging trees **C**, **D** and **E**. Indicated are borders according to gap definitions given by Brokaw 1982a), Runkle 1981) and Riéra 1982).*

The side at a particular place on the perimeter is located at the innermost point reached by foliage, at any level, at that place on the perimeter." In each gap, the centre point was located. The distance from the centre point to the gap edge was measured in the direction of fall of the gap creating tree and 7 other directions at intervals of 45°. The edge of the gap was determined by the vertical projection of the first vegetation over 2 meters encountered in each direction. The gap size was calculated as the surface of the area enclosed by the 8 edge-points.

Runkle (1981, 1982) defines a gap as *"the ground area under a canopy opening extending to the bases of the canopy trees surrounding the canopy opening"*. Runkle considers trees as part of the surrounding forest canopy when they have reached a height of between 10-20 meters and a diameter of over 25 cm. In this study, canopy trees were defined on the basis of (1) tree height > 20 m and (2) being part of the surrounding forest. Runkle's gap size was calculated using the gap centre as a starting point. Direction and distance from the gap centre to the bases of all surrounding canopy trees was measured. The gap size was calculated as the surface of the area enclosed by the bases of the surrounding canopy trees.

Riéra (1982), defines a "chablis" (see Oldeman 1978) rather than a gap as *"the liberation of a biovolume, in which regeneration is possible"*. For as many points as necessary, the outermost border was determined of the vertical projection of the biovolume of the vegetation which had disappeared as a result of the gap creation. The gap size was calculated as the surface of the area enclosed by these border points.

Differences in gap size between gap definitions were statistically tested using Wilcoxon's test (non-parametric; matched pairs). Correlation and regression analyses were done to investigate the relationship between gap sizes according to different gap definitions. The consequences of different gap sizes (as a result the gap definition used) on stand turnover time calculations were estimated.

Results & Discussion

Gap size and turnover time

At the studied area, we detected 18 gaps which were created less than three years ago (Riéra, pers. obs.) and which were suitable for our analysis. Gap size differs greatly when measured according to one of the three gap definitions studied (Figure 2; Table 1). When a gap is measured according to Brokaw its size is significantly smaller than when measured

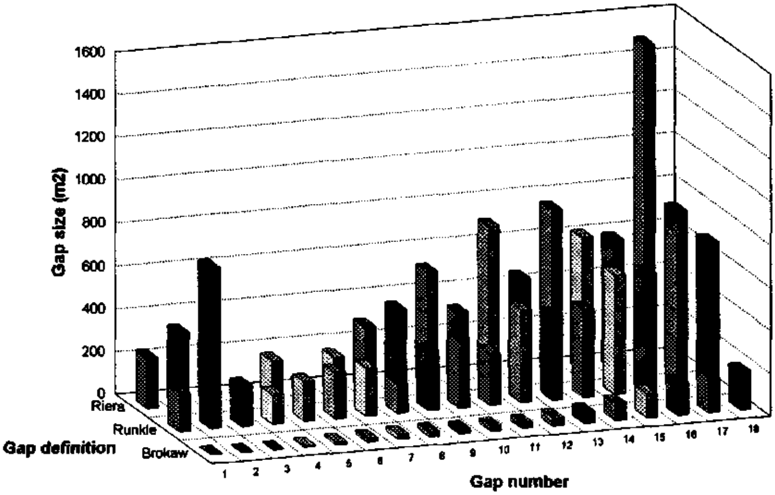

Figure 2. *Gap size of 18 canopy gaps measured according to definitions given by Brokaw (1982a), Runkle (1981) and Riéra (1982).*

according to either Runkle or Riéra (Wilcoxon Matched-Pairs Signed-Ranks Test; 2-tailed $P < 0.001$). Gap sizes according to Runkle are significantly smaller than gap size according to Riéra (Wilcoxon Matched-Pairs Signed-Ranks Test; 2-tailed $P = 0.01$). The differences in gap size can be explained by the different methods of the three gap definitions to border the gap area. Also, gap sizes according to different definitions show a strong to very strong positive correlation (Table 2).

Table 1. *Mean, standard deviation (S.D.) and range of gap size (in m^2) of 18 canopy gaps, according to the gap definitions of Brokaw (1982a), Runkle (1981) and Riéra (1982). Different letters in superscript at the Mean Gap Size's indicate a significant difference (Wilcoxon Matched-Pairs Signed-Ranks Test, $p < 0.01$)*

	Gap Size (m^2)		
	Brokaw	**Runkle**	**Riéra**
Mean	54^{A}	338^{B}	476^{C}
S.D.	57	181	331
Min.	4	138	54
Max.	183	731	1498

Table 2. *Pearson correlation between gap size of 18 canopy gaps according to Brokaw (1982a), Runkle (1981) and Riéra (1982).*

Gap Sizes (Definitions)	r	p
Brokaw x Runkle	0.95	0.000
Brokaw x Riéra	0.71	0.002
Runkle x Riéra	0.82	0.000

Regression analysis revealed a strong significant linear relation between Brokaw's gap size and Runkle's gap size ($R^2 = 0.90$; cv = 18 %; Figure 3). Although significant, the linear relationship between Brokaw's gap size and Riéra's gap size was not very relevant as a result of the very high coefficient of variation (c.v. = 52%). There was no significant linear relationship found between Runkle's gap size and Riéra's gap size. Interestingly, the constant value in the linear relation between Brokaw's gap size and Runkle's gap size implies that when there is no canopy gap (Brokaw's gap size = 0), Runkle's gap size would still be circa 180 m^2. This is caused by the distance between the stem bases of neighbouring canopy trees. When we would assume the "Runkle" gap of 180 m^2 to be round in shape, it would have a diameter of

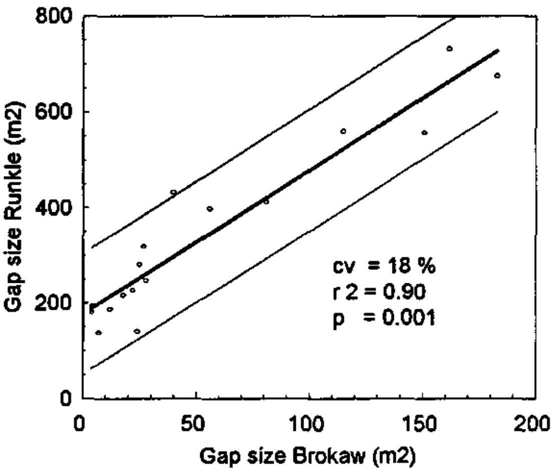

Figure 3. *Regression between Brokaw's gap size (1982a) and Runkle (1981). Runkle's gap size = 178 + 3 x Brokaw's gap size. Dotted lines indicate the 95 % confidence limits.*

15 meter. In the case of symmetrically, evenly shaped tree crowns, this would imply an average crown radius for canopy trees of some 7 meter. This is roughly in agreement with field observations, where for 60 canopy trees surrounding 7 gaps, an average crown radius of 6 meter was found (van der Meer; unpublished data).

Studies in which the disturbance regime of a forest is quantified generally use gap size measured at canopy level (direct consequences) instead of gap size at the forest floor (indirect consequences) (e.g. Clark 1990). Also, in many studies dealing with the ecological effects of treefall gaps on forest regeneration, gaps are being defined as the size of a hole in the forest canopy after Brokaw (1982a) (e.g. De Steven 1988; Schupp 1988; Turner 1990a, 1990b). However, as indicated by the results of Popma *et al.* (1988), the ecologically altered area at the forest floor is often larger than the size of the gap at the forest canopy level. This makes it difficult to relate the disturbance regime at the canopy level to regeneration processes at the forest floor. In future studies on the relation between disturbance regimes and population dynamics of seedlings, a gap definition defining gap size at the forest floor should therefore be used.

The linear regression between Brokaw's and Runkle's gap size was used to estimate how differences in gap size as a result of different gap definitions affect the calculation of turnover time. At the same time, the relation between the turnover time at the forest floor and the turnover time in the forest canopy was investigated. Preliminary results from a study of the light availability in and around canopy gaps indicate that Runkle's gap size greatly coincides with the area at the forest floor with an enhanced light level compared to the surrounding forest (van der Meer, unpubl.). Therefore, Runkle's gap size is assumed to be a reasonable measure of the gap size at the forest floor. Brokaw's gap size is taken here as a measure of gap size in the forest canopy, being the best available alternative (see p. 8; evaluation of the significance). With these two assumptions, the relation between the turnover time of the forest canopy (Brokaw) and the turnover time at the forest floor (Runkle) was analysed.

No actual stand turnover time of the studied forest could be calculated because the forest area had only partly been searched for gaps and complex gaps were not considered. Instead, the mean gap size in the forest canopy (Brokaw's gap size; 54 m^2) was used to predict (with the aid of the linear relation between Brokaw's gap size and Runkle's gap size) the mean gap size at the forest floor (Runkle's gap size; 338 +/- 127 m^2). With this, it was possible to predict the turnover time at the forest floor on the basis of the turnover time at the forest canopy (Figure 4). This illustrates clearly that for the same forest, turnover time at the forest canopy would be some 4 to 8 times higher than turnover time at the forest floor.

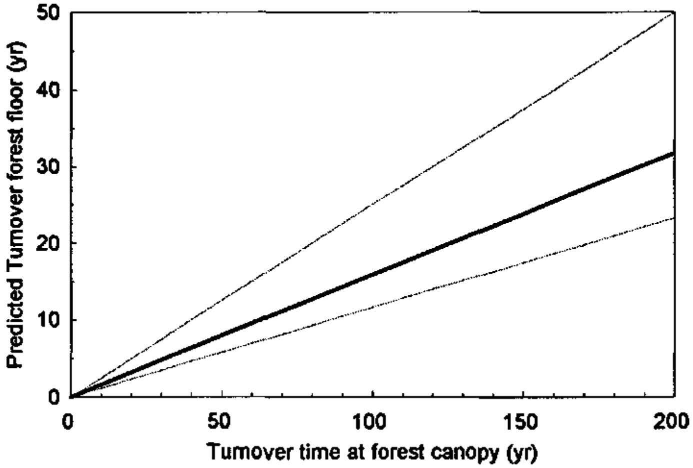

Figure 4. *Turnover time at the forest floor, predicted on the basis of the turnover time at the forest canopy. The mean gap size in the forest canopy (Brokaw's gap size; 54 m^2) was used to predict the mean gap size at the forest floor (Runkle's gap size; 338 m^2), using the linear relation between Brokaw's and Runkle's gap size. The stand turnover time was calculated for imaginary disturbance rates in terms of different numbers of gaps formed per ha per year (e.g. 1 gap/ha/yr would yield a turnover time of 185 years at the forest canopy and 29.5 years at the forest floor; 2 gaps/ha/yr a turnover time of 93 years at the forest canopy and 15 years at the forest floor). Dotted lines indicate the 95 % confidence limits of the predicted turnover time at the forest floor.*

This stresses, as stated by Clark (1990), the importance of indicating exactly which gap definition is used in stand turnover time studies. For instance, a turnover time at the forest canopy of 100 years, which is a average value for Neotropical forests (e.g. Hartshorn 1990), equals a turnover time at the forest floor of between 11.5 and 25 years (Figure 4). This would imply that on average every 11.5 to 25 years, each seedling in the forest would be affected by enhanced light conditions as a result of a canopy disturbance. This is roughly in agreement with the findings of Popma *et al.* (1988), whose gap size is measured on the basis of the occurrence of seedlings of pioneer plants at the forest floor. When their results on gap size measurements (gap size according to Popma et al. = 3.4 x Brokaw's gap size) would be translated into stand turnover time calculations, the difference between the turnover time at the forest canopy and the turnover time at the forest floor would be in the same order of magnitude as the difference found in this study.

So far, in other studies on gap dynamics and stand turnover time, the apparent difference between turnover time at the forest canopy and turnover time at the forest floor has been scarcely recognised. However, the increase in light availability is generally considered to be a very important factor in regulating the population dynamics of plants in a tropical rain forest (e.g. Canham *et al.* 1990). Further research should be done to investigate the exact relationship between canopy disturbance and changes in light availability at the forest floor.

Some complex older gaps were not included in the analyses. These gaps did not have an opening in the canopy larger than 4 m^2, but often had several small (< 4 m^2 each) openings in the gap regrowth. Consequently, these gaps were not considered as gaps following Brokaw's definition, and were thus not considered here. Also, gaps in the understorey, where vegetation was destroyed without creating a whole in the canopy through all levels, were not considered here. However, not considering these complex and understorey gaps might affect the calculation of the disturbance regime of a forest, as well as it might underestimate the effects of the disturbance regime of a forest on the population dynamics of seedlings.

Evaluation of the gap definitions

The significance, accuracy and practical workability of the gap definition are discussed below. The findings are summarised in Table 3.

SIGNIFICANCE

To estimate the significance of a method, one has to consider the aim of the gap measurements. As stated before, the aim of a gap study is in general to quantify either the direct results (gap size at the forest canopy; to quantify the disturbance rate of a forest) or the indirect results (gap size at the forest floor; in studies on the effects of gaps on seedling populations) of the creation of gaps. Depending on the aim, one has to consider whether the application of a certain gap definition, in theory, will result in a meaningful or significant measure of the gap.

*** Forest canopy**

Brokaw's gap size is measured at 2 meters above the ground. The size of the gap at two meters high is often much smaller than when measured higher up in the canopy. This was shown for instance by Hubbell & Foster (1986) by their profile diagram of the average gap in their study site in Panama. Also, in a companion study with the present one at Nouragues, preliminary results indicate that the gap size at 2 meters height is smaller than the canopy gap size at 20 meters height (van der Meer, unpubl.). This should be taken into account when using Brokaw's gap size as a measure of gap size in the forest canopy. Of the three definitions studied here, Brokaw's gap size is the only one measuring the size of an actual opening in the forest canopy, and therefore considered the best in quantifying the direct consequences of the creation of a canopy gap.

Runkle's gap size is measured to the stem bases of the canopy trees surrounding a gap. In general, most of these trees have a crown extending several meters in the gap. As a consequence, the Runkle's gap size is nearly always larger then the vertical projection of the opening in the forest canopy (see Figure 2). This is independent of the height at which the canopy gap is defined. Runkle's gap size is therefore of practically no use as a measure of gap size in the forest canopy.

Riéra (1982) defines a gap as a volume. The affected vegetation can be at any height, situated under or above intact vegetation. Also, the volume can be of any shape. However, Riéra's gap size is expressed as the area of the vertical projection of the estimated volume. This is mathematically not correct, since there is no linear relation between a volume and the area of the vertical projection of a volume. Therefore, Riéra's gap size is of limited use in measuring gaps in the forest canopy.

*** Forest floor**

As indicated by several authors (e.g. Popma *et al.* 1988; Brown 1990), the area at the forest floor which is affected by the gap creation (increase in light availability & vegetation damage) greatly extends the Brokaw's gap size. This is confirmed by preliminary results of a study concentrating on light availability in canopy gaps (van der Meer, unpubl.). Brokaw's definition is therefore of no use in defining gaps at the forest floor level.

As stated earlier, preliminary results indicate that the Runkle's gap size greatly covers the area at the forest floor with changed light availability (van der Meer, unpubl.). Therefore, for the moment it is assumed that Runkle's definition gives a reasonable estimate of the affected area at the forest floor. In future research, this will be further investigated.

Riéra's gap size seems to be of very limited use in defining gap size at the forest floor. As stated before, the affected biovolume can be very irregularly shaped. This can range from one thin layer of 1 or 2 meters thick (at any height) to a hole extending through all levels. Consequently, the effects of these changes in biovolume on the forest floor (e.g. in terms of light availability) are of varying magnitude. This makes it hard to relate Riéra's gap size to changes in light availability at the forest floor.

Table 3. *Evaluation of gap definitions according to Brokaw (1982a), Runkle (1981) and Riéra (1982). Findings are based on impressions in the field while measuring 18 canopy gaps. All figures are relative and not absolute. See text for further explanation.*

	Gap definition		
	Brokaw	**Runkle**	**Riéra**
Significance			
* *forest canopy level*	±	-	±
* *forest floor level*	-	±	-
Accuracy			
* *objectivity*	-	±	-
* *measuring precision*	-	+	-
Practical Workability			
* *time*	±	+	-
* *physical ease*	±	+	±

ACCURACY

Independently of the aim of the gap measurements, a method should preferably have a high level of accuracy. The accuracy of a gap defining method depends on the potential errors one can make while measuring gap size. Errors can occur (1) through misinterpretation of the definition, resulting in a wrong determination of the gap edge, or (2) during the actual measurement of the enclosed gap area. Therefore, (1) objectivity and (2) measuring precision in applying each definition in the field was estimated.

* **Objectivity**

Applying Brokaw's definition proved to be quite subjective, in spite of suggestions by Clark (1990) who considered Brokaw's definition objective. Firstly, determining the gap centre is often not easy and often subject to personal interpretation. Secondly, in larger gaps the gap area is often fragmented by isolated gap vegetation over 2 meters height, making it inevitable to distinguish more than one centre (four gaps in this study). However, the choice to decide for one instead of two centres is not defined and thus quite subjective. Finally, going from the gap centre towards the gap border, it proved troublesome to decide what should be considered as the first vegetation (1 leaf; 5 leaves; a whole branch ?) over 2 meters tall.

In applying Runkle's definition, the determination of the surrounding canopy trees proved sometimes to be subjective. This was especially so when several surrounding canopy trees higher then 20 meter were standing close together and partially overtopping each other.

Working with Riéra's definition proved to be very subjective. It was often very hard to determine the extent of the vegetation which has disappeared as a result of the gap creation.

*** Measuring precision**

The precision in measuring Brokaw's gap size is considered to be low. Firstly, it proved sometimes to be difficult to determine the exact location on the ground of the vertical projection of the gap edge. Second, Brokaw's gap size is measured using only 8 directions to determine the border of a gap. As most gaps are very irregularly in shape, the actual size of the gap may differ from the Brokaw's gap size.

Runkle's gap size can be determined precisely when the surrounding canopy trees are identified. Measuring precision of Runkle's method is thus considered to be high.

In measuring the Riéra's gap size, it also (like Brokaw) proved hard to determine the exact vertical projection of the determined gap edge. Measuring precision is therefore estimated as poor.

PRACTICABLE WORKABILITY

Finally, it is important that a gap definition can be applied in the field without too many practical problems. The practicable workability of the 3 gap definitions was evaluated by (1) the time needed to measure a gap and (2) the physical ease whilst using each definition.

*** Time**

The measurement of Runkle's gap size appeared to take less time then measuring Brokaw's gap size. On its turn, measuring Brokaw's gap size took on average less time then measuring Riéra's gap size.

*** Physical ease**

Runkle's method is considered to be the most easy way to determine the gap area. Most surrounding canopy trees can be determined while standing in the centre, measuring distances with a range finder. The physical constraints whilst measuring Brokaw's gap size and Riéra's gap size can be quite high. Determination of the gap edges according to these methods is often hindered by stacks of branches and other debris.

Measuring gap sizes is very difficult, mainly because of the complexity of shape of gaps and the absence of a clear border between gap area and the surrounding forest. None of the tested gap definitions was considered to be truly significant for determining either the direct or the indirect consequences of gap creation. However, of the three definitions considered, Brokaw's definition was considered to be the most significant for measuring gap size at the forest canopy, and Runkle's definition for measuring gap size at the forest floor. The accuracy of both Brokaw's and Riéra's method was considered to be poor; Runkle's method proved to be more accurate. Working in the field, Runkle's definition could be applied more easily than the other 2 methods.

Conclusions

In tropical rain forests, the border between a canopy gap and the surrounding closed forest is gradual and often very irregular in shape. As a result, defining canopy gaps is not easy. However, in quantitative studies on the disturbance regime of forests, as well as in studies on the effects of canopy gaps on population dynamics of plants (e.g. tree seedlings), the measurement of the size of canopy gaps is important.

Gap size measures appeared to be significantly affected by the use of different gap definitions. The significance for either measuring gap size at the forest floor or at the forest canopy was fair to poor for the three gap definitions considered. Nevertheless, Brokaw's definition was considered to be the most significant for measuring gaps at the forest canopy, and Runkle's definition for measuring gaps at the forest floor. The accuracy of gap size measurements of two of the three tested gap definitions was considered to be poor; one gap definition was considered to have a fair to good accuracy in the measurement of gap size.

As in different gap studies different gap definitions might have been used, there is reason to be very cautious in comparing the frequency distributions of gap sizes and turnover times. Another reason to be cautious with comparing results of gap studies, is that in studies in which Brokaw's definition was used, the complex, small and/or understorey gaps are probably not considered. Also, in studies on gap regeneration, more attention should be given to using a significant gap definition, which determines the gap size at the forest floor.

Gap size according to all three definitions were strongly to very strongly positively correlated. On average, a gap measured using Runkle's definition would have a gap size which is between 4 to 8 times larger than when measured using Brokaw's definition. This is an indication that the turnover time at the forest floor of the studied forest in French Guiana is probably some 4 to 8 times lower than the turnover time at the forest canopy.

It is important to reach a consensus on the choice and application of one or more clearly defined gap definitions, to measure both direct and indirect consequences of gap creation. A good gap definition has to be significant, accurate and easy to apply in the field. In looking for such a gap definition, canopy openness as proposed by Whitmore *et al.* (1993) seems to be a promising way of quantifying gap size in the forest canopy. However, a problem to be solved in this method is how the canopy openness can be translated into a measure of surface area and, consequently, a measure of stand turnover time. The method proposed by Popma *et al.*

(1988) is in potential a useful way to determine the gap size at the forest floor, provided that there is sufficient knowledge about the ecology of the pioneer species at a site.

When gaps are accurately measured using a standard gap definition, stand turnover time, together with some basic data on the mean and range of the gap sizes, can be validly used to compare the disturbance regimes of different forests. This can be an important tool in studying how the disturbance regime affects the species composition of a forest.

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CHAPTER 3

Patterns of treefalls and branchfalls

Patterns of treefalls and branchfalls in a neotropical rain forest in French Guiana

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Abstract

Treefalls and branchfalls of all trees with a diameter at breast height (dbh) of over 10 cm were studied in 12 ha of primary rain forest at Nouragues, French Guiana. Consequences in terms of the number of damaged trees and number and sizes of resulting canopy gaps were investigated. Spatial distribution of treefalls and spatial relation with pre-existing canopy gaps were analysed. Forest turnover rates were calculated on different bases.

Of the 6314 trees initially present in the plot 1.5% had fallen and 1.3% lost at least one major branch after one year. In total, 4.9% of the standing basal area had been felled or damaged. The major cause of treefalls and tree damage is falling trees and limbs: 75% of the fallen and 83% of the damaged trees were felled or damaged by others ("domino-wise" felled or damaged trees). Of the remaining ("initiating") fallen trees, 38% were uprooted and 62% were snapped-off above the ground. Simular percentages were observed for domino-wise felled trees. The spatial distribution of the 38 trees which initiated events was random. Pre-existing canopy gaps did not increase the chances of surrounding trees to initiate a tree- or branchfall. However, initiating tree- and branchfalls were found clustered at around 50m from large gaps, while few gaps occurred at around 25m from old gaps.

Some 35% of the fallen trees did not create canopy gaps, and 42% of the damaged trees were not involved in the creation of a canopy gap. Initiating treefalls that resulted in a canopy gap had no larger dbh than initiating treefalls not resulting in a canopy gap. In contrast, gap creating branchfall trees had a larger dbh than non-gap creating branchfall trees. Gap size increased with the number and basal area of the trees involved. Gap size measured following the Brokaw (1982a) definition was not very relevant in quantifying the direct consequences of gap creation, and a modified gap definition is proposed. Both the forest turnover rate based on the number of fallen trees and the turnover rate based on the area of canopy gaps underestimate the actual disturbance regime of the forest. To quantify the disturbance regime of a forest, the basal area of the annually fallen and damaged trees deserves more attention.

Keywords: *branchfalls - canopy gaps - forest dynamics - French Guiana - Monte Carlo test - spatial pattern - treefalls - tropical rain forest - turnover rate*

Introduction

The fall of trees and large branches are important phenomena in tropical rain forests. In primary lowland rain forests some 1-3% of the trees larger than 10 cm in diameter fall down in any year (e.g. Phillips & Gentry 1994; Rankin de Merona *et al.* 1990). In most of the forests studied, falling trees account for some 74-90% of the tree mortality (but see Durrieu de Madron 1994), the remaining part being due to the death of standing trees (Lieberman *et al.* 1985; Rankin de Merona *et al.* 1990; Putz & Milton 1982). In many, but not all cases, treefalls and branchfalls create openings in the forest canopy (canopy gaps), where environmental circumstances differ from closed forest conditions (Brown 1993; Canham *et al.* 1990; Chazdon & Fetcher 1984). These newly created gaps are of importance in the life cycles of many tree species (e.g. Clark 1990; Denslow 1987; Martinez-Ramos 1985, Oldeman & van Dijk 1990, Pickett & White 1985; Bongers & Popma 1988).

Causes of tree- and branchfalls

The causes of treefalls and branchfalls are complex and poorly understood so far. Some gap studies differentiate between the initiator of a gap ("gapmaker") and the remaining felled trees (e.g. Durrieu de Madron 1994; Runkle 1982; Veblen 1985), and in an analogous way, we can distinguish between *initiating* tree- and branchfalls the subsequent *domino* events. An important distinction is that the causes of domino treefalls are initiating treefalls, whereas the causes of initiating treefalls are not so easily explained.

Initiating treefalls and branchfalls may be caused by several factors. Vooren (1986) distinguishes between tree deaths caused by sudden events (external causes) and a slowly progressing dieback process (internal causes), and in many cases, the fall of trees or branches is caused by a combination of these external and internal factors. Rain and wind for instance can be the proximate cause of treefalls, bringing down trees already weakened by fungus or disease (Brokaw 1985; Uhl *et al.* 1988). External factors affecting this process are local climate, topography, soil conditions and stand structure and species composition (Jans *et al.* 1993; Kapos *et al.* 1990; Hallé *et al.* 1978). Internal factors affecting the fall of trees and branches are often related to fungus attack, insect infestations or other diseases. De Graaf (1986) for instance found that many fallen trees suffered from root decay. It is however hard to predict rates and location of treefalls since chance also plays an important role in both external and internal factors.

Another factor which might cause trees to fall over is their proximity to canopy gaps. Several studies mention that trees surrounding canopy gaps are more likely to fall than other trees (Brokaw 1985; Lang & Knight 1983; Putz & Milton 1982). The creation of a canopy gap may have destabilised or damaged surrounding trees, enhancing the chance that these trees will fall in the near future. Also, tree crowns may become asymmetrical when they grow into a gap, increasing the possibility of toppling over (c.f. Young & Hubbell 1991). This would lead to enlargement of existing gaps and clustering of gaps. Poorter *et al.* (1994) indeed found canopy gaps to be clustered in two of three studied rain forest sites in Ivory Coast. However, in temperate forest in Ohio, USA, canopy gaps did not affect the tree mortality of the neighbouring canopy trees (Runkle 1990).

It is rare to observe the actual fall of trees and/or branches and this makes it even more complicated to determine their causes. However, the mode of fall (uprooted or snapped-off) may indicate which external factor caused the treefall. Uprooting of trees is often associated with soil loosening, whilst the snapping of trees is often the result of above ground agents like the rainload of a tree (e.g. Brokaw 1985, Strong 1977). Durrieu de Madron (1994) found uprooting to increase around creeks, suggesting that the proximate cause of treefalls around creeks are related to unstable soils.

Consequences of tree- and branchfalls

The fall of trees and branches in tropical rain forests has both direct (destruction of vegetation) and indirect (environmental factors; seedling response) consequences (e.g. Van der Meer *et al.* 1994). In the present study, we will concentrate on the direct consequences of treefalls in terms of the disturbance of the forest vegetation.

The disturbance caused by treefalls and branchfalls can be described in two different ways, either at the tree level, for instance in terms of the number of trees affected by treefalls, or in terms of canopy gaps (defined as a hole in the forest canopy existing through all levels; as in Brokaw 1982a), for instance as the rate at which canopy gaps are created. Accordingly, turnover rates of forests, often used to compare disturbance regimes of forests, are calculated in two different ways: on the basis of treefall and tree mortality data (e.g. Hartshorn 1990; Lang & Knight 1983; Lieberman *et al.* 1985; 1990; Phillips & Gentry 1994; Putz & Milton 1982; Rankin de Merona 1990) and on the basis of canopy gap formation rates (see reviews of Clark 1990; Denslow 1987; Denslow & Spies 1990; Hartshorn 1989; Jans *et al.* 1993; Platt & Strong 1989). Because of the imperfect correspondence between tree mortality and gap formation, turnover rates calculated on the basis of gap formation may differ from the turnover rate calculated on the basis of tree mortality (Denslow 1987; Denslow and Hartshorn 1994; Lieberman *et al.* 1985; 1990).

Objective

In this paper we describe the patterns of treefalls and branchfalls in a tropical rain forest in French Guiana and reveal some of its causes and consequences. Specifically, we address the following questions: (1) what is the amount and spatial distribution of annually fallen and damaged trees ?; (2) what are the causes of tree- and branchfalls ?; (3) are initiating treefalls and branchfalls spatially related to existing canopy gaps ?; (4) which treefalls and branchfalls create canopy gaps of what size ?; (5) how is the disturbance caused by treefalls and branchfalls described by turnover rates based on (i) treefalls and (ii) canopy gap formation ?

Methods

Study Site

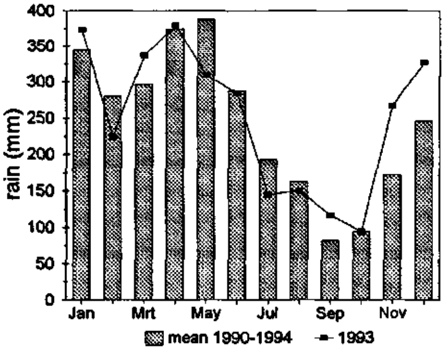

Figure 1. *Mean monthly rainfall in Nouragues, based on observations over 46 months between 1990 and 1994. Mean annual precipitation was 2920 mm. In 1993, observations were made during all months; total precipitation was 3005 mm.*

The study was conducted at the Nouragues field station, French Guiana (4°05'N; 52°40'W). In this area, a permanent sample plot of 12 ha was established in 1991. Canopy gap formation has been monitored since the end of 1990 (van der Meer, unpublished data). Location, size and age of all canopy gaps in the study area are known. The plot is situated on a relatively flat plateau, the elevation ranging between ca 90-110 m above sea level. It has well drained, clayey to sandy-clayey ferralitic soils on weathered granite parent material. At some places, soils are shallow, with bare granite parent material several centimetres beneath the soil surface. The forest is old-growth evergreen rain forest, with the canopy height ranging between 20-40 metres and emergents up to 60 metres tall. No long-term rainfall data are available for Nouragues, but observations between 1991 and 1994 suggest that the annual rainfall averages around 3000 mm. This corresponds with the rainfall map of French Guiana as presented by De Granville (1982). There is a distinct dry season from September-October, and a less conspicuous dry season around February (Figure 1). In 1993 (study period), pattern and total amount of rainfall did not differ much from the four-year average.

Tree- and branchfalls

At the end of 1992, all trees > 10 cm in diameter at breast height (dbh) in the 12 ha plot were permanently tagged, numbered, measured (dbh) and mapped to the nearest metre. In the case of trees with buttresses, diameter was measured or estimated directly above the buttress. At the end of 1993, the plot was checked again for all fallen and damaged trees. Damaged trees were trees which had lost at least one major branch with a base > 10 cm diameter. The dbh and basal area of the fallen and damaged trees was determined by taking the dbh value from the 1992 inventory. No tree were classified as standing dead trees in either inventory, as one year is too short to confirm the death of a tree. However, effects of the fall of dead stems on live stems were included.

The place where the forest canopy had been disturbed during the preceding year by the fall of one or more trees, major branches or dead stems was considered to be the site of an event. All fallen and damaged trees were grouped in events. When more than one tree had been involved in an event, a distinction was made between an initiating tree- or branchfall ("fall of a tree or branch which was not caused by the fall of another tree or branch") and a domino tree- or branchfall ("trees or branches which are brought down by the fall of another tree or branch"). The initiator of the event was determined on the basis of the position of the fallen stems and/or branches, and other damaged and/or fallen trees in such events were marked as domino treefalls or domino branchfalls.

For each event it was determined whether initiating was due to the fall of (1) a tree, (2) a branch or (3) a standing dead stem. The causes of each of the domino falls was also assigned to one of these categories. The mode of treefall (uprooted or snapped) was determined for both initiating trees and domino trees.

To test for differences between the mean dbh of different groups of trees (e.g. initiating treefalls compared to domino treefalls, fallen trees compared to damaged trees), the Mann-Whitney U test was used. To test if dbh distributions of different groups of trees differed, the Kolmogorov-Smirnov two-sample test was performed.

Spatial patterns

The spatial distribution of the initiating treefalls and branchfalls was investigated using a nearest neighbour analysis. For each of the initiating tree- and branchfalls (with n=38; see results), the distance to its nearest initiator was determined. These distances were ranked from smallest to largest, and converted to a cumulative distribution function. This cumulative distribution function was compared with cumulative distribution functions of 38 randomly selected trees to their nearest neighbour. The random or non-random nature of the cumulative nearest neighbour distances was tested using the Monte Carlo simulation technique (Besag & Diggle 1977). This cumulative distribution function of the nearest neighbours of the 38 initiators was tested against 200 simulations. In each simulation, 38 trees were randomly selected from the total number of trees (n = 6314) in the 12 ha. For each simulation, a cumulative distribution function of the distances of each tree to its nearest neighbour was made. The 200 distribution functions were ranked and the 95% confidence interval was determined by plotting the 6th and the 195th simulation in a figure and compared with the cumulative distribution function of the actual distances.

The relation between the spatial distribution of the 1993 events and canopy gaps already present at the start of the observations ("present gaps", formed before 1993) were also investigated by means of a nearest neighbour analysis. A cumulative distribution function of the distances from 38 initiating tree- and branchfalls to the centre of the nearest "present" gap was made. This cumulative distribution function was compared with cumulative distribution functions of 38 randomly selected trees to the nearest "present" gap (200 simulations). The Monte Carlo simulation technique was used to test for randomness. Furthermore we tested whether the location of the 38 initiators of 1993 was spatially related to (1) the most recently formed canopy gaps ("recent gaps", formed between January 1991 and December 1992; n = 16); (2) the oldest canopy gaps ("old gaps", formed before January 1991; n = 71); and (3) the largest canopy gaps, indifferent of age ("large gaps", gap size over 50 m^2; n = 14). In this analysis, the minimum gap size was 4 m^2 (after Brokaw 1982a). The spatial relation of initiators to gaps formed in the same period (between end 1992 and end 1993) could not be analysed due to lack of exact dates within this period.

Formation of canopy gaps

We recorded whether or not each event resulted in the creation of a new canopy gap. The size of the new gaps was measured using (1) the commonly used gap definition given by Brokaw (1982a) and (2) a modified Brokaw definition to determine the size of the opening at 20 metres height. For the first definition, the distance was determined from the centre of the gap to the vertical projection of the first vegetation above 2 metres in eight directions. The centre of the gap was determined by estimating the centre of the vertical projection of the hole in the canopy. The eight gap border points were connected with straight lines, and the enclosed surface was determined by calculating the area of the eight triangles. Only gaps larger than 4 m^2 were considered. The second gap definition used was a modified Brokaw definition: here, the same centre and the same eight directions were used, but the gap was now limited when vegetation over 20 metres tall was encountered. The height of the vegetation was checked using an optical range finder (Ranging Optimeter 120; range 2-30 m); the exact location of the vertical projection of the vegetation was determined using a pentagon prism. The relation between gap size and the number and basal area of the fallen and damaged trees in the events was investigated using the Spearman Rank correlation coefficient. One event had been created at the edge of an old, large gap. Here, an estimate was made how large an area had been opened up by the event, based on the length, orientation and crown width of the fallen trees. This gap was not used to analyse the relation between fallen and damaged trees and gap size.

Disturbance rate

The annual rate of tree disturbance was calculated as the percentage of the number and the basal area of (1) the fallen, (2) the damaged and (3) both fallen & damaged trees. The rate of gap disturbance was calculated as the percentage of the surface in canopy gaps according to the two used gap definitions. The "traditional" turnover rates, normally calculated based on either (i) the number of fallen trees or (ii) the area opened up by canopy gaps sensu Brokaw (1982a), were compared to rates of tree disturbance using the basal area and gap disturbance using the modified gap definition.

Results

Fallen and damaged trees: events

During one year (1993), 96 trees fell in the 12 ha of rain forest studied, an average of 8 trees per ha (Table 1). Of the fallen trees, 25.0% (24 trees) were the initiators of an event (initiating treefalls) and 75.0% (72 trees) were brought down by falling trees, dead stems or branches (domino treefalls). In terms of basal area, 54.5% of the fallen trees were initiating treefalls, and 45.5% of the fallen trees were domino treefalls. The mean dbh of fallen initiating trees was significantly larger, and of fallen domino trees significantly smaller then the dbh of undisturbed trees (Mann-Whitney U; $p < 0.01$). Initiating treefalls ranged in size from 10 to 90 cm dbh, whilst domino treefalls ranged between 10 and 55 cm dbh (Figure 2). The frequency distribution of the dbh of fallen initiating trees differed significantly from that of both domino treefalls and all trees in the original inventory (Kolmogorov-Smirnov, $p < 0.01$). The latter two were not different.

Over the same period (1993), 81 trees or 1.3% of the trees in the original inventory were damaged, averaging some 7 trees per ha (Table 1). Of the damaged trees, 17.3% (14 trees) were the initiator of an event by the spontaneous breakage of a major branch (initiating

Table 1. *One year of treefalls and branchfalls of trees > 10 cm dbh in 12 ha of rain forest, Nouragues, French Guiana. For the fallen and damaged trees, a distinction is made between trees which initiated events and trees which were felled or damaged domino-wise by other falling trees or branches. Different letters in the last column indicate a significant difference between the dbh of trees (Mann-Whitney U Wilcoxon Rank Sum W Test, $p < 0.01$).*

	Number of trees			Basal Area (m^2)			DBH
	n	(mean/ ha)	% (of total in 1992)	b.a.	(mean/ ha)	% (of total in 1992)	mean (cm)
1992 Inventory							
Standing trees	6314	(526)		412.0	(34.3)		23.5
1993 Inventory							
Fallen Trees							
- Initiating treefalls	24	(2)	0.4	2.9	(0.2)	0.7	34.1^{A}
- Domino treefalls	72	(6)	1.1	2.4	(0.2)	0.6	18.5^{B}
Damaged Trees							
- Initiating branchfalls	14	(1.2)	0.2	11.3	(0.9)	2.7	88.3^{C}
- Domino branchfalls	67	(5.6)	1.1	3.5	(0.3)	0.9	22.3^{BD}
Undisturbed Trees	6137	(511.2)	97.2	391.9	(32.6)	95.1	23.4^{D}

branchfalls). The remaining 82.7% (67 trees) were damaged by the domino effect of other treefalls, branchfalls or falling dead stems. Of the damaged basal area, 76.2% (11.5 m^2) was damaged through initiating branchfalls, the remaining 23.8% (3.5 m^2) being damaged by others. Similarly, the mean dbh of trees damaged by initiating branchfalls was significantly larger than the dbh of trees damaged by domino branchfalls (Mann-Whitney U; $p < 0.01$). Trees which initiated branchfalls ranged in size from 35 to 180 cm dbh, and 50% were > 80 cm dbh (Figure 2). Trees damaged by others ranged in size between 10 and 70 cm dbh. The frequency distribution of the dbh of trees which initiated branchfalls differed significantly from that of trees damaged by the domino effect, and differed also from all trees in the original inventory (Kolmogorov-Smirnov, $p < 0.01$). In addition, the frequency distribution of the dbh of trees which initiated branchfalls differed from that of fallen initiator trees (Kolmogorov-Smirnov, $p < 0.01$). The difference in frequency distribution of the dbh between trees felled domino-wise and undisturbed trees was not significant (Kolmogorov-Smirnov, $p = 0.07$), despite the significant difference in mean dbh between these two groups (see above).

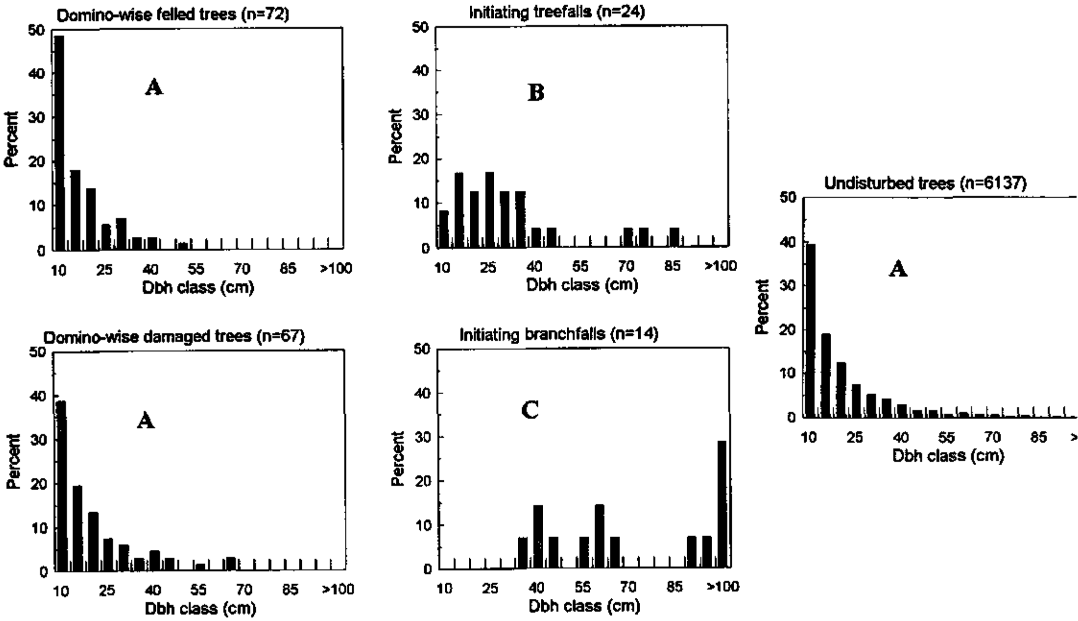

Figure 2. *Frequency distribution of the dbh of the disturbed and undisturbed trees (> 10 cm dbh) in 1993 on a plot of 12 ha of rain forest in French Guiana. For the fallen and damaged trees, a distinction was made between the initiating and domino trees (see text for futher explanation). Different letters in the graphs indicate significantly different distributions (Kolmogorov-Smirnov 2 sample test; $p < 0.01$).*

Trees were felled or damaged in 45 events. Of these events, 24 were initiated by a treefall (51%), 14 by a falling branch (31%), and 7 by a falling dead stem (18%). In 11 events, no trees fell down but trees were damaged, averaging some 1.4 damaged trees per event. In the remaining 34 events, an average of 2.8 trees fell and 1.9 trees were damaged per event. The number of fallen trees in these events varied between 1 and 17, the number of damaged trees between 0 and 18 (Figures 3 a & b). Events in which one tree fell and no trees were damaged were most frequent. In events in which trees were both felled and damaged, the number of fallen trees was linearly related to the number of damaged trees (R^2adj = 0.81; $p < 0.05$; Figure 3c).

In 11 events initiated by a treefall, at least one other tree was felled. Within each of these events, initiating trees had a significantly larger dbh than trees felled domino-wise (Wilcoxon Matched Pairs test, $p < 0.01$). In 8 events initiated by a branchfall, at least one other tree was damaged. Here too, the dbh of trees initiating branchfalls was significantly larger than the dbh of trees from which domino branchfalls originated (Wilcoxon Matched Pairs test, $p < 0.01$).

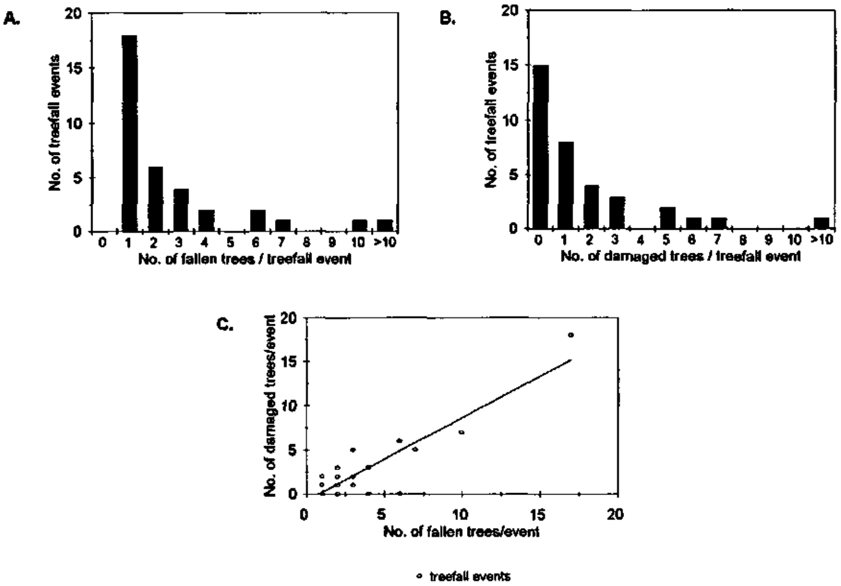

Figure 3. *Frequency distribution of the number of fallen trees (A; n= 96) and number of damaged trees (B; n=66) involved in events in which trees fell ("treefall event"; n=34) during one year in 12 ha of tropical rain forest, Nouragues, French Guiana. The relation between the number of fallen trees and damaged trees per treefall event is given in C* ($N^{damaged\ trees} = 0.9 \times N^{fallen\ trees} - 0.7$; $R^2_{adj} = 0.81$).

Causes of fallen and damaged trees and modes of treefalls

Of the 72 domino treefalls, 53% were felled in events initiated by treefalls and 33% in events initiated by branchfalls. The remaining domino treefalls (14%) were felled in events initiated by the fall of dead stems. The average dbh of the three groups did not differ (Mann-Whitney U test, $p < 0.01$).

About one-third (34%) of all fallen trees were uprooted, the rest of the trees (66%) fell as a result of snapping the tree bole. The dbh of fallen and uprooted trees did not differ (Mann-Whitney U test, $p < 0.01$). Of the fallen trees which initiated events, 38% were uprooted and 62% snapped off. Of the domino treefalls, some 33% uprooted and 67% snapped off. For both groups dbh did not differ between uprooted and snapped trees (Mann-Whitney U test, $p < 0.01$).

Spatial patterns

The Monte Carlo test revealed a random pattern for the 38 trees which had initiated a tree- or branchfall. There was a slight trend towards clustering, but never outside the 95% confidence envelope (not shown). Non-random patterns occurred in the dispersion of initiating

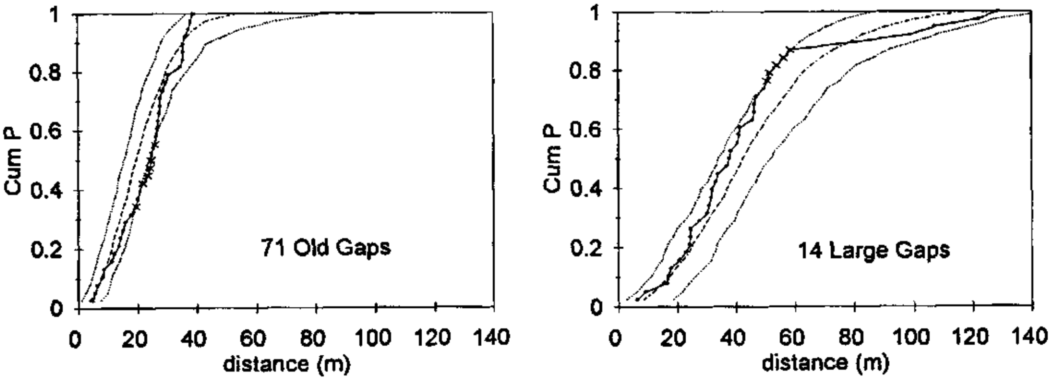

Figure 4. *Cumulative distribution functions (Cum P) for the nearest neighbour distances from 38 observed initiating tree- and branchfalls in 1993 for observed and simulated patterns of (a) 71 old canopy gaps (created before January 1991), and (b) 14 large canopy gaps (i.e. > 50 m², after Brokaw; both new and old gaps). The solid line indicates the actual cumulative distribution functions, the thin striped-dotted line shows the estimated cumulative distribution functions. The thin dotted lines indicate the 95% confidence envelope based on 200 simulations. "X" indicates where the actual nearest neighbour distance lies outside the 95 % confidence envelope. See text for further explanation.*

treefalls and branchfalls around old or large canopy gaps. For initiators and old gaps (Figure 4a), nearest neighbour distances of 19 to 24 metres occurred less frequently than expected, indicating a hyperdispersed or uniform pattern. For initiating tree- and branchfalls and large gaps (Figure 4b), nearest neighbour distances of 50 to 58 metres were more frequent than expected, indicating clustering. Recently created canopy gaps did not seem to affect the location of initiating treefalls and branchfalls.

Which events create canopy gaps ?

One third of the events in 1993 resulted in the creation of a canopy gap larger than 4 m^2 (Table 2). This was not related to the type of initiator (treefall, branchfall or dead stem fall) of the event. Both more fallen and more damaged trees were involved in events which created canopy gaps than in non-gap creating events. The majority of both the fallen (65%) and damaged (58%) trees resulted from events which created canopy gaps. The initiators of a branchfall had a larger dbh in gap creating events than in non gap creating events (Mann-Whitney U-test, $p < 0.01$). Neither the dbh of the initiators of treefalls, nor the dbh of domino-wise felled or damaged trees differed between gap creating and non-gap creating events.

Table 2. *Number of natural events where trees were felled and/or damaged during one year in 12 ha of rain forest. Events are grouped in (1) events which resulted in a canopy gap of at least 4 m² (sensu Brokaw 1982a) (gap creating events) and (2) events which did not result in a canopy gap (non-gap creating events).*

		Involved fallen trees		Involved damaged trees		Type of initiator of the event		
	no.	n	n/ event	n	n/ event	Tree fall (n)	Branchfall (n)	Dead Stem fall (n)
Gap Creating Events	15	62	4.1	47	3.1	8	4	3
Non-Gap Creating Events	30	34	1.1	34	1.1	16	10	4

Table 3. *Spearman correlation coefficients between the number and basal area of fallen and damaged trees, and the size of the canopy gap. This was done for 14 gap creating events; one gap creating event was not considered (see text). Gap size was determined using two different methods.*

	Number of involved Trees		Basal Area of involved Trees	
	Fallen	Damaged	Fallen	Damaged
Gap Size:				
Modified (20m) method	0.45*	0.53*	0.50*	0.53*
Brokaw's (1982a) method	0.31	-0.12	0.24	0.20

** significant correlation ($p<0.05$).*

The gap size at 20 metre height in the canopy was positively related to the number and basal area of both the fallen and damaged trees (Table 3). We found no evidence for a relation between fallen and damaged trees and the gap size sensu Brokaw (1982a).

Disturbance regime

Some 1.5% of the trees containing 1.3% of the basal area fell during the observed year, and 1.3% of the trees containing 3.6% of the basal area were damaged (Table 1). Thus, in the 12 ha, 2.8% of all trees containing 4.9% of the basal area were disturbed by treefalls, branchfalls and the fall of dead stems. The tree- and branchfalls created 15 canopy gaps covering 341 m^2 using Brokaw's (1982a) gap definition and 1591 m^2 using the modified Brokaw definition.

The disturbance rate based on stem turnover rate was 1.5%. Based on the area opened up by canopy gaps the disturbance rate was 0.3% (Brokaw 1982a) or 1.3% (modified Brokaw).

Discussion

Causes of tree- and branchfalls

The most important cause of treefalls and branchfalls was other falling trees or branches. Some 75% of the fallen trees were felled by falling trees or branches, and 83% of the damaged trees were damaged by the fall of other trees or branches. Falling trees and branches have been acknowledged as causes of tree mortality in several other studies. Clark & Clark (1991) found that 41% of the mortality in stems between 1-30 cm was caused by falling debris but in other studies, domino-wise felled trees never accounted for more than 25% of the annual tree mortality (e.g. Durrieu de Madron 1994; Franklin *et al.* 1987; Milton *et al.* 1994; Rankin de Merona *et al.* 1990). It is not clear whether the large difference between this study and the other studies is caused by ecological differences between the studied sites, or by differences in the methods used.

Tree- or branchfalls were more often initiated by larger rather than smaller trees. An explanation for this might be that older trees, by their larger size, are more susceptible to storms or the waterload on leaves and branches than younger, smaller trees (e.g. Runkle 1985). Also, an ageing tree will eventually start to decline, which increases the chances that the tree will fall or will drop its branches. In contrast, we found that smaller trees were more often felled or damaged by the domino effect than larger trees. Interestingly, Clark & Clark (1991) found that large saplings were relatively more often damaged or killed by falling branches or falling trees than smaller saplings. The results of the present study suggest that once saplings have reached a dbh of 10 cm, physical damage becomes less important with increasing dbh.

The dbh distribution of trees felled or damaged domino-wise did not differ from the dbh of undisturbed trees. Although this implies that both large and small trees had an equal chance of being damaged or felled by a falling tree or branch, large emergent trees are not likely to be harmed by other falling trees or branches. For instance, although there were trees of dbh > 80 cm, the dbh of the largest felled and damaged domino trees had a dbh < 55 cm and < 70 cm respectively (Figure 2). The apparent absence of a significant size effect is probably due to the small number of large trees in the forest.

The mode of treefalls is of help in understanding the causes of initiating treefalls. Putz *et al.* (1983) found that of the variables studied (dbh, height, wood density, slope, buttressing), the mode of was most affected by wood properties. Uprooted trees generally had denser, stiffer and stronger wood than snapped trees. Wood properties of trees are also affected by the health of trees (disease, fungal attack etc.). Putz *et al.* (1983) found uprooted trees to have a larger dbh than snapped trees. This suggests that snapped trees are less healthy than uprooted trees, trees snapping as a result of factors such as disease or insect attack before they reach their maximum height. In contrast with this, the uprooting of trees seems to be more related to abiotic factors. For instance, Durrieu de Madron (1994) found that the percentage of uprooted trees increased towards creeks and valley bottoms, while Brokaw (1985) suggested that uprooting of trees is related to soil loosening.

In this study, 38% of the trees which initiated a treefall were uprooted and 62% snapped off. This is roughly in agreement with the findings of Putz *et al.* (1983; 70% snapped and 30% uprooted or snapped at the ground) and Rankin de Merona *et al.* (1990; 47% snapped, 27% uprooted, 26% standing dead), but not with Carey *et al.* (1994) who reported, for lowland rain forests in Venezuela, a very high number of trees dying standing (60%, uprooted 13.5%, snapped 12.3%, other 14.1%). Milton *et al.* (1994) found 123 dead trees ≥ 19.1 cm dbh in three one-ha plots over 13.6 years in Panama. They could only be sure about 20.3% snapped-off and 11.4% uprooted trees. The remaining treefalls were unclear due to decay of many trees and complicated multiple treefall events. In these studies no distinction was made between initiating and domino treefalls. Durrieu de Madron (1994) did make such a distinction and found that some 75% of initiating treefalls were uprooted and 25% snapped off. It is unclear how the large difference in the mode of treefalls between the forest studied by Durrieu de Madron and the forest in the study presented here (a forest only 100 km away) can be explained. One possible explanation might be that this forest is situated on a plateau, with relatively little area in valley bottoms or near creeks. However, even on plateau, Durrieu de Madron found 65% of the initiating treefalls were uprooted.

It is well known that rates of treefalls are correlated with rainfall (Brandani *et al.* 1988; Brokaw 1982b; Oldeman 1974). At Nouragues too more large trees fall at the start of the rainy season than during the dry season (Van der Meer, pers. obs.). These trees often fell during calm weather, so their fall was not caused by storms but possibly by the heavy waterload in the treecrown. Exogenous factors (wind, rain etc.) which cause initiating treefalls are most likely to affect the larger trees in the forest. The waterload of a tree is probably an important factor in this, as large trees are potentially more vulnerable to waterload due to larger crown size (e.g. Runkle 1985) and/or higher epiphyte load (e.g. Strong 1977). Another potential cause of initiating tree- and branchfalls is the asymmetry of tree crowns. Young and co-workers (Young & Hubbell 1991; Young & Perkocha 1994) showed that trees with asymmetrical crowns were more likely to fall than trees with symmetrical crowns and that trees had a strong tendency to fall towards the heavy side of the crown.

In this study we did not investigate the tree mortality caused by the standing death of trees. It is very hard to determine whether a standing tree is actually dead or is suffering from a disease or insect attack which it eventually will overcome. Also, dying of standing trees can be a gradual process which takes several years (Franklin *et al.* 1987).

Spatial patterns

The results on the spatial distribution of the initiating tree- and branchfalls do not support the often mentioned idea that canopy gaps may destabilise surrounding trees (e.g. Brokaw 1985; Hubbell & Foster 1986; Putz & Milton 1982). No effect on the rate of initiating treefalls could be detected within one year after gap creation. Initiating tree- and branchfalls were clumped away from both old gaps and large gaps. Although some non-random patterns were detected, there was thus no evidence that initiating tree- and branchfalls occurred more often close to existing canopy gaps. We know of only two studies that provide evidence for such a relation. Young & Hubbell (1991) on Barro Colorado Island, Panama, found that trees bordering gaps tended to fall into the gaps. Poorter *et al.* (1994) working in Taï National Park, Ivory Coast, showed that in 2 of the 3 sites studied new gaps were very close to old gaps.

Our field observations and impressions suggested that events in which many trees were felled and damaged were close to large gaps. To check this, an additional test was carried out to see whether **all** tree- and branchfalls (both initiators and domino) were spatially related to large gaps. The nearest distances between the 14 large gaps and the 177 fallen and damaged trees were calculated and compared with 100 simulations in which the nearest distances were determined between the 14 large gaps and 177 randomly selected trees. This revealed more or less the same patterns as is shown by the 38 initiating trees and 14 large gaps. Clumping was much stronger in the case of the 177 trees, but also at a rather large distance from the gap centre (between 40 - 58 metres). This again does not support the idea that trees surrounding large gaps are more likely to fall than other trees. A possible explanation for this wrong impression is that when doing fieldwork, large gaps attract more attention than closed forest, so that trees which fall into a gap are more conspicuous than trees which fall in a patch of closed forest (without creating a canopy gap).

Tree- and branchfalls, and canopy gaps

When branchfalls initiated an event, those from large trees had a larger chance of creating a canopy gap than falling branches from smaller trees. In contrast, we found that when a whole tree initiated an event, the probability that this resulted in a canopy gap was not related to tree size. This seems strange, and may only be true for canopy and sub-canopy trees, as a falling emergent tree will always create a canopy gap. Our one-year survey was too short to include the fall of emergents, which are not likely to fall frequently: in our survey, the largest tree which fell was < 90 cm dbh (Figure 2). The dbh of fallen dead stems could not be determined as dead stems were not measured in the first inventory, and most of those that fell were too severely damaged and/or had decayed too much to be measured accurately. However, we estimate that, on average, they are quite large (over 40 cm dbh).

We expected that a falling tree would have a greater chance of creating a canopy gap than a falling branch or a falling dead stem (e.g. Arriaga 1988), but this is not the case. This can possibly be explained by the larger dbh of the initiators of branchfalls which create a canopy gap compared to the initiators of branchfalls which do not create canopy gaps. Many canopy gaps are created by branchfalls from very large trees, a phenomenon which was also recorded by Jans *et al.* (1993). The reason that dead stemfalls are relatively likely to create a canopy gap may also be explained by the large dbh of the stems.

The size of canopy gaps at 20 metres height increased with an increase of both the number and size (basal area) of the trees involved. This is in accordance with the findings of others (e.g. Brokaw 1982b). However, we did not find a significant correlation between the number and size of trees involved and the gap size according to Brokaw's definition. As we discussed elsewhere (Van der Meer *et al.* 1994; see also Popma *et al.* 1988), Brokaw's definition is not very relevant in determining the direct consequences of the creation of a canopy gap. The fact that the new, modified gap definition (developed on the basis of Brokaw's definition) was significantly correlated to the number and basal area of the involved trees might indicate that this definition is more relevant in terms of determining the direct consequences of gap creation than Brokaw's original definition.

Forest turnover rates

The direct consequences of tree- and branchfalls can be quantified in terms of the disturbance regime of a forest which, in its turn, can be an important tool in trying to explain structure and species composition of a forest (e.g. Hartshorn 1978). The disturbance regime of a forest is often expressed as the turnover rate, based on the rate of tree mortality or gap formation. There is no direct relation between the two (e.g. Denslow & Hartshorn 1994) and the apparent differences may lead to major differences in turnover calculations. For instance, both Putz & Milton (1982) for BCI, Panama, and Lieberman *et al.* (1990) for La Selva, Costa Rica, found that the tree mortality turnover rate was twice as fast as the gap turnover rate for the same forest.

The annual rate of fallen trees in this study (1.5%) is consistent with other studies on treefalls and tree mortality in neotropical rain forests. Recent overviews by Phillips and Gentry (1994) and Rankin de Merona (1990) show that annual mortality rates of neotropical rain forests range between 0.7 and 3.1%. In another study on tree mortality in French Guiana, the mean annual tree mortality rate was 1.1%, with a variation between 0.8 and 1.6% over 7 consecutive years (Durrieu de Madron 1994).

Using Brokaw's gap definitions, we arrived at a disturbance rate of 0.3%. This is very low compared to other neotropical forests, where the disturbance rate typically ranges between 1-2% (e.g. Clark 1990, Jans *et al.* 1993), suggesting that the forest at Nouragues is less dynamic than other neotropical rain forests. However, the tree mortality rate indicates that in terms of fallen trees, the forest is equally dynamic as other forests. We believe the low gap disturbance rate in Nouragues to be the result of a rather strict application of Brokaw's definition. To be as objective as possible in measuring gaps, we classified the gap border as any vegetation above two metres height. This vegetation could be anything from a small branch at 3 metres height to a large tree crown at 40 metres. We have the impression (pers. comm. with several gap researchers) that in many other gap studies, Brokaw's gap definition is applied more loosely, without taking into account the often abundant small (between 2 and 5 m) vegetation in the gap area and only considering the vegetation of large surrounding trees. To overcome the problem of small gap vegetation in measuring gap size, we developed the modified gap definition, measuring the gap size at 20 metres height. Using this method, the gap disturbance rate was 1.3%, which is more within the range of other findings. Suprisingly, this latter gap disturbance rate of 1.3% is comparable to our turnover rate based on fallen trees (1.5%). As of the fallen trees 35% did not create canopy gaps, 42% of the damaged trees were not involved in the creation of a canopy gap, and two canopy gaps were created by the falling of branches only (with no treefall involved), there is no biological reason why this should be so.

The difference or similarity between rates of tree death and rates of gap formation may however be an important parameter in describing the dynamics of a particular stand (Diana Lieberman pers. comm.). For instance, it may reveal whether large trees die slowly, dropping of branches one by one, or whether they die abruptly by toppling over. An example of this is the paradoxical situation found in Ivory Coast, where Jans *et al.* (1993) found that of three rain forest sites studied, the site with the largest trees had the smallest gaps. At this site, single branches dropped from dying emergent trees, creating relatively small gaps.

In Nouragues, both the turnover rate based on tree death and on gap formation underestimate the actual disturbance regime of the forest. The rate of tree disturbance (both fallen and damaged trees) based on either the number (2.8%) or the basal area (4.9%) is larger than the traditionally calculated turnover rates, which are based on either the number of fallen trees (1.5%) or the area in new gaps (0.3% or 1.3%, using Brokaw's gap definition and the modified gap definition respectively). Damaged trees open up the forest canopy, and their falling branches can kill smaller plants (e.g. Aide 1987; Clark & Clark 1991). Therefore, both fallen and damaged trees should be taken into account in determining the disturbance regime of a forest, as should both the basal area and the number of the disturbed trees.

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CHAPTER 4

Formation and closure of canopy gaps

Formation and closure of canopy gaps in the rain forest at Nouragues, French Guiana.

P.J. Van der Meer & F. Bongers

(submitted)

Abstract

Formation and closure of canopy gaps was monitored for three years in 12 ha of primary rain forest at Nouragues, French Guiana. At the first inventory, in April 1991, 74 openings in the canopy > 4 m^2 (sensu Brokaw 1982a) were located; 60 of these gaps were formed before January 1990. Between January 1990 and December 1993, 5 to 15 gaps were annually formed, opening 0.64 - 1.33 % of the forest canopy each year. Of all gaps, 41 % were created by a falling, snapped tree, 34 % by a falling, uprooted tree, 22 % by a falling branch, and 3 % by a falling dead stem.

A refined nearest neighbour analysis showed that gaps formed after January 1990 were clustered. The clustering of new gaps appeared to be caused by the abundant shallow soils at Nouragues. Uprooting of trees seemed to be related to shallow soils, and relatively many other trees were felled when a trees uprooted, independent of the dbh of the uprooted tree.

In 37 gaps, canopy openness in the gap centre (determined by hemispherical photographs) was monitored over three years. In 54 % of the gaps, canopy openness increased in two successive years. It is argued that edges of especially large gaps may frequently be re-disturbed by falling trees or branches. Results suggest that gaps have closed after around 15 years. More data are needed to verify this.

Keywords: *canopy gaps - canopy openness - French Guiana - gap closure - gap formation - hemispherical photographs - rain forest - shallow soils - spatial pattern*

Introduction

Canopy gaps are holes in the forest canopy existing through all height levels (sensu Brokaw 1982a). In tropical rain forests, canopy gaps are an important factor controlling the species diversity (e.g. Denslow 1987). There formation can be considered the starting point of the forest growth cycle, after which the forest starts to regrow and will eventually reach the mature canopy stature (Oldeman 1978; Whitmore 1978). During this process, both spatial and temporal heterogeneity in the gap micro-climate is large, providing habitats for many plant species (Bazzaz & Wayne 1994; Bongers & Popma 1988).

Canopy gaps in tropical rain forests are hard to define, and difficult to measure (Van der Meer *et al.* 1994). Often there is no clear border between gap area and forest area: in general, micro-climatic factors change gradually with a high variation (and overlap) in both gap and forest understorey (Canham *et al.* 1990; Rich *et al.* 1993). It is clear that the often mentioned gap versus non-gap dichotomy of tropical rain forests is an oversimplification of reality (Lieberman *et al.* 1989). However, it is indisputable that canopy gaps have a major effect on the recruitment, growth and/or mortality of plant species: during the last decades, the effect of canopy gaps on the performance of plants was investigated at an ever-increasing rate (e.g. Denslow *et al.* 1990; Martinez-Ramos & Alvarez-Buylla 1986; Newell *et al.* 1993; Popma & Bongers 1988).

Canopy gaps in tropical rain forests are created by the fall of trees, either by snapping or uprooting. Also, falling branches may create gaps in the forest canopy. The rate at which canopy gaps are formed indicates the frequency with which plant resource availability (e.g. light and nutrients) is enhanced. In general, between 1 and 2 % of a tropical rain forest canopy is opened by gaps per year (overviews in Brokaw 1985a; Clark 1990; Hartshorn 1990; Jans *et al.* 1993). The composition of regeneration in canopy gaps is affected by gap size, and by the mode of tree death. For instance, Brokaw (1985b) found the density of pioneer species to increase with increasing gap size, and Riéra (1985) found that root-mounds were important regeneration sites for some pioneer species. Also, the spatial distribution of gaps, which might be clumped (e.g. Brokaw 1985a; Hubbell & Foster 1986; Poorter *et al.* 1994), is of importance when estimating the effect of gap formation on recruitment, growth and mortality of plants.

Finally, it is important to know how fast canopy gaps close, in order to be able to estimate how long canopy gaps influence plant population dynamics. It is generally acknowledged that small gaps mainly fill by means of lateral ingrowth of branches from adjacent trees (Bazzaz 1984; Denslow 1987). The rate at which this happens however has hardly been investigated. In larger gaps, the dominant gap fillers are seedlings and saplings, Their growth rates have been investigated intensively at the species or population level (e.g. Barton 1984; Brokaw

1985b; Clark *et al.* 1993; Welden *et al.* 1991). Van der Meer (subm.) studied gap filling on the vegetation level: small gaps closed 5-6 years after formation, and large gaps were estimated to have formed a more or less closed canopy of at least 10 m height after 5-10 years.

In this paper, we provide information on the formation and closure of canopy gaps in the tropical rain forest around Nouragues, French Guiana, and compare this with information on other neo-tropical rain forests. We will address the following questions: (1) How, and how often is the forest canopy opened by canopy gaps each year (mode of creation; gap size frequencies; variation between years) ?; (2) How are canopy gaps spatially related to each other ? and (3) How fast do canopy gaps close ?

Methods

The study was conducted in a pristine lowland rain forest in French Guiana, in the northern part of the Amazon Rain Forest. Research took place at the Nouragues field station, located some 100 km inland (4°05'N; 52°40'W). No long term data on rainfall are available yet, but between 1990 and 1994, the average annual rainfall was 2920 mm. There is a distinct dry season from September to November and a less conspicuous dryer period around February-March. The region is hilly; elevation ranges between 60-120 m above sea level. There are some small mountains between 300 - 450 m high, and one granitic outcrop ("inselberg") of 411 m high. Canopy gap formation was monitored in a permanent sample plot of 300 x 400 m (12 ha), situated on a plateau (between 90-110 m a.s.l.).

In April 1991, we determined the exact location, the size, and the age of all canopy gaps > 4 m^2 (" a canopy opening extending through all levels down to an average height of 2 m above the ground"; after Brokaw, 1982a) in the study area. The gap centre was permanently marked with a plastic picket. Locations of the pickets were plotted on a map, using a 100 x 100 m trail system through the area, a compass, and an optical range finder (Ranging Optimeter 120; range 2-30 m). Gap size was determined using two commonly used gap definitions. First, gaps were measured using Brokaw's (1982a) definition; in eight directions (at 45° intervals), the distance was determined from the gap centre to the vertical projection of the first vegetation above 2 meters. The eight gap border points were connected with straight lines, and the enclosed surface was determined by calculating the surface of the eight triangles. Secondly, gaps were measured using Runkle's (1981) gap definition: the expanded gap surface is the area bordered by the stembases of the canopy trees > 20 m tall surrounding the canopy opening. Of each gap, the year of gap formation was determined using 5 classes (< 1985; 1986-87; 1988-89; 1990; 1991). Gap age was estimated through observations on the gap vegetation and environment: (1) the state of decomposition of fallen debris; (2) "freshness of snap" of snapped trees or saplings; (3) the size of resprouts on snapped trees, and (4) freshness of the uprooted soil mount. In some cases, gap age was known through field observations in the preceding years (Riéra, pers. comm.). These cases served as a check to our method of gap age determination.

The formation of new canopy gaps (> 4 m^2) in the 12 ha was monitored during five stays of 2-3 months between October 1990 and December 1993. Location and date of formation was determined, and the centre was marked with a plastic picket. Gap size was measured as soon as possible after gap formation. In addition to the two gap definitions used in the April 1991 inventory, a third gap definition (modified after Brokaw) was added to measure the gap size at 20 meters height (Van der Meer & Bongers, in press). The distance from the gap centre to the first vegetation > 20 m tall was determined in eight directions. The eight gap border points were connected with lines, and the enclosed surface was calculated. In applying this method, the height of the vegetation was checked using an optical range finder; the exact location of the vertical projection of the vegetation was determined using a pentagon prism. All gaps formed in or after 1991 were measured using all three methods. Henceforth, the three methods will be called by their definer's name (Brokaw, Runkle, Van der Meer).

For each gap, it was noted whether the tree which had created the gap ("gap initiator") was uprooted or snapped, or whether the gap had been created by the fall of a branch. The diameter at breast height (dbh) of the fallen tree was measured, and its direction of fall was determined. In case of branch fall, the dbh of the tree from which the fallen branch originated was measured. When other trees (> 20 cm dbh) were felled by the gap initiator, their dbh was measured too. Local topography (slope, direction) was determined.

To test whether the spatial distribution of canopy gaps departed from randomness, a refined nearest neighbour analysis (Upton & Fingleton 1985) was used. For each of the canopy gaps in the 12 ha, the distance to its nearest neighbour was calculated. These distances were ranked from small to large, and converted to a cumulative distribution function. The frequency distribution was plotted in a graph, and compared with the (two-sided) 95% confidence envelope of a random pattern, using the Monte Carlo simulation technique (Besag & Diggle 1977). With this technique, 200 simulations were performed, each simulation being (a) the generation of random points, (b) the calculation of the distance to its nearest neighbour for each point, (c) ordering of the distances from small to large. In the field, gap centres are at least as far apart as the sum of their gap radii. Therefore, when generating the random points, the minimal distance between two points was set at four meters, as the minimum gap radius is two m. The 200 cumulative distribution frequencies were ordered again per distance: all smallest distances in the 200 simulations were ordered from small to large, all second-smallest distances were ordered, and so forth. The boundaries of the 95 % confidence envelope are defined by the 6th and 195th cumulative distribution frequencies. When values of the cumulative distribution function of the distances of the actual canopy gaps fall inside this confidence envelope, the pattern is considered as being random.

For the canopy gaps present in the 12 ha in April 1991, a hemispherical photograph was made of the canopy above the gap centre (1 m height) in April 1991. In about half of these gaps (the gaps in the central 6 ha), hemispherical photographs were made again in November 1992 and December 1993. Photographs were made in early morning or late afternoon, during overcast weather, to avoid direct sunlight. In the newly formed gaps, hemispherical photographs were made in October 1991, November 1992 and December 1993. In 1991, photographs were made using a Minolta X-700 body with a Sigma Fisheye lens 8 mm. In 1992 & 1993, a Canon Ti70 body was used with a Canon Fisheye lens 7.5 mm/5.6. For each photograph, the canopy openness ("percentage unobstructed sky on the photograph"; cf. Mitchell & Whitmore 1993) was calculated using the program Hemiphot (Ter Steege 1993).

Results

In total we located 102 gaps: 60 of them were created before January 1990 ("old gaps"), and 42 had been created between January 1990 and December 1993 ("new gaps"). Many of both old and new gaps were tiny: 55.0 % and 47.6 % respectively had a gap size between 4-10 m^2 (sensu Brokaw). The average gap size decreases with gap age: gap size (sensu Runkle) of old gaps was significantly smaller than gap size of new gaps (Mann-Whitney U-test; $p < 0.05$).

Gap status of Nouragues forest, April 1991

In April 1991, we located 74 canopy gaps larger than 4 m^2 in the 12 ha, of which 14 were not older than 16 months (Table 1). Average gap size appeared to vary between age classes, but differences were not significant (Kruskal-Wallis test, $p < 0.05$). The 74 canopy gaps opened 1.13 % of the forest canopy (sensu Brokaw). Some 15.4 % of the forest floor was affected by the canopy openings, assuming that Runkle's gap definitions is a reasonable estimate of the extent to which micro-environment at the forest floor is changed through the gap formation (see Van der Meer & Sterck submitted). Of the total area covered by gaps in April 1991, older gaps (formation before January 1990) contributed 69.5 % to the gap area at the forest canopy, and 72.5 % to the gap area at the forest floor.

Table 1. *Gap status of the studied plot in April 1991. All canopy gaps over 4 m^2 (Brokaw) were measured in 12 ha of rain forest, using two methods: Brokaw (gap size at two meters high) and Runkle (expanded gap, bordered by stembase of surrounding canopy trees). Age of gaps formed before October 1990 was estimated.*

Year of gap formation	No. of Gaps	Total Gap Size (m^2) (*average per gap*) Brokaw	 Runkle
< '85	16	213 (*13*)	2541 (*159*)
'86-'87	25	318 (*13*)	6071 (*243*)
'88-'89	19	407 (*21*)	5281 (*278*)
'90	11	338 (*31*)	3501 (*318*)
'91	3	74 (*25*)	1084 (*361*)
Total	74	1350 (*18*)	18478 (*250*)

Total % forest area in gaps April 1991:

cf Brokaw:	1.1 %
cf Runkle:	15.4 %

Table 2. *Annual Gap Formation Rate between January 1990 and December 1993 in the Nouragues forest. Sizes of gaps (> 4 m^2 Brokaw) were measured using three methods: Brokaw, Runkle, and Van der Meer. Gap formation rate per year is expressed as the percentage of the forest area opened up by gaps.*

Year of gap formation	No. of Gaps	Total Gap Size (m^2) (*average per gap*)			Annual Gap Formation Rate (% of forest area)		
		Brokaw	Runkle	VdMeer	Brokaw	Runkle	VdMeer
'90	11	338 (*31*)	3501 (*318*)	-	0.28	2.92	-
'91	5	163 (*33*)	3114 (*623*)	770 (*154*)	0.14	2.60	0.64
'92	11	212 (*19*)	2726 (*248*)	1087 (*99*)	0.18	2.27	0.91
'93	15	341 (*24*)	4442 (*296*)	1591 (*106*)	0.28	3.70	1.33
Avg '90-'93	11	264 (*26*)	3446 (*371*)	1149 (*120*)	0.22	2.87	0.96

Annual gap formation rate between January1990 and December1993

Over a period of 4 years, between 5 -15 gaps (with an average of 11 gaps) were annually formed in the 12 ha (Table 2). Average gap size seemed to vary between years, but this was not significant (Kruskal-Wallis test, $p < 0.05$). The annual amount of forest area affected by new gaps ranged between 0.14 - 0.28 % (sensu Brokaw), 2.38 - 3.70 % (sensu Runkle), and 0.64 - 1.33 % (sensu Van der Meer).

Gap features

Some 41 % of the gaps were created by snapping, and 34 % by uprooting of trees. About 22 % of the gap initiators were falling branches. Falling dead stems created 3 % of the canopy gaps (Figure 1). This ratio did not differ between years (Kolmogorov-Smirnov test; $p < 0.05$).

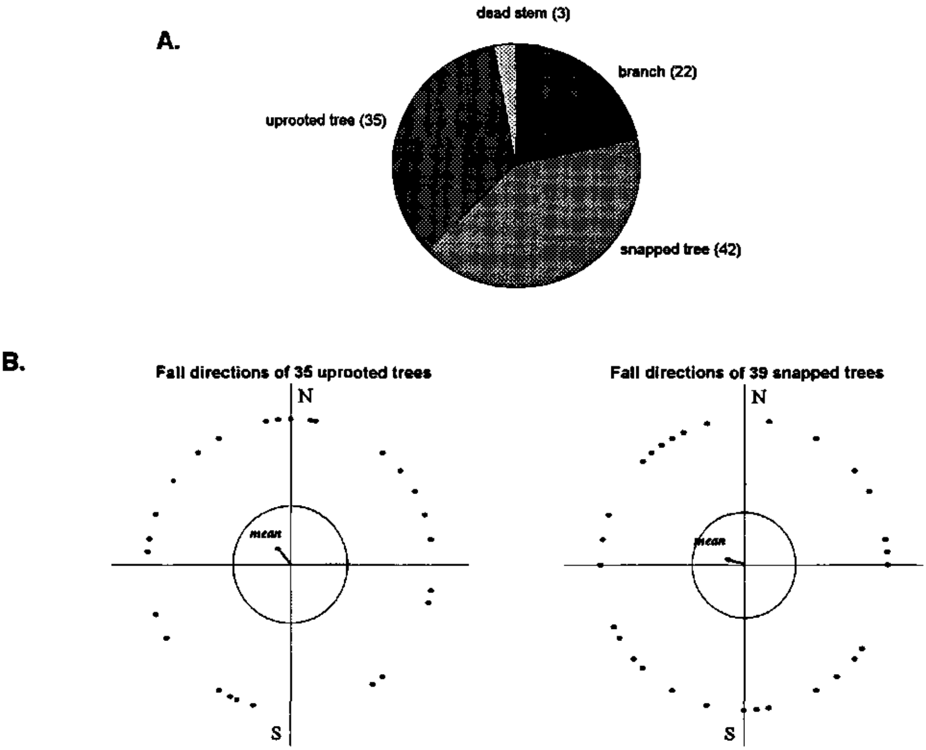

Figure 1. *A. Type of gap-creator of 102 canopy gaps. B. Direction of falling of snapped and uprooted trees which created a canopy gap. The mean vector ("mean") does not exceed the 95 % confidence limit (inner circle) for either uprooted or snapped trees. The falling direction is random in both cases (Rayleigh test for randomness).*

Table 3. *Dbh of different type of gap creators, and the average gap size per gap creator type. Dbh of branchfalls is the dbh of the trees from which the branchfall originated. For gap size, only new gaps were used (created after January 1991). Gap size was determined using three definitions (see text). Significant differences are indicated with different letters in superscript (Anova one-way test; Students t-test, $p < 0.05$).*

		Gap Creators		
		Snapped	**Uprooted**	**Branchfalls**
Dbh *(cm)*		61.6^{B}	48.9^{A}	69.7^{B}
(all gaps)		*(n=42)*	*(n=35)*	*(n=22)*
Gap Size *(m^2)*		*(n=11)*	*(n=9)*	*(n=8)*
(gaps formed after Jan. 1991 only)*	**sensu Brokaw**	23.5	28.2	20.8
	sensu Runkle	377.1	407.7	234.6
	sensu Van der Meer	113.6^{AB}	163.8^{B}	66.4^{A}

Ad *: Three gaps created by falling dead stem were not considered here

Furthermore, gap creators had not fallen into a specific direction. A Rayleigh test for randomness (Batschelet 1981) revealed that the fall direction of uprooted trees, of snapped trees, and of uprooted and snapped trees together, did not differ significantly from randomness (Figure 1). The slope of the local terrain where trees fell did not differ between snapped (10.5 % slope) and uprooted trees (11.4 % slope) (Mann-Whitney U-test, $p < 0.05$).

Different types of gap creators had a significantly different dbh (Anova test; $p < 0.05$; Table 3). Uprooted trees were significantly smaller than (1) snapped trees and (2) trees which initiated branchfalls (t-test; $p < 0.05$). Furthermore, gaps created by an uprooted tree were generally larger than gaps created by snapped trees or branchfalls, although differences were significant in only one case (Table 3). In analysing the relation between the type of gap creator and gap size, only gaps created after January 1991 were considered, as these gaps were measured within maximally 10 months after gap formation. The size of gaps created before January 1991 may initially (just after gap formation) have been larger than the size which was measured in the April 1991 inventory.

Gap size frequencies for the one-time gap survey and for the gaps formed between 1990 and 1993 did not differ (Kolmogorov-Smirnov test, $p < 0.05$). Also, in separate years between 1990 and 1993, frequencies were not significantly different. Patterns varied when different gap definitions were used (Figure 2).

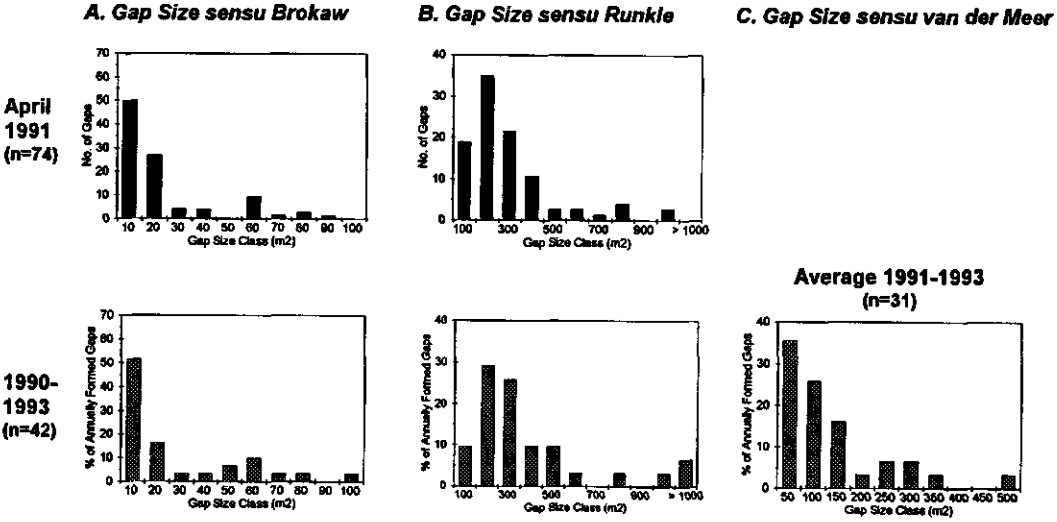

Figure 2. *Gap size frequencies for the one-time gap survey in April 1991, and of the annually formed gaps between 1990 and 1993. Frequencies are given for three different gap definitions.*

Table 4. *Correlation coefficients (Pearson) between gap size and (1) number of trees involved, and (2) dbh of gap creator for the gaps formed after January 1991. Gap size was determined using three different methods (see text). Significance of the coefficients is indicated with * (2-tailed $p < 0.05$) or ** ($p < 0.01$).*

		Gap Size		
	Gap creator type	**sensu Brokaw**	**sensu Runkle**	**sensu Van der Meer**
(1) No. of trees involved	**Snapped** *(n=11)*	0.60*	0.60*	0.69*
	Uprooted *(n=8)*[A]	0.58	0.73*	0.60
	Branchfall *(n=8)*	0.99**	0.89**	0.97**
	All *(n=27)*[B]	0.69**	0.65**	0.70**
(2) Dbh of gap creator	**Snapped** *(n=11)*	0.69*	0.19	0.49
	Uprooted *(n=8)*[A]	0.14	0.21	-0.24
	Branchfall *(n=8)*	0.35	0.39	0.36
	All *(n=27)*[B]	0.41*	0.08	0.10

Ad [A]: One uprooted gap creator was not considered, as it fell in the edge of an old, large gap.

Ad [B]: Three gaps created by dead stem falls were not considered here.

The size of gaps formed after January 1991 was modestly to very strongly correlated (cf. Fowler & Cohen 1990) with the number of trees involved in the event which created the gap (Table 4). Especially in the case of gaps created by falling branches, correlation coefficients were very strong. The dbh of (1) snapped gap creators, and (2) trees which dropped a branch which created a gap were positively correlated with gap size. The dbh of uprooted gap creators was not correlated with the gap size. The results were highly affected by gap definitions. Finally, in events initiated by uprooted trees, more other trees (> 20 cm dbh) were involved than in events initiated by snapped trees (2.8 versus 2.0 respectively). However, this difference was not significant (Mann-Whitney U-test, $P < 0.05$).

Gap size and canopy openness (at the moment the gap size was determined) as calculated from hemispherical photographs showed a modest positive correlation: correlation coefficients (Pearson) were 0.69 (n=100), 0.60 (n=100) and 0.48 (n=30) for gap size according to Brokaw, Runkle and Van der Meer respectively (Figure 3).

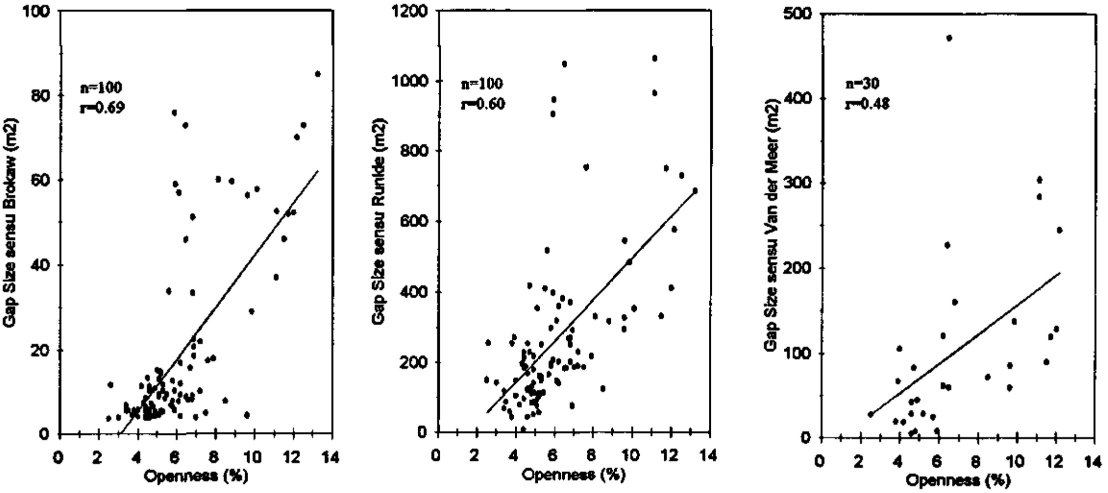

Figure 3. *Correlation between canopy openness as determined by hemispherical photographs, and gap size sensu three gap definitions. Pearsons correlation coefficients given.*

Spatial Distribution of Gaps

In the studied 12 ha area, the cumulated gap area varied markedly between separate one-hectare plots: between 67 to 332 m^2 (0.7 - 3.3 %) of each hectare was covered by both old and new gaps (sensu Brokaw; Figure 4). Differences in cumulated gap area between the 12 one-hectare blocks were significant (Chi^2, $p < 0.05$). When grouping hectare's in independent (at least 100 m apart) blocks of three or four hectares, differences between the cumulated gap area remained significant. The cumulated gap area did not differ between two blocks of six hectares (Chi^2- test, $p < 0.05$).

New gaps (formed between January 1990 and December 1993) were clustered: nearest neighbour distances between 12-17 m occurred more frequently than expected (Figure 5). The spatial distribution of all gaps did not differ significantly ($p > 0.05$) from a random distribution, although there was a tendency towards uniformity. Old gaps showed a trend towards clustering, but this too did not differ significantly from a random distribution.

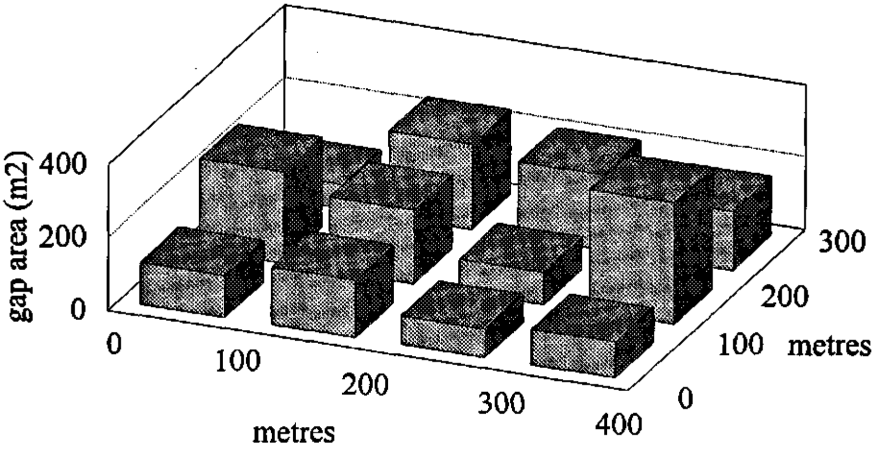

Figure 4. *Cumulative gap surface (sensu Brokaw 1982a) of the one-time gap survey in April 1991 and of the period till 1993 for each one-hectare block in the 12 ha plot.*

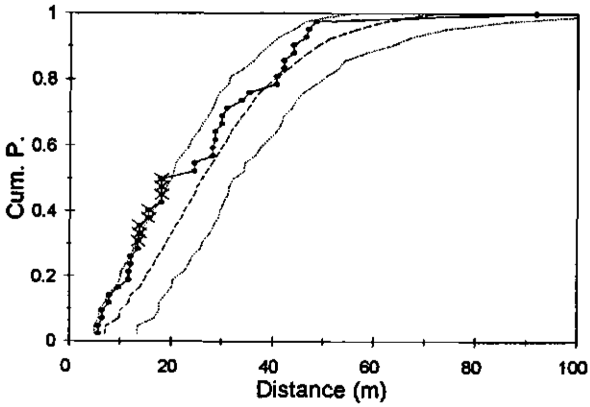

Figure 5. *Cumulative distribution functions (Cum P) for the nearest neighbour distances of gap locations of 42 new gaps (formed after January 1990). Dots connected with the solid line indicates the actual cumulative distribution functions, the thin striped-dotted line showing the estimated cumulative distribution functions. The thin dotted lines indicate the 95% confidence envelope based on 200 simulations. A "X" indicates that the actual nearest neighbour distance lies outside the 95 % confidence envelope. See text for further explanation.*

Closure Rate of Gaps

The canopy openness in gap centres was monitored for three years in 37 gaps created before 1990, in seven gaps created in 1990, and in five gaps created in 1991. In other gaps, photographs were not made for all three years for various reasons (gaps formed after 1991, over- or under exposed photographs etc.). In general, canopy openness decreased with the ageing of gaps, although variation was large. Canopy openness of older (pre 1990) gaps increased slightly between 1992 and 1993 (Figure 6). For instance, 54 % of the pre 1990 gaps showed an increase in canopy openness between 1992 and 1993 (versus 19 % between 1991 and 1992).

We used the gap status in December 1991 to estimate the rate of gap closure during the first 6 years after gap formation: considering the 12 ha at the end of 1991, (338+161=) 501 m^2 of the forest area is in gaps younger than 2 years, 407 m^2 in 3-4 years old gaps, and 318 m^2 in 5-6 year old gaps. We assumed hereby that the gap sizes had not changed between April and December 1991, and that the two-annual gap formation rates did not differ between years. The cumulated gap areas per age class (two-years) were converted to percentages of the forest area in gaps, and plotted in a graph above the middle point of the two-annual age classes they represent (Figure 7). These points served as a guide for a possible route of gap closure, indicating that gaps, on average, will have closed after around 15 years.

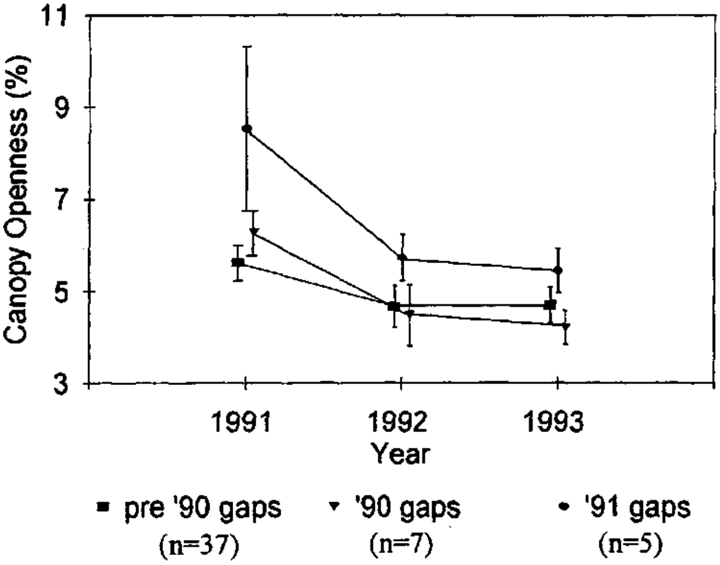

Figure 6. *Canopy openness during three successive years in the gap centre of canopy gaps of different age. Standard error of the mean are indicated with lines.*

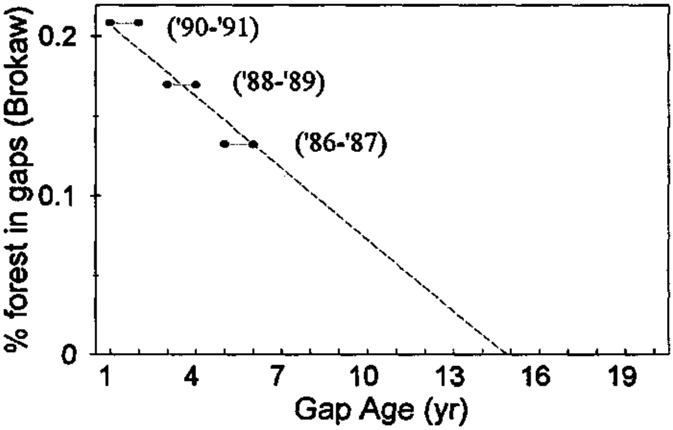

Figure 7. *An example of the simulated rate of gap closure (dotted line), using the observed area in gaps 1-2, 3-4 and 5-6 years old in 1991. See text for further explanation.*

Discussion

Uprooting of trees, and its consequences for spatial patterns.

Most of the canopy gaps (78.5%) in Nouragues were formed by falling trees. Causes of treefalls which initiate gap creating or non-gap creating events are poorly understood, and were discussed elsewhere (Van der Meer & Bongers in press). Analysis of the mode of falling (i.e. uprooted vs. snapped), and the spatial patterns in gap formation, may help to reveal some of the causes and consequences of the falling of trees.

Uprooting of trees is related to soil factors. Fraser (1962; in Putz *et al.* 1983) found that a small increase in rooting depth resulted in a considerable increase in the resistance to uprooting. In their study on gap formation in Ivory Coast, Jans *et al.* (1993) found that the mode of gap creation differed between sites, and concluded that poor soil conditions resulted in a greater incidence of uprooting of trees (versus snapping on more favourable soil conditions). Also in other studies it was suggested that the uprooting of trees was associated with unstable soil conditions, e.g. as found around creeks (Brokaw 1985a, Durrieu de Madron 1994). In Nouragues, uprooting of trees is a more important mode of falling than at other neo-tropical rain forest sites. Of the fallen trees which had created a canopy gap, 46 % had uprooted, and 54 % had snapped. In Mexico and Panama, only 30 % of the fallen trees which were involved in canopy gaps had uprooted (and 70 % snapped) (Martinez-Ramos *et al.* 1988a; Putz *et al.* 1983). This indicates that unstable soils in Nouragues are a relatively important factor which affects treefalls and gap formation. This is most likely to be related to shallow soils: in the 12 ha in Nouragues, at least 13 locations (generally not larger than 25 m^2) had a very thin or absent top soil layer, with sometimes bare rock visible at the surface.

Interestingly, uprooted trees in Nouragues had a significant smaller dbh than snapped trees, which may be explained as follows. When trees grow at places with unstable, shallow soils, they are not able to develop well extended, deep root systems. At such places, trees have higher chances to uproot before growing very large than at places with well developed, well drained soils. Eventually, trees on well developed soils will fall too, but here other factors than soil (e.g. wood properties: Putz *et al.* 1983) are more likely to determine whether trees uproot or snap. In contrast with our results, Putz *et al.* (1983) found uprooted trees in Panama to be larger than snapped trees. And in Mexico, Martinez-Ramos *et al.* (1988a) found no difference in dbh between uprooted and snapped trees. This indicates that at these sites, trees are not prevented to grow into large individuals due to unstable soil conditions. For instance, during most of the year, valley bottoms provide good growth conditions (e.g. high nutrient and water availability), and are only occasionally unstable (e.g. during exceptionally wet conditions).

In Nouragues, uprooted trees have a smaller dbh than snapped trees, but gaps made by uprooted trees appeared to be larger (although not significantly) than gaps made by snapped trees. This seems paradoxical, as a smaller dbh of a fallen tree would normally result in a smaller gap size (e.g. Brokaw 1982a). The number of fallen trees in gaps created by uprooted trees was higher than in gaps created by snapped trees (2.8 versus 2), although this difference was not significant (Mann-Whitney, $p < 0.05$). Furthermore, the dbh of uprooted trees was not correlated with gap size. All this suggests that when trees uproot, relatively many other trees are felled in the same event, independent of the dbh of the uprooted tree.

The variation in cumulated gap area between the one-hectare blocks indicates that gap formation may be related to the local variation in soil depth, or variation in topography. For instance, the one-hectare plot with the highest area in gaps is an area with some steep slopes, and several places of bare rock (Van der Meer, unpubl. data). In other tropical rain forests, gap formation was found to be affected by local differences in topography and related soil factors. In La Selva, Costa Rica, there are permanent canopy openings in the forest where early successional vegetation is abundant, and relatively small trees fall at high frequency (Hartshorn 1990; Sanford *et al.* 1986). These places are associated with swamps and poorly drained soils, and occupy 3.4 % of the forest area. In the same forest, the gap formation rate was higher on a plateau (1.25 %) than on slopes (0.74 % and 0.72 %) and in a swamp (0.84 %) (Hartshorn 1978). On Barro Colorado Island, Panama, Hubbell & Foster (1986) found that disturbance regimes varied within their 50 ha plot, which was reflected in the species composition of these places. Poorter *et al.* (1994) found non-random patterns in the location of gaps in a rain forest in Ivory Coast, West Africa, which was related to catena position. Gap densities, sizes, and percentage forest in gap phase were higher on the upper and middle slope than at the crest or lower slope.

The clustering of new gaps in Nouragues as revealed by the nearest neighbour analysis (Figure 5) may well be caused by soil factors. When gaps are more likely to occur on places with shallow soils, gaps (notably those created by uprooted trees) will cluster around these places. On other, deeper soils, gaps created by either branchfalls, uprooted trees, or snapped trees, may cluster too. Our results, and the results of others, suggest that canopy gaps are not random in space, but are clustered around specific sites (e.g. Hubbell & Foster 1986; Poorter *et al.* 1994; Sanford *at al.* 1986). Exact data on the relation between soil distribution and gap locations in the Nouragues forest may help to explain patterns of gap clustering at a more detailed level, but are largely lacking up to date.

Rates of gap formation

Average annual gap formation rates in Amazonian rain forest ranges between 0.96 - 1.33 % (Table 5). The average annual gap formation rate in Nouragues, expressed in terms of Van der Meer's gap size (0.96 %), is comparable with these findings. As indicated by Van der Meer & Bongers (in press), we applied Brokaw's gap definition in a rather strict sense which is not commonly done by other gap researchers. Therfore, we presume that gap sizes sensu Van der Meer in this study are comparable with Brokaw's gap size data of other studies. In Central America, average annual gap formation rates on five tropical lowland rain forest sites ranged between 0.69 and 1.5 % (Bongers *et al.* 1988; Brokaw 1982b; Hartshorn 1978; Hubbell & Foster 1986; Martinez-Ramos & Alvarez-Buylla 1986). Although this variation may at first sight seem small, in reality it means that one forest may be twice as dynamic as another forest.

As indicated by Hartshorn (1990), surprisingly few studies in tropical America provide information about gap formation rates over longer periods of time. We know about only one study that gives the annual gap formation rate over a period of 70 years: Martinez-Ramos *et al.* (1988a) used bent palms to date back gap formation in a Mexican rain forest, and found that the annually opened area of forest varied between 0 and 10 %. None of the other Amazonian gap studies provide information about annual variation in gap formation rate. Variation in gap formation between years was considerable in Nouragues: annual gap area varied between 0.64 % and 1.33 % in three years. Also the number and sizes of gaps formed each year varied importantly. This may be related to variation in the annual rainfall regime, as rain and wind are often the proximate cause of treefalls, felling weakened or unstable trees (Brokaw 1985a). In many forests, trees fall most often at the start or the middle of the rainy season (e.g. Brandani *et al.* 1988; Brokaw 1982b; Oldeman 1974). Chandrashekara & Ramakrishnan (1994) and Martinez-Ramos *et al.* (1988a) found positive correlations between variation in rainfall and gap formation. In Nouragues, treefalls peaked during the rainy season. Unfortunately, for many canopy gaps the exact date of creation was not known, but had to be estimated after a period of up to nine months of absence. Also, rainfall data were not complete, so that we could not analyse the precise relation between rainfall and the formation of canopy gaps.

In recent years, several researchers compared gap formation rates of different sites (e.g. Brokaw 1985a; Clark 1990; Hartshorn 1990; Jans *et al.* 1993). Results of canopy gap research however are potentially subject to large errors (e.g. Clark 1990). The use of different gap definitions is an important factor in this (e.g. Popma *et al.* 1988; Van der Meer *et al.* 1994). Other methodological constraints in measuring gaps are (a) the annual variation in gap formation rate, (b) the use of different minimum gap sizes, (c) different surface area's studied, (d) the low reliability of gap measurements (Van der Meer unpublished data), and (e) the

Table 5. Overview of canopy gap studies in Amazonian lowland rain forests.

Location	Plot Size (ha)	Study period (yr)	Gap definition	Min. Gap Size (m^2)	Gap formation rate (%)		No. stems > 10 cm dbh/ha	Basal Area (m^2)	Avg. Canopy Height	Source
					Annual rate	Gap status				
San Carlos (Venezuela)	1	1	?	?	0.96^{xx}	4.8	786	34.3^{xxx}	17.2	Uhl & Murphy (1981)
Rio Sumino & Rio Quilla (Equador)	RS: 0.7	1	Hole in the forest canopy to: A. 2 m B. 5 m C. 10 m	?	-	A. 1.4 B. 3.3 C. 6.7	1433^{x}	44.3^{x}	19.4	Kapos et.al. (1990)
	R.Q.: 0.7	1		?	-	A. 5.1 B. 17.5 C. 28.4	1132^{x}	47.5^{x}	19.1	
St. Elie (French Guiana)	21.3	3	hole in canopy	?	1.1	-				Riera & Alexandre (1988)
Paracou (French Guiana)	18.75	7	?	?	1.33		618	31	-	Durrieu de Madron (1994)
Nouragues (French Guiana)	12	3	A. Brokaw (1982a) B. Runkle (1981) C. Van der Meer & Bongers (1995)	4 (Brokaw)	A. 0.22 B. 2.87 C. 0.96	A. 1.13 B. 15.40	526	34.3	24	This study

^{x} = trees > 5 cm dbh

^{xx} = based on the assumption that gaps persist for 5 years

^{xxx} = trees > 1 cm dbh

difference between the annual area created by gaps (0.22 % sensu Brokaw in Nouragues; Table 2), and the area in canopy gaps at one moment (1.1 % sensu Brokaw; Table 1). Considering these large potential errors, and the expected variation between sites as a results of differences in soils, topography, climate, and species composition, it is remarkable that data on gap formation rates among (neo-) tropical rain forests show such a small variation.

Closure of canopy gaps

Ageing gaps are colonised by new vegetation (e.g. Oldeman 1978; Whitmore 1978). Accordingly, canopy openness in the gap centre is expected to slowly diminish, and finally to reach values which are found in the forest understorey. Gap size (sensu Brokaw 1982a) and canopy openness were strongly correlated. Whitmore *et al.* (1993) too found strong positive correlations between gap size and canopy openness based on hemispherical photographs, which are widely used to study light availability in tropical rain forests (e.g. Mitchell & Whitmore 1993; Rich *et al.* 1993). The hemispherical photographs made in gap centres during successive years suggest that new gaps close faster than older gaps, and consequently, that the closure rate of gaps slows down with the ageing of gaps. Surprisingly, with the ageing of gaps, an increasing number of gaps show an increased canopy openness.

Obviously, canopy openness in gap centres may increase with the ageing of gaps, which is caused by several factors. Firstly, canopy gaps are regularly re-disturbed by new treefalls and branchfalls. Crowns of gap-edge trees often become asymmetrical, and gap-edge trees are more likely to fall towards canopy gaps than in other directions (Young & Hubbell 1991; Young & Perkocha 1994). Also, increased turbulence around gaps may provoke treefalls and branchfalls in gap edges (Brokaw 1985a, Hubbell & Foster 1986). Furthermore, trees in gap edges which were damaged during the gap formation have higher chances on mortality (Putz & Chan 1986). Secondly, the canopy openness in a gap can be increased through the creation of a new gap in its direct neighbourhood, as canopy gaps may increase the light availability (and canopy openness) well beyond their projected canopy opening (e.g. Canham *et al.* 1990). Thirdly, small scale vegetation changes nearby the photo-location may have un-proportional large effect on the calculation of canopy openness in canopy gaps. Photographs were made each year at the same position in the gap centre. In some cases, vegetation may have developed between 1991-1992 directly above this location (for instance a palm leaf), which may have died and disappeared in 1993.

The process of repeated disturbances in and around gaps makes it hard to use hemispherical photographs to estimate actual rates of gap closure. The area in 1-2, 3-4, and 5-6 year old gaps indicate that after some 15 years, the area initially in gaps will not be in gaps any longer (i.e. a canopy height of at least 20 metres). As we have no actual information on rates of gap closure, we assumed for simplicity's sake that gaps closed in a linear way. Martinez-Ramos *et al.* (1988b) indicate that regeneration routes may differ between small and large gaps. Also, they found that large gaps may take 35 years to reach the mature canopy stature. Van der Meer (subm.) suggests that small gaps close within 5 to 6 years. This illustrates that the variation in gap closure routes and rates is large and not necessarily linear, and that more long term observations on vegetation development in canopy gaps are needed to reveal more precise routes and rates of canopy gap closure in tropical rain forests.

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CHAPTER 5

Vegetation development in canopy gaps

Vegetation development in canopy gaps in a tropical rain forest in French Guiana.

P.J. Van der Meer

Selbyana (in press)

Abstract

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

The percentage of space occupied by vegetation ("vegetation occupation") was determined at one metre intervals through the expanded gap area (divided in a central and outward gap zone), and the first metres 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 advance 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 metres high.

***Keywords:** canopy gaps - French Guiana - gap closure rate - gap floor regeneration - lateral branch growth - tropical rain forest*

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) recognised gap, building, mature, and degenerate phases in his studies on heather vegetation, which was later adapted by Oldeman (1974, 1978) and Whitmore (1975, 1978) to tropical rain forests. Oldeman (1978, 1990) identified patches in the forest as reorganising, aggrading, biostatic and degrading stages, calling them 'eco-units'. Whitmore (1975, 1978) distinguished three structural forest phases (gap, building and mature forest), and named this the forest growth cycle. It is clear that canopy gaps in tropical rain forests, 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 have now been performed in which the ecological importance of canopy gaps for population dynamics of tree species in tropical rain forests was demonstrated (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, has been studied in 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 studied less profoundly. Runkle & Yetter (1987) did so, and found the vertical increment of the gap floor regeneration in canopy gaps in the temperate Smoky Mountains 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. Bazzaz 1984; 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 gaps than in small gaps, as fast-growing pioneer species only germinate in large gaps (e.g. Brokaw, 1985a).

Within canopy gaps, vegetation structure and micro-climate may vary greatly (Brown 1993; Canham *et al.* 1990; Chazdon & Fetcher 1984). Accordingly, processes of gap regeneration may differ amongst different gap zones. Brandani *et al.* (1988) found differences in seedling germination in gaps between the root zone (location around the stembase of fallen trees), bole zone (area alongside the stem of the fallen tree), and crown zone (area covered by the fallen tree crown) (after Orians 1982). Barton (1984) found higher pioneer densities in the centre 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 outward 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 after some period of languishing. Also, in several studies it is mentioned that trees adjacent to canopy gaps are more likely to fall than trees further away from gaps (Brokaw 1985a; Lang & Knight 1983; Putz & Milton 1982; Young & Hubbell 1991).

The rate of gap formation in tropical forests has been studied extensively: in many tropical rain forests, 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 gaps 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 the change in vegetation structure of 50 ha of rain forest, 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 over time 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 checked whether they differed between small and large gaps. Finally, I investigated how fast canopy gaps were filled in 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). The forest canopy height ranges between 20-40 metres, with emergent trees up to 60 metres tall. Rainfall averages around 3000 mm annually, with a distinct dry season from September to November and a less conspicuous dryer period around February-March. The topography is hilly and ranges between 60-120 m a.s.l., with some small mountains between 300-450 m high. The area where this study was performed is situated on a 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 area, a permanent sample plot of 12 ha was established in 1991 to investigate natural treefalls and canopy dynamics.

In the study area, I selected three large and three small, young 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 (expanded gap size; area bordered by the stembases of the 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 1). 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, (in press), and the *outward gap zone* (gap area between the central gap border and the expanded gap border). Secondly, outside the expanded gap area, the first 1-5 metres 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" (also the adjacent forest zone, which is strictly speaking no real gap zone).

Vegetation occupation

Two perpendicular inventory lines (North-South and East-West) were located through the gap centre, extending over the whole gap area and the first 1-5 metres of the adjacent forest (Figure 1). Inventory lines were between 20 - 65 m long, and were permanently marked with plastic pickets at 5 metre intervals. During both inventories, a measuring tape was placed along the inventory line, and vegetation structure was determined above each metre (after Hubbell & Foster 1986): presence or absence of vegetation was determined in imaginary vertical cylinders with a radius of 25 cm above each metre point. This was done in three height

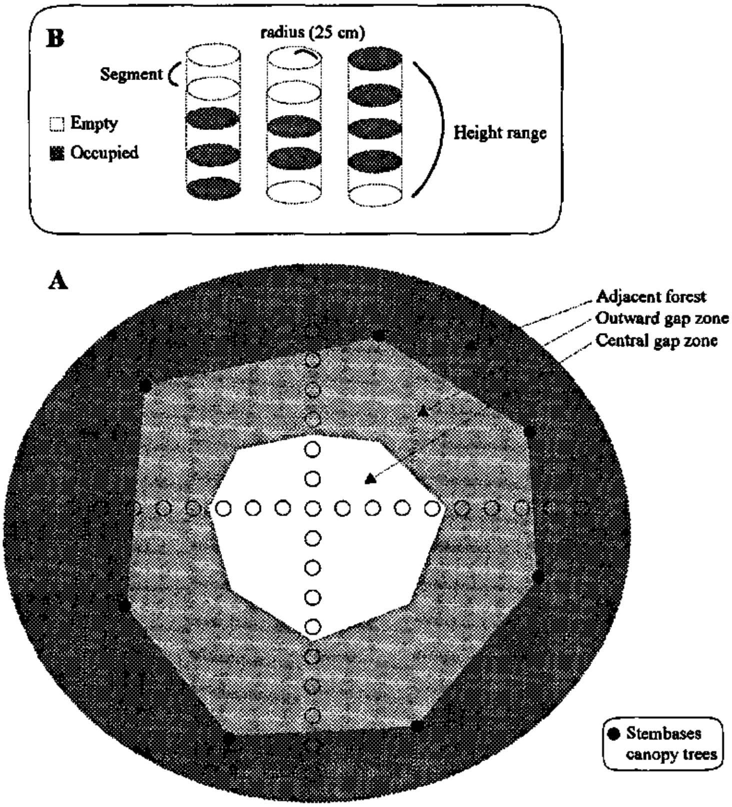

Figure 1.
A. Schematic aerial view of a (small) imaginary canopy gap. The central gap zone is bordered as soon as vegetation is > 20 tall. The outward gap zone is bordered by the stembases of the canopy trees (> 20 m tall) surrounding the canopy gap. Small circles indicate the line of inventory points (at one metre intervals) where vegetation occupation was determined.
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.

ranges, using different height intervals or levels of resolution: (1) whole range (0 - > 30 m), in five metre intervals; (2) range between 0 - 10 m, in one metre intervals; (3) range between 0-2 m, in 0.25 metre intervals.

Vegetation occupation (percentage of gap-space occupied by vegetation) was calculated as follows (Figure 1). When we consider 10 inventory points, there are 10 cylinders in which the presence or absence of vegetation is determined. At a vertical resolution of 5 metres, there are seven vertical height intervals or "segments" per cylinder, so that in total 70 (10 x 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. In 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 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 between large and small gaps. Within a gap, vegetation occupation in gap zones are not independent observations, so that no statistical test was done to investigate differences in vegetation occupation between gap zones.

Gain & loss in vegetation occupation

The net change in vegetation occupation is the result of vegetation growth at the one hand, and vegetation mortality at the other hand. The *gain in vegetation occupation* was defined as the gap segments which had been open in 1991, and had been 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 (Students 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 at which the net change in vegetation occupation between 1991-1993 occurred, 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 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 of the imaginary segments 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 metres) 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 width of the central gap zone was 17 m for large, and 6 m for small gaps. The expanded gap zone (central and outward gap zone; see Figure 1) of large gaps and small gaps had an average width of 32 m and 15.5 m respectively.

Vegetation occupation in 1991 and 1993

The percentage vegetation occupation in both 1991 and 1993 was generally higher in large gaps than in small gaps, but differences were not always significant (Table 2). Vegetation occupation in the central gap zone of both small and large gaps was generally less than in the outward gap zone and adjacent forest zone .

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. Gap size (expanded, after Runkle, 1981) is given behind gap number. The average width of the central and expanded gap zone are given.*

		Number of inventory points				Width of gap zone (m)	
		Gap Zones				Gap Zones	
		Central	Outward	Adjacent Forest	Total	Central	Outward
Large Gaps	Gap 1 (965m^2)	39	45	12	96	19.5	42
	Gap 2 (758m^2)	34	19	8	61	17	26.5
	Gap 3 (575m^2)	30	24	7	61	15	27
	All	103	88	27	218	17	32
Small Gaps	Gap 4 (255m^2)	12	20	14	46	6	16
	Gap 5 (232m^2)	13	20	13	46	6.5	16.5
	Gap 6 (187m^2)	11	17	13	41	5.5	14
	All	36	57	40	133	6	15.5

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 between the rows with an "x" (t-test; $p < 0.05$).*

		Vegetation Occupation 1991 (%)			Vegetation Occupation 1993 (%)		
		Gap Zones			Gap Zones		
Height range	Gap Size	Central	Outward	Adjacent Forest	Central	Outward	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)	28.2	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

Although the net vegetation change between 1991 and 1993 did not differ significantly between large and small gaps, there seemed to be a trend that (1) the net vegetation change in small gaps occurred mainly at higher levels (0 - > 30 m), and (2) in large gaps, vegetation changed mainly in the height range from 0 - 10 m (Figure 2). In small gaps, net vegetation change seemed to decrease from the gap centre towards the adjacent forest, especially in the in the 0 - > 30 m height range. In large gaps, trends between gap zones were less clear.

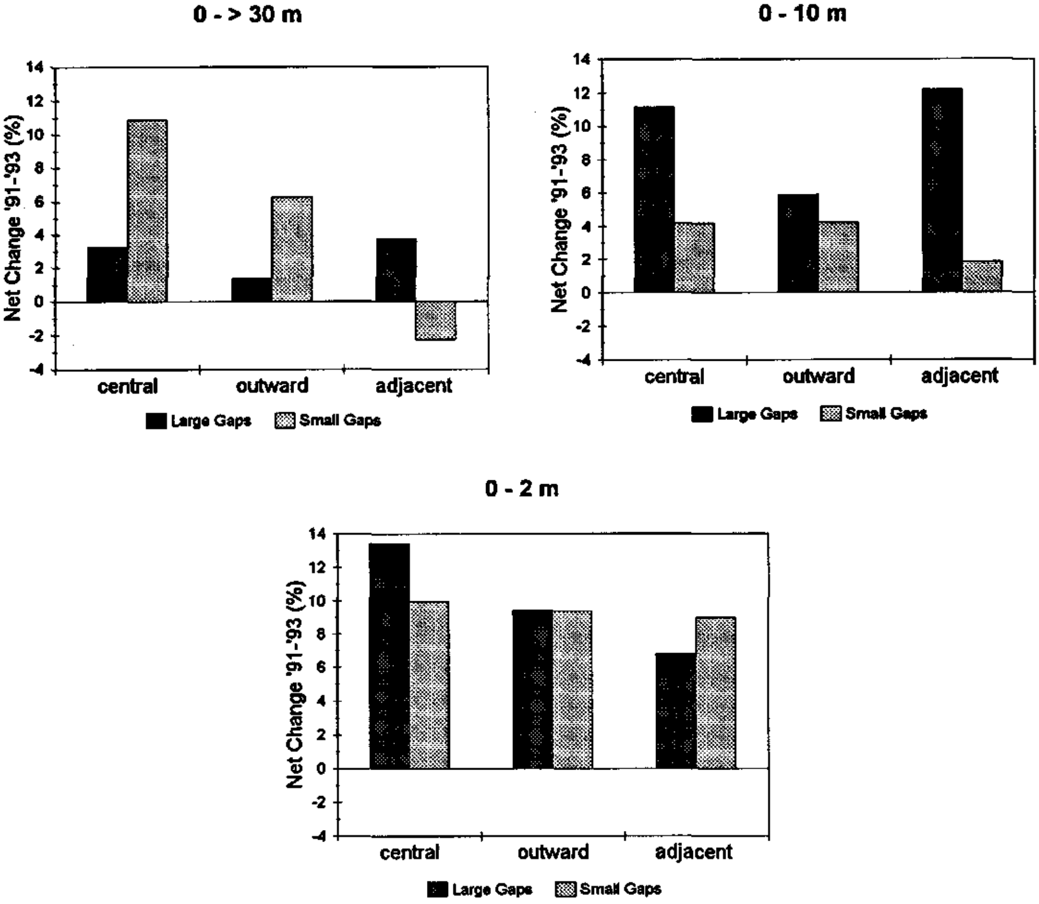

Figure 2. *Net change in vegetation occupation between 1991 and 1993 in three large and three small gaps. For each height interval, net change was measured in central, outward, and adjacent forest gap zone. Differences between large gaps and small gaps were not significant (Students t-test).*

Gain & loss in vegetation occupation

In the 0 - > 30 m range of central gap zones, the gain in vegetation occupation was significantly faster in small gaps than in large gaps (Table 3). In contrast with this, gain in vegetation occupation was 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 seemed to differ between gap zones: in general, gain decreased from the gap centre towards the adjacent forest. Only in large gaps, the gain seemed to increase from the gap centre towards the adjacent forest. Differences between vegetation loss in large gaps and 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 outward gap zone (t-test; $p < 0.05$). In the 0 - 10 m and 0 - 2 m height range I did not find 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.

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 between the rows with an "x" (t-test; $p < 0.05$).*

		Gain in Occupation (%)			**Loss in Occupation (%)**		
		Gap Zones			**Gap Zones**		
Height range	**Gap Size**	**Central**	**Outward**	**Adjacent Forest**	**Central**	**Outward**	**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

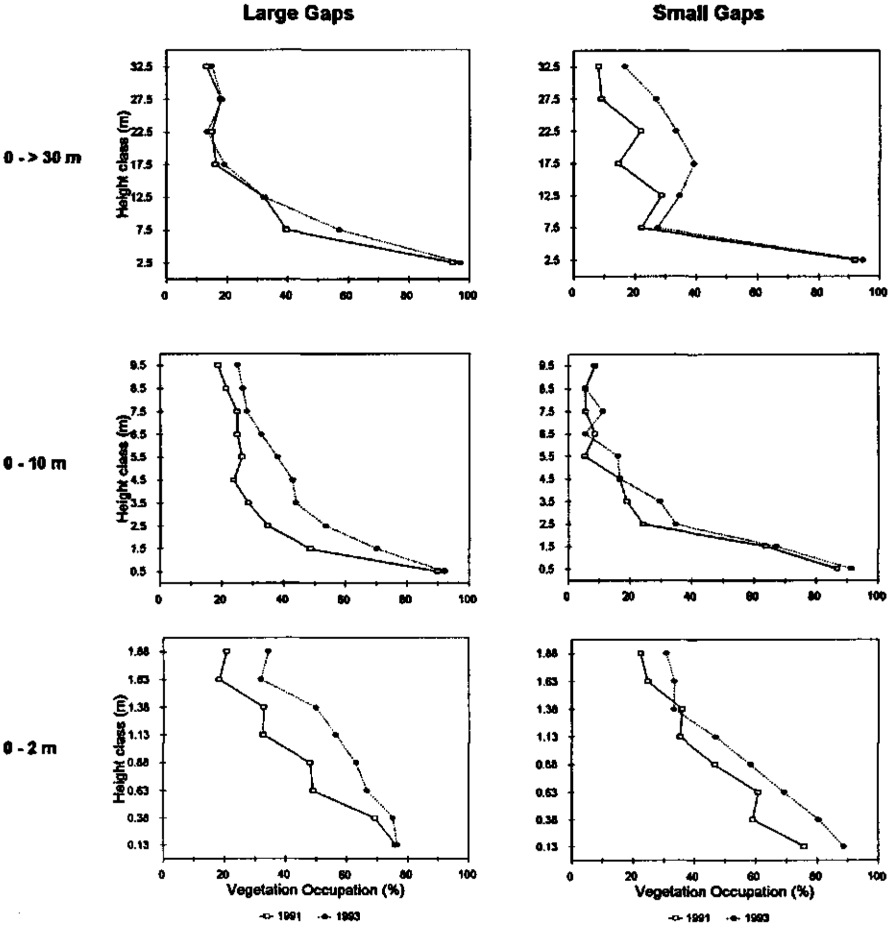

Figure 3. *Vegetation occupation per height interval in 1991 and 1993 in the central gap zones: averages of three large and three small gaps. Vegetation occupation is expressed as the percentage of the gap were vegetation was present, and was determined in three height ranges (see text for further explanation).*

Central gap zones: vegetation occupation & canopy layer

The central gap zone of small gaps, vegetation occupation between 0 - > 30 m seemed to change more and at larger vertical heights than in the central gap zone of large gaps (Figure 3). 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 seemed to increase faster in small gaps than in large gaps (Table 4). The increase in vertical height of the lower canopy layer (0 - 10 m) seemed to be slightly faster in large gaps than in small gaps. However, in neither case, differences were significant (t-test).

Table 4. *Height of the canopy layers in the central gap zones in 1991 and 1993. Of 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 (Students t-test).*

		Height of Canopy Layer (m)			
		(0 - > 30m)		**(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**

To visualise 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 centre of the gap, and increasing heights were placed (at both sides of the centre) at increasing distance of the centre. This was done for both 1991 and 1993 (Figure 4). These idealised canopy layer diagrams do not represent the exact situation as observed in the field for two reasons. First, each diagram is the sum of canopy organisation of three gaps. Secondly, canopy heights in 1991 and 1993 above each point in the diagram are most likely to shift because of different rates of growing and dying of plant parts. 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 these simplification, the diagrams clearly illustrate 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.

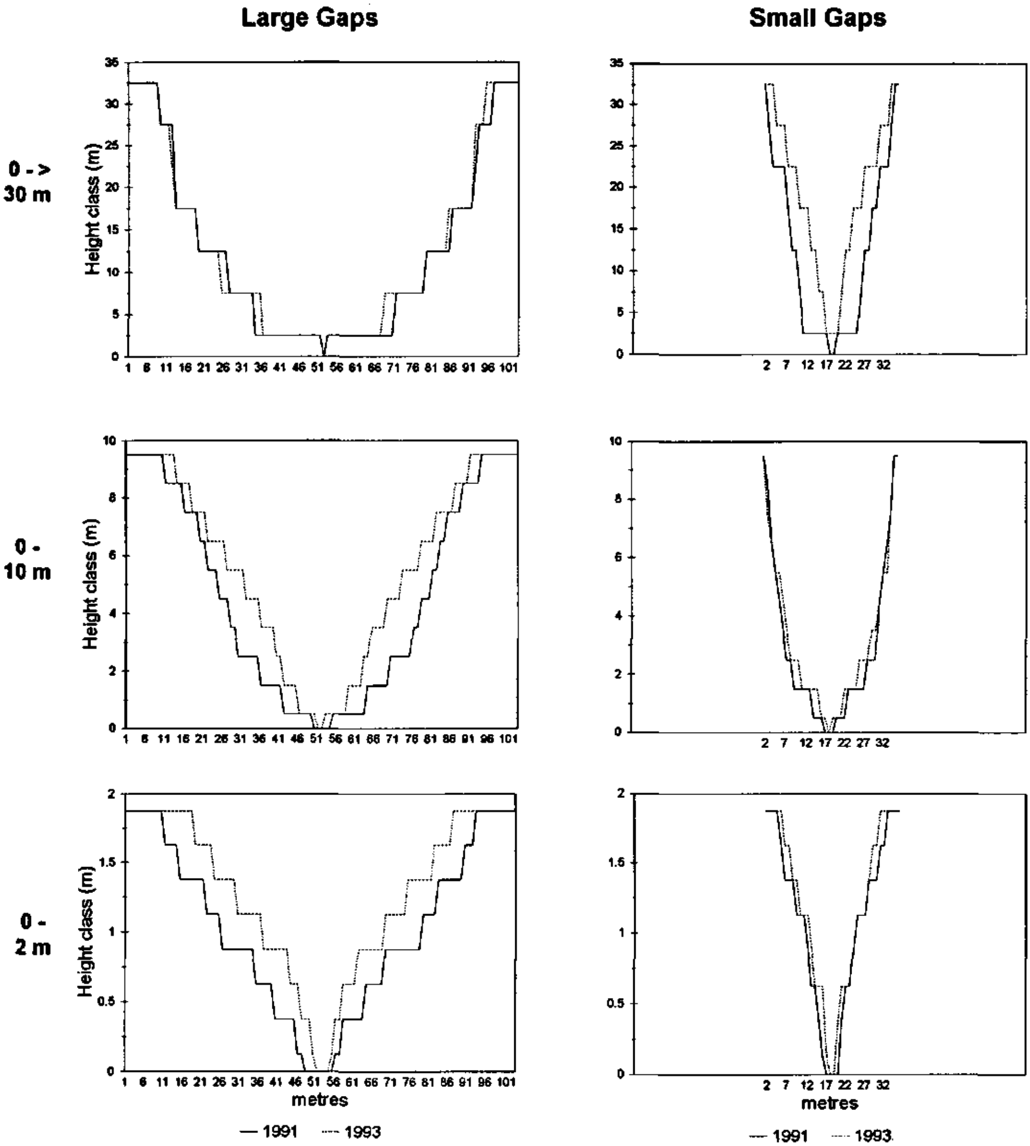

Figure 4. *Idealised canopy layer in the central gap zones in '91 and '93 between 0 - > 30 m. Canopy height (maximum height of observed vegetation) above each point in the central zones of large gaps (103 points or cylinders) and small gaps (36 points or cylinders) were "symmetrically" ordered. The lowest 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.*

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 the most appropriate to study the lateral ingrowth of branches. As the central gap zone is the zone where the largest changes will occur, we will 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; Runkle & Yetter 1987). Also, the rate of 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 2 & 3). Vegetation growth rather than vegetation mortality seems to be 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 2 & 3), which may indicate that the lateral ingrowth of branches is especially important in small gaps. Vegetation growth 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 in general place at larger vertical heights than vegetation gain in large gaps. Although I did not directly measure the origin of the vegetation gain, gain in the central zones of small gaps is most likely to originate 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 metre resolution.

Vegetation occupation and change in occupation are calculated in terms of the percentage of the gap volume. This may have consequences when comparing large and small gaps: one metre lateral ingrowth has a relative larger effect in small gaps than in large 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).

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 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 most trees adjacent to large gaps had asymmetrical crowns into their adjoining gap.

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, there will always be a certain local variation in vegetation occupation due to for instance 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 2). This indicates that canopy gaps also affects vegetation dynamics in the adjacent forest at several metres distance from the gap edge, 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. This is understandable as it is unlikely that the complete forest volume would contain foliage and branches. For instance, when more than around 99 % of the light is intercepted by higher vegetation layers, the light levels will generally be too low to allow for plant growth below these vegetation layers.

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 sub-alpine 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 25 and 40 metres, with sometimes emergents up to 50 or 60 metres. On average, 85 % of the forest adjacent to the six gaps had a canopy layer with a vertical height 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 been 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 gap zone of the large gaps, the average height of the canopy layer between 0 - > 30 m virtually did not increase between 1991 and 1993 (Figure 4). However, in small gaps, the canopy layer between 0 - > 30 m increased by some seven metres. When the increase in average canopy height would continue at the same rate (3.5 m annually) in future years, and considering that the small gaps were between one - two years old at the first inventory, the small gaps will have a closed canopy layer (between 25 - 30 m) some five to six years after gap creation. Lateral ingrowth of branches is expected to be the main contributor to the gap filling. The speed at which this happens seems to decrease with an increase in height (Figure 4). This may be related to a more severe midday depression of photosynthesis higher in the canopy (as a result of the 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) seedlings and saplings. In the large gaps, some fast-growing pioneers (like *Cecropia spp.*, *Miconia spp.*, etc.) had established between 1991 and 1993 (Van der Meer, personal observation). They eventually may have growth rates of several metres 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 metres height. Further extrapolation in height filling seems not warranted by the available data.

Height increment of the canopy layer between 0 - 10 m was slightly less fast in the central zone of small gaps than of in the central zone of large gaps (1.1 m versus 1.6 m annually). As mentioned earlier, growth rates of seedlings and saplings generally increase with an increase of gap size. Also, the proportion of fast growing pioneer species compared to slower growing shade tolerant species increases with an increase of gap size (e.g. Bazzaz 1984). In small gaps, the vegetation layer between 0 - 10 m will be over-topped relatively fast by a canopy layer at higher vertical heights, and growth rates of seedlings and saplings may drop faster than in larger gaps.

The average height in 1991 of the canopy layer of each gap varied considerably within both large gaps and small gaps (Table 4). This may be caused by differences in the amount of advance 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 centres, and decreased towards the gap edges. Also in the forest adjacent to gaps, vegetation occupation increased in the two years following gap formation.

Vegetation gain (open space in 1991 which was occupied by new vegetation in 1993) was mainly situated in the central gap zones. In the outward 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 related to 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 metres 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 currently largely missing.

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CHAPTER 6

Tree seedling performance in canopy gaps

Forest and gap partitioning of tree seedlings in a tropical rain forest: the role of light availability

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(submitted)

Abstract

Naturally occurring seedling populations of the tree species *Cecropia obtusa*, *Dicorynia guianensis*, and *Pourouma bicolor* were studied in canopy gaps and under closed forest in a tropical rain forest in French Guiana. Density of all three species was significantly higher in gaps than under closed forest. *Pourouma* seedlings grew faster in gaps than under closed forest, whereas height growth of *Dicorynia* seedlings did not differ between gaps and closed forest. *Cecropia* seedlings grew only in the largest gap, and not under closed forest.

In one large canopy gap, we found significant differences between the densities of seedlings established before ("pre-gap" seedlings), and seedlings established after gap formation ("post-gap" seedlings). Pre-gap *Dicorynia* seedlings grew slower than post-gap seedlings, and did not adapt to the gap environment. In contrast, post-gap *Pourouma* seedlings grew faster during the second year than during the first year after gap formation. *Cecropia* seedlings that germinated on dead wood had higher survival and growth rates than individuals germinated on the ground. *Cecropia* seedlings germinated in the lightest spots of the gap, whereas post-gap *Dicorynia* seedlings had a clear preference for the darker places. Pre-gap *Pourouma* seedlings were more abundant at the darker places of the gap. Height growth of post-gap *Dicorynia* and *Cecropia* seedlings, and of pre-gap *Pourouma* seedlings showed a modest positive correlation with light availability.

We conclude that the regeneration strategy of *Cecropia* supports the specialisation concept (cf. Denslow 1980; Rickleffs 1977), whereas *Pourouma* and *Dicorynia* are partly in favour of the generalisation concept (cf. Hubbell 1979). More long-term studies on the performance of naturally occurring seedlings in and outside canopy gaps are needed for other species, as this is a critical factor in the population dynamics of many species.

Keywords: *canopy gaps - Cecropia obtusa - Dicorynia guianensis - French Guiana - gap partitioning - light availability - Pourouma bicolor - population dynamics - seedling establishment - seedling growth - seedling mortality -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, around 1 % of the canopy of tropical rain forests is annually opened up 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 (e.g. Bazzaz & Wayne 1994; Bongers & Popma 1988; Brokaw 1985; Clark 1990; Denslow 1987). Some species, i.e. the pioneer or light demanding species, are highly specialised and can only germinate in canopy gaps. Other, 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). Of course, this is a rough 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 (e.g. 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 were used, including greenhouse experiments (e.g. Ashton & De Zoysa 1989; Augspurger 1984; Cornelissen *et al.* 1994; Kamaluddin & Grace 1993), and experiments with planted or placed seedlings in the field (e.g. 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 (Brown & Whitmore 1992; Bongers *et al.* 1988; Ter Steege *et al.* 1994; Kennedy & Swaine 1992; Newell *et al.* 1993). 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, seedling performance has been studied of naturally occurring tree seedling populations in naturally formed canopy gaps (Clark & Clark 1987; Nunez-Farfan & Dirzo 1988; Sork 1987; Turner 1990a; 1990b).

Most 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 (e.g. 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 on tree seedlings relate seedling performance to gaps of different sizes (e.g. Denslow 1980; Whitmore 1978). However, light availability may vary considerably within gaps (e.g. Canham 1988; Chazdon & Fetcher 1984; Raich 1989; Rich *et al.* 1993), which has hardly been considered in studying seedling performance in gaps. 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, in a lowland tropical rain forest, the performance of naturally occurring tree seedling populations was affected by naturally formed canopy gaps. This was done at two levels of scale. First, for three tree species, we investigated how patterns of germination, growth, mortality and density of seedlings differed between canopy gaps and closed forest. Secondly, for one large canopy gap, we compared the performance of pre-gap seedlings with that of post-gap seedlings, 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 done in part of a 12 ha sample plot, which was established in 1991 to investigate natural treefalls and canopy dynamics (Van der Meer & Bongers in press). The 12 ha plot is situated on a plateau, ranging 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 20-40 m, with emergents up to 60 m tall. Annual rainfall averages around 3000 mm, with a distinct dry season from September to November, and a dryer 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 chance in light availability: (1) *Dicorynia guianensis* Amsh. (CAESALPINIACEAE), a shade tolerant canopy tree, with an adult stature of 50 m; (2) *Pourouma bicolor* Mart. *spp. digitata* Tréc. (CECROPIACEAE), a shade tolerant canopy tree, with an adult stature between 30 - 40 m; (3) *Cecropia obtusa* Tréc. (CECROPIACEAE), a pioneer tree, with and adult stature between 30 and 40 m (e.g. Schulz 1960). The species will be called by their generic names only.

Closed forest versus canopy gaps

In a 0.5 ha transect (20 x 250 m) in the central part of the 12 ha plot, seedlings 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 two to three years old, and they covered 750 m^2 of the transect. For each seedling, we determined whether it 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 ^{year1} - ln ^{year0} ; cm cm^{-1} yr^{-1}) were determined per species. The effect of species and location (i.e. closed forest vs. canopy gaps) on seedling density, growth and survival was investigated (Chi^2-test for density and survival; Kruskal-Wallis and Mann-Whitney U-test for height growth).

Large canopy gap

On 10 May 1991, a large canopy gap was formed in the 12 ha pot by the natural fall (snap at 4 metre) of a large (dbh=84 cm) senescent tree (Van der Meer, personal observation). The tree felled and damaged several other trees, and created a large opening in the forest canopy. The central gap area measured 284 m^2 (i.e. the area delimited by the vertical projection of the adjacent canopies taller than 20 m; Van der Meer & Bongers in press), and the extended gap area 965 m^2. The gap centre was located at some 80 metres distance from the above mentioned 0.5 ha transect.

Seedling performance was determined on two (five metres wide) perpendicular transects through the extended gap area. These two perpendicular transect covered 400 m^2 . Between September 1991 and November 1993, three inventories were carried out. In September 1991, four months after gap creation, the gap area was searched for tree seedlings of the three species. Seedlings were mapped to the nearest 10 cm, tagged, and their height was measured. A distinction was made between seedlings already present before the gap was created (i.e. pre-gap seedlings), and those that established after the gap formation (i.e. post-gap seedlings).

Seedling appearance (e.g. presence of cotyledons; freshness of leaves), enabled distinction between old (pre-gap) and newly recruited (post-gap) tree seedlings of *Dicorynia*. Adult trees of *Dicorynia* were close enough to the gap to cover the whole extended gap area with their seed dispersal range (Van der Meer, unpublished data). *Dicorynia* sheds its anemochorous seeds usually within 30 metres from the seed source (Loubry 1993). Fruit shedding generally peaks around June, and germination is usually within one month (Forget 1988). *Pourouma* trees generally fruit around February and March (Julien-Laferriere and Riera, unpublished data), and we assumed that all 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 months after gap creation, we determined the survival and height of tagged seedlings, and recorded establishment of new seedlings (location, height). In November 1993, 30 months after gap creation, we determined the survival and height of tagged seedlings. The effects of species and of the period of establishment, i.e. pre-gap versus post-gap seedlings, on the annual relative height growth and annual survival rate were investigated (Chi^2-test for density and survival; Mann-Whitney U-test for height growth).

Large canopy gap: light availability

We placed a five by five metre grid system in and around the gap, covering the extended gap area and the first 5 metres 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 one metre above the 67 pickets during the three inventories (September 1991; November 1992; November 1993). For each photograph, the light availability in terms of the direct site factor (the percentage of direct radiation which penetrates the forest canopy, e.g. Mitchell & Whitmore 1993) was calculated using the program Hemiphot (Ter Steege 1993). In 1991, we made photographs using a Minolta X-700 body with a Sigma Fisheye lens 8 mm. In 1992 & 1993, a Canon Ti70 body was used with a Canon Fisheye lens 7.5 mm/5.6. For each of the 67 grid points, we calculated an average direct site factor (DSF) by averaging the DSF values of the 3 years. A light climate map of the extended gap area was created by applying a spatial interpolation (Kriging) between the gridpoints, using the average DSF values. For this purpose we used the software program SURFER Access System (Vers. 4.13). Using the point and edit device of the program, we could derive values for the average DSF for every seedling in the extended gap area.

We tested how the frequency distribution of seedlings with respect to the light availability was affected by species, or time of establishment (i.e. pre- or post-gap seedlings). For the transect, the total area in each DSF class of 2 % was calculated with the aid of 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 (Kolmogorov-Smirnov test). Accordingly, we could detect whether groups of seedlings showed preferences for particular light availability classes. For statistical analysis, the statistical package SPSS version 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.

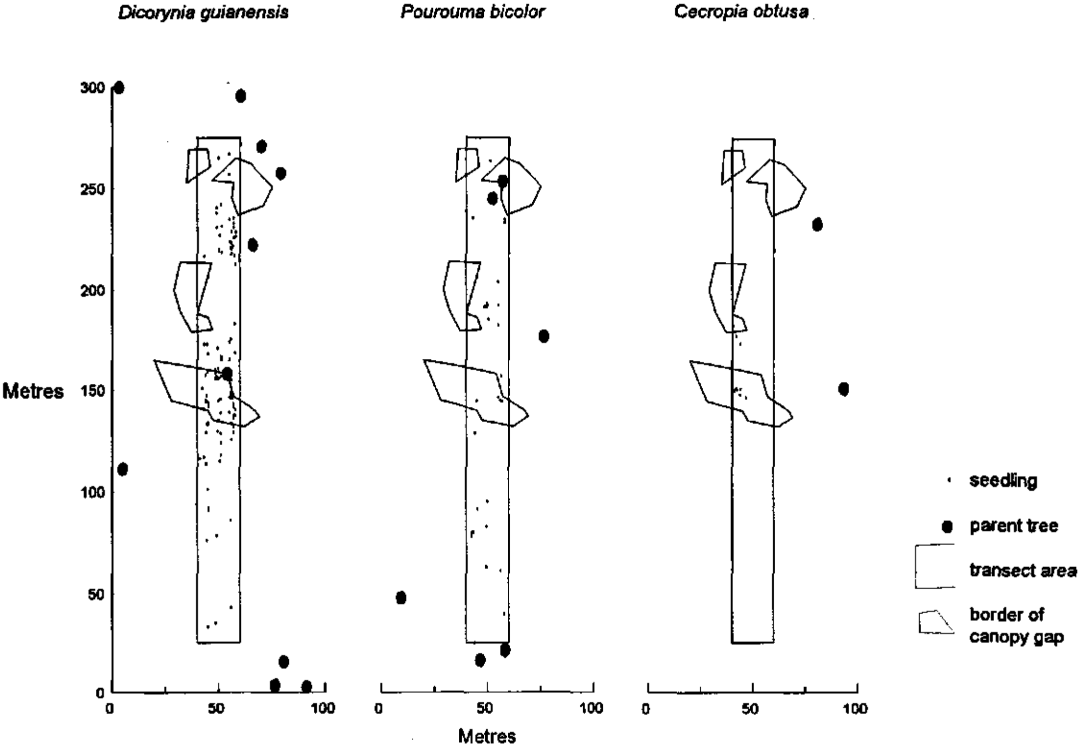

Figure 1. *Distribution patterns of seedlings (.) of three tree species on a 20 x 250 m rain forest plot in French Guiana. Location of large trees (O) with a potential to produce seeds are given for the forest within and around the transect (for Dicorynia, trees > 50 cm dbh, for Pourouma and Cecropia,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

Seedling densities differed significantly between the three species, and between canopy gaps and closed forest. Seedling density was highest for *Dicorynia*, intermediate for *Pourouma*, and lowest for *Cecropia* in the gaps as well as in the closed forest. For each of the three species, seedling densities were higher in gaps than in closed forest (Table 1). The clustering of *Dicorynia* seedlings in 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 investigated seedling density within the seed dispersal range (30 metres after Loubry 1993) around one large *Dicorynia* tree (dbh=71) which was situated at the edge of one of the canopy gaps. Seedling density was significantly higher ($Chi^2 = 30.3$; $p < 0.001$) 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* establishment was low, and did not differ significantly between canopy gaps (1.3 / 100m^2) and closed forest (0.5 / 100m^2; Chi^2 -test). Establishment of *Pourouma* seedlings was very low, and did not differ between closed forest conditions and canopy gaps (both 0.1 per 100 m^2). *Cecropia* seedling establishment was not observed between November 1992 and November 1993. Seedling establishment densities were too low (*Pourouma* and *Cecropia*) to be tested for significant differences between species.

Table 1. *Seedling performance in relation to forest structure for three tree species in a tropical rain forest in French Guyana. The total area of forest with closed canopies is 4250 m^2, and with canopy gaps 750 m^2.*

	Dicorynia		***Pourouma***		***Cecropia***	
Density in 1992 (n/100m^2)						
Closed Forest	3.4^{D}	*(n=145)*	1.5^{B}	*(n=64)*	0.02^{A}	*(n=2)*
Canopy Gap	10.9^{E}	*(n=82)*	2.7^{CD}	*(n=20)*	1.9^{BC}	*(n=14)*
Survival 1992-1993 (%)						
Closed Forest	71.7	*(n=104)*	57.8	*(n=37)*	0.0	*(n=0)*
Canopy Gap	82.9	*(n=68)*	95.0	*(n=19)*	57.1	*(n=8)*
Relative Height Growth (cm/cm/yr)						
Closed Forest	0.15^{A}	*(n=104)*	0.07^{A}	*(n=37)*	-	*(n=0)*
Canopy Gap	0.11^{A}	*(n=68)*	0.28^{B}	*(n=19)*	0.21^{AB}	*(n=8)*

* Chi^2-test was performed to investigate differences in densities and annual survival. Kruskal-Wallis test and Mann-Whitney U-test were used to investigate differences in relative height growth ($p<0.05$). Significant differences are indicated with different letters in superscript.

Percentages of annual survival did not differ between species, nor did they differ between canopy gaps and closed forest. Annual survival of *Pourouma* seedlings seemed to be higher in gaps than in the forest, but this was not significant ($Chi^2 = 3.16$; $p = 0.08$). The two closed forest individuals of *Cecropia* did not survive, while 57.1 % of the 14 individuals in canopy gaps did survive.

Species showed contrasting patterns for the effects of forest structure on relative height growth rates. In canopy gaps, *Pourouma* seedlings grew significantly faster than *Dicorynia* seedlings. Conversely, under closed forest, *Dicorynia* seedlings seemed to grow faster than *Pourouma* seedlings (although not significantly). The height growth of *Cecropia* gap seedlings did not differ significantly from the height growth of *Pourouma* and *Dicorynia* seedlings in gaps. *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.

Large canopy gap

We found significant differences in density between the pre- and post-gap seedlings per species, and among the three species (Table 2). Pre-gap seedling density of *Dicorynia* was higher than that of *Pourouma*, while pre-gap seedlings of *Cecropia* did not occur. *Cecropia* and *Dicorynia* had higher post-gap seedling densities than *Pourouma*. Post-gap *Dicorynia* seedling density was higher than the pre-gap seedling density. In contrast, post-gap *Pourouma* seedlings were less abundant than pre-gap seedlings. *Cecropia* seedlings were not present before the gap was created, but recruited at a relatively high density after gap formation.

Annual survival did not differ significantly between the pre- and post-gap seedlings per species (Table 2). Also, the annual survival of pre-gap seedlings (*Dicorynia* and *Pourouma* only) did not differ significantly between the first and second year after gap formation. Post-gap *Dicorynia* seedlings survived better than post-gap *Cecropia* seedlings. Pre-gap *Dicorynia* seedlings have similar levels of annual survival as pre-gap *Pourouma* seedlings. Annual survival of pre-gap *Dicorynia* and *Pourouma* seedlings between 1991 and 1992 did not differ from the survival between 1992 and 1993.

Post-gap *Dicorynia* seedlings grew significantly faster than pre-gap *Dicorynia* seedlings. Pre-gap *Pourouma* seedlings grew slower in the first year than in the second year after gap formation. Between species, pre-gap *Pourouma* seedlings grew faster than pre-gap *Dicorynia* seedlings. Also, post-gap *Cecropia* seedlings grew faster than post-gap *Pourouma* seedlings, and than pre- and post-gap *Dicorynia* seedlings (Table 2).

Table 2. *Seedling performance of three tree species in a large canopy gap (extended gap area = 965 m^2 after Runkle 1982) in tropical rain forest in French Guyana. Tree seedlings were assigned to two groups: seedlings established before gap creation (pre-gap seedlings), and seedlings that established after gap creation (post-gap seedlings).*

		Dicorynia		*Pourouma*		*Cecropia*	
Density in 1991 (n/100m^2)							
Pre-gap		2.0^{B}	*(n=8)*	4.8^{C}	*(n=19)*	0.0	*(n=0)*
Post-gap		12.5^{D}	*(n=51)*	1.3^{A}	*(n=5)*	15.3^{D}	*(n=61)*
Annual Survival (%)							
Pre-gap	'91-'92	87.5^{A}	*(n=7)*	94.7^{A}	*(n=18)*	-	*(n=0)*
	'92-'93	57.1	*(n=4)*	77.8^{A}	*(n=14)*	-	*(n=0)*
Post-Gap	'92-'93	60.8^{A}	*(n=31)*	60.0	*(n=3)*	21.3^{B}	*(n=13)*
Relative Height Growth (cm/cm/yr)							
Pre-gap	'91-'92	0.12^{A}	*(n=7)*	0.28^{B}	*(n=18)*	-	*(n=0)*
	'92-'93	-0.09	*(n=4)*	0.44^{C}	*(n=14)*	-	*(n=0)*
Post-gap	'92-'93	0.32^{B}	*(n=31)*	0.44	*(n=3)*	0.71^{D}	*(n=13)*

* Chi^2-test was performed to investigate differences in densities and annual survival, Kruskal-Wallis test, and Mann-Whitney U-test were used to investigate differences in relative height growth ($p<0.05$). Significant differences are indicated with different letters in superscript.

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 survival of seedlings germinated on dead wood (55 %) was significantly higher than survival of the seedlings on the ground (14 %) (Chi^2 -test; $p < 0.05$). Also, relative height growth of the seedlings on dead wood was significantly higher than of seedlings on the ground (Mann-Whitney U-test, $p < 0.05$).

Large canopy gap: variation in light availability

We constructed a light availability map using the 3 year average DSF values of the 67 gridpoints (Figure 2). 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 metres of the adjacent forest (avg. = 7.9 % (3.0 - 15.1 %); n=25; Mann-Whitney U-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; Mann-Whitney U-test; $p < 0.05$).

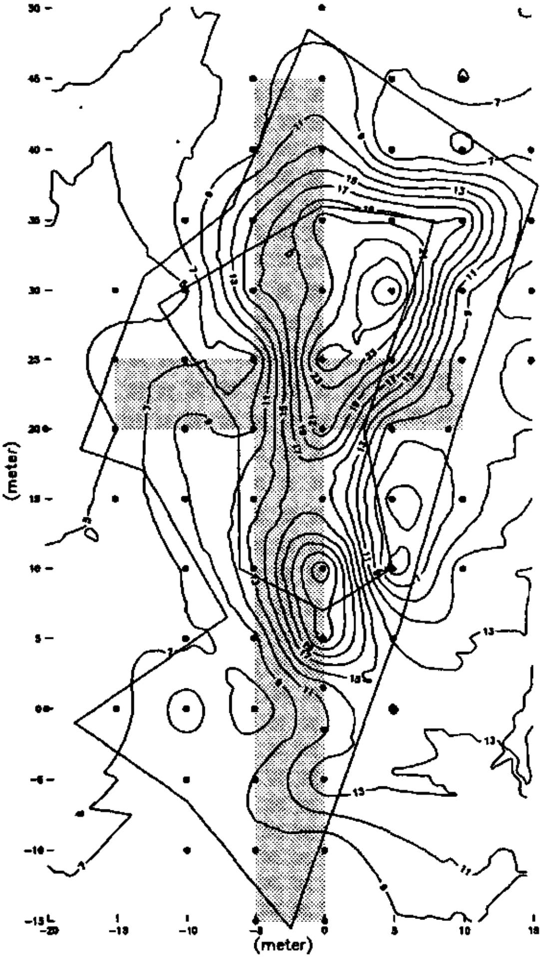

Figure 2. *Light distribution in a large canopy gap (extended gap size = 965 m², sensu Runkle 1981) in a tropical rain forest in French Guiana. Isolines represent 2 % intervals of the average direct site factor between 1991 and 1993. Black dots indicate the location of the gridpoints were hemispherical photographs were made. The extended and central gap area are indicated (outer and inner polygon respectively). Transects where seedling performance was monitored are indicated by the shaded areas.*

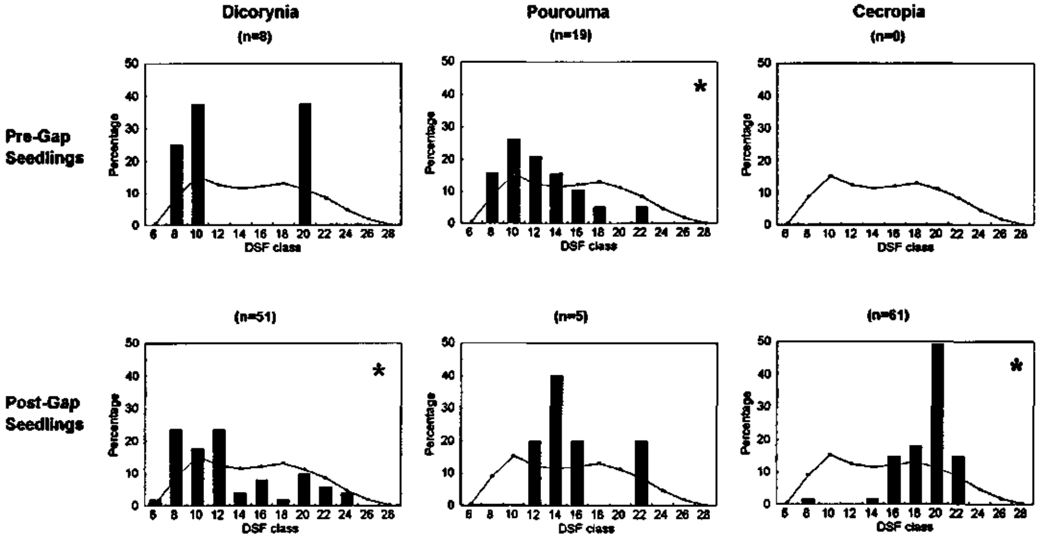

Figure 3. *Frequency distribution of the light availability (the average direct site factor between 1991 and 1993) above the transect area in a large canopy gap (line), and above tree seedlings on that transect of three species (bars). Tree seedlings were assigned into two groups: seedlings established before gap formation (pre-gap seedlings), and seedlings which established after gap formation (post-gap seedlings). An * indicates a significant difference between the two frequency distributions (seedlings vs. studied transect area) (Kolmogorov-Smirnov test, $p < 0.05$).*

Post-gap *Dicorynia* seedlings showed a clear preference for the darker places within the gap (Figure 3). In contrast, pre-gap *Dicorynia* seedlings did not show a clear pattern with respect to the light availability, probably as a result of the low number (8) of individuals. 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 3).

The average DSF above pre-gap *Pourouma* seedlings and post-gap *Dicorynia* seedlings did not differ significantly (Mann-Whitney U-test; $p < 0.05$). The DSF above post-gap *Cecropia* seedlings was significantly higher than the DSF above pre-gap *Pourouma* seedlings and post-gap *Dicorynia* seedlings (Mann-Whitney U-test; $p < 0.05$). 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 (Mann-Whitney U-test; $p < 0.05$).

The height increment between 1992 and 1993 of post-gap *Dicorynia* seedlings which had recruited after September 1991 showed a modest correlation (cf. Fowler & Cohen 1990) with the DSF (r = 0.51). In contrast with this, height increment of post-gap *Dicorynia's* which recruited before September 1991 (0-4 months after the gap formation) did not show a correlation with DSF. Height increment between 1992 and 1993 of pre-gap *Pourouma* seedlings was modestly correlated with the DSF (r = 0.66), but height increment between 1991 and 1992 was not correlated with DSF (r = -0.05). Height increment of (post-gap) *Cecropia* was modestly correlated with DSF (r = 0.56).

Discussion

Gap size and species specialisation

According to the gap specialisation and partitioning concept, different tree species specialise on canopy gaps of different sizes (e.g. Grubb 1977; Denslow 1980; Rickleffs 1977; Whitmore 1978). However, as indicated by Brown (1993), gap size specialisation by different tree species may not occur because (1) gaps of similar size may have substantially different micro-environments, and (2) because light availability may vary considerably within gaps. For instance, Barton (1984) found the densities of several non-pioneer species not to differ between large and small gaps, and this seems to contradict the gap partitioning theory. Popma *et al.* (1988) showed that the floristic variation in pioneer communities in gaps was only partly related to gap size. Also, Brown & Whitmore (1992) found that growth and survival of seedlings of three tree species was most importantly affected by the seedling height at the time of gap creation, and not by location in the gap or gap size. They suggest that the factor time should be incorporated in the gap partitioning theory, in terms of frequency and duration of the disturbances which plants experience.

In contrast with the gap specialisation concept, it has been proposed that most species are generalists, which is promoted by biotic uncertainty (Hubbell 1979; Hubbell & Foster 1986). In order to survive in a highly variable environment, caused for instance by the random process of gap creation, plants must be able to germinate and survive in a wide range of environments. Accordingly, gap filling is largely determined by the growth of seedlings or saplings which were accidentally present before the gap was created. Welden *et al.* (1991) found that of 108 studied species (saplings between 1-5 cm dbh), 79 were generalists, and only six could be classified as pioneer species.

Niche differentiation within gaps

Orians (1982) suggested that the internal heterogeneity of (large) gaps affect 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 of our study 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), this resulted from a gradual increase in overtopping tree crowns and other vegetation towards the adjacent forest. Light availability is highest in the crown zone of the 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 different habitats, which may be exploited by different species. In the following paragraphs we will discuss how the three studied species reacted to canopy gaps, and how they exploited the different habitats within gaps.

Cecropia obtusa

It is well known that the *Cecropia* only recruits in large, young (one-two year old) canopy gaps (e.g. Brokaw 1987; Schulz 1960; 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 two years. In the large canopy gap, *Cecropia* was not present before gap creation, but established at relatively high densities in locations with high levels of light availability (DSF ranged between 16 and 22%). High levels of light availability may be related to high variations in temperature and other micro-environmental factors (e.g. Bazzaz and Wayne 1994), which may trigger germination of *Cecropia* (Vazquez-Yanes & Orozco-Segovia 1987).

We did not observe *Cecropia* seedling establishment during the first inventory (4 months 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 (Van der Meer, personal observation). Fruiting of *Cecropia* species may be almost continuous, and seeds may be dispersed at least 86 m from mother trees, for instance by birds or bats (Charles-Dominique 1986; Estrada *et al.* 1984; Alvarez-Buylla & Martinez-Ramos 1990). We therefore assume that newly arrived seeds in the gap are more important contributors to *Cecropia* seedling establishment than 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 expect no seeds to survive more than two years after they reached the soil, although others found that *Cecropia* seeds buried for long periods still were able to germinate (Holthuijzen & Boerboom 1982).

Annual survival was not correlated with light availability. This is not surprising as nearly all *Cecropia* seedlings occurred within a small range of relatively high light levels. However, height growth was positively correlated with light availability. These significant height growth responses may have important effects on the future survival of *Cecropia* individuals, as the fast growers are expected to over-top and thus out-compete their smaller neighbours. We expect that after establishment, seedlings in the more open sites have a higher probability to survive than those in darker sites, although survival rates of *Cecropia* are generally low.

Germination on top of dead wood was highly advantageous. Riéra (1985) also observed the importance of treefall mounds for successful germination and survival of *Cecropia obtusa*, and suggested that this was related to micro-climatic 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 (Mann-Whitney U-test). 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. Also, 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.

Pourouma bicolor

Pourouma did virtually not recruit in canopy gaps. *Pourouma* seems to depend on seedling establishment under closed forest conditions, where they are able to survive without much growth for long periods of time (e.g. Bongers, unpublished data; King 1993). The higher density of *Pourouma* seedlings in gaps compared to closed forest is likely to be caused by the higher survival and growth rate of seedlings in canopy gaps. Also, seedlings are clustered in small groups, which is probably a results of its mode of seed dispersion. The relatively large (1-2 cm long) *Pourouma* seeds are abundantly consumed by the Kinkajou *(Potos flavus)*, Red

Howler Monkeys *(Alouatta seniculus),* and other arborous animals (Julien-Laferriere, unpublished data). Accordingly, seeds will be mainly dispersed under a closed forest canopy, as arboreous animals are unlikely to defecate in canopy gaps (e.g. Schupp *et al.* 1989). Concentrations of seeds and seedlings may show up at places where animals frequently defecate (e.g. under sleeping sites: large trees where animals frequently sleep).

In the large gap, pre-gap *Pourouma* seedlings which survived gap formation are more abundant than post-gap seedlings. The location where the gap was formed may have been a "hot spot" of *Pourouma* regeneration, as pre-gap seedling density (4.8 / 100m^2, Table 2) is significantly higher than closed forest seedling density in the forest plot (1.5 / 100m^2; Table 1) (Chi^2-test; $p < 0.01$).

Pre-gap *Pourouma* seedlings are more abundant in darker places than in lighter places in the gap, which is probably the effect of the destruction of seedlings in the more brighter parts 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). In this way, seedlings have the time to adjust to the new micro-environment, which may take more than six months (Popma & Bongers 1991).

For both pre- and post-gap seedlings, annual survival was not correlated with light availability. Relative height growth rates (between 1992 and 1993) were greater in the relatively open sites of the gap. The correlation between height growth and light availability during the two years indicate that *Pourouma* seedlings need at least one year to adjust to the new light environment. 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 and Bongers 1991). An explanation for this discrepancy may be that the tree seedlings of 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.

Dicorynia guianensis

In 1992, *Dicorynia* seedling density was significantly higher in canopy gaps than under a closed forest canopy. This may be 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). In 1993, when gaps were at least two years old, we did not find a significant difference between seedling establishment in old gaps and in closed forest sites, which indicates that *Dicorynia* recruits mainly in young gaps.

For successful regeneration in canopy gaps, *Dicorynia* depends more on the seedling establishment after gap formation than on pre-gap seedlings which survived the gap formation.

Pre-gap seedlings may have trouble in adjusting to the changed environment (low growth rate between 1991 and 1993), although the number of observations is low. Post-gap seedlings may be better adjusted to the gap environment in which they recruited, as they show a significantly higher growth rate than pre-gap *Dicorynia* seedlings.

Post-gap *Dicorynia* seedlings had a preference for the darker sites of canopy gaps, although seedlings established within a wide range of light levels (DSF ranged between 6 and 24 %). The preference for the darker places may be explained by the lowered (compared to lighter places) physiological drought stress. Annual survival of both pre- and post-gap seedlings was not correlated with the light availability.

Differences in relative height growth indicate that post-gap *Dicorynia* seedlings are better adjusted to the gap environment than pre-gap seedlings. Also, the relative height growth of seedling established in the first 4 months after gap formation was not related with light availability, whereas height growth of seedling established between 5 and 18 months after gap formation was positively correlated with light availability. We have no clear explication for this apparent difference, although it may indicate that the environmental stress (high temperatures, soil heating, water stress) diminishes with the ageing of gaps, and that older gaps are better habitats for *Dicorynia* recruitment than new gaps.

Relative height growth of pre-gap seedlings was not correlated with light availability. Tree seedlings and saplings of *Dicorynia* grow faster under high light levels related to gaps than under low light levels of closed forest (Sterck, unpublished data), so that we believe that a period of two years was to short to demonstrate a significant height growth response for the pre-gap seedlings. Apparently, it takes them very long to respond to the new environment. Here too, the low response may be explained by the suffering of tree seedlings from drought stress.

Conclusions

Seedling establishment, early growth, and survival of the three species were clearly affected by canopy gaps. *Cecropia* is not only highly specialised on large gaps, but also on specific sites in large gaps: seedling performance is increased by light, and by dead wood. *Pourouma* seems to germinate mainly under closed forest conditions, where it can wait for a long period until a canopy gap is formed. Once a gap is formed, surviving *Pourouma* seedlings adjust well to the new gap environment, 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 successfully grow in a wide range of micro-environments: it is able to germinate both in gaps and under closed forest conditions. However, seedling performance is enhanced in gaps.

In large gaps, *Dicorynia* specialises for darker places. Pre-gap seedlings have difficulties to adjust to the changed micro-environment.

Seedling performance (at least for the three studied species) varies greatly within gaps, which may for a large part be related to the variation in light availability within a gap. The regeneration strategy of *Cecropia* supports the specialisation concept (cf. Denslow 1980; Rickleffs 1977), whereas *Pourouma* and *Dicorynia* are partly in favour of the generalisation concept (cf. Hubbell 1979).

There are few published studies on seedling establishment and the first years of seedling performance in canopy gaps. This is remarkable, as it is generally acknowledged that canopy gaps play a major role in the regeneration of many species. Factual evidence for this is scarce, and mainly based on observations done under experimental conditions, or based on studies concentrating on saplings. We feel that more attention should be given to long-term studies on seedling performance in and around canopy gaps, as this is a critical factor in population dynamics of many species.

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CHAPTER 7

Synthesis

Chapter 7

Canopy gaps, seedling performance and forest management: a synthesis.

Formation of canopy gaps in tropical rain forests

Rates of gap formation and the measurement of canopy gaps.

The canopy of a tropical rain forest is dynamic. Treefalls and branchfalls regularly create canopy gaps where new vegetation starts to grow. Canopy gaps provide opportunities for new plants to establish themselves, grow and mature, and they affect the population structure of many species in tropical rain forests (Hartshorn 1978). Different rates of gap formation may help to explain differences in species richness and species composition between forests. Frequent formation of gaps will favour light-demanding species, whereas a less frequently disturbed forest will be advantageous for shade-tolerant species. At an intermediate level of disturbance, both light-demanding and shade-tolerant species will thrive, and species richness is expected to be highest (Connell 1978).

The first work on the cyclic nature of gap formation in tropical rain forest was published by Aubréville (1938). Richards (1952) elaborated these ideas into the "mosaic theory of regeneration". During the seventies, there emerged a renewed interest in canopy gaps in tropical forests, initiated by Hartshorn (1978), Oldeman (1974; 1978), and Whitmore (1975; 1978). From 1980 onwards, canopy gaps have been studied extensively at several rain forest sites in different continents: 26 studies published after 1980 provide data on the area of forest in gaps, or the actual rate of gap formation (Appendix 1). The annual gap formation rates vary between 0.3 % (Jans *et al.* 1993) and 4.4 % (Torquebiau 1986) of total forest area surveyed, but they can not readily be compared. Results presented in this thesis and by others reveal some important problems with regard to the calculation of gap formation rates.

Firstly, gap formation measurements are subject to large potential errors (e.g. Clark 1990). Usage of different gap definitions greatly affect gap size measures (Popma *et al.* 1988; Chapter 2). Borders of canopy gaps are usually irregular and vague, and the exact location of the gap edge is often difficult to determine (e.g. Brokaw 1985). The creation of new gaps in the edge of existing gaps makes the measurement of the new gap area even more complicated. Both determination of gap borders and measurement of gap sizes may be highly affected by differences between persons: the measured sizes of five gaps measured by five persons revealed a two- to ten-fold difference in 80 % of the gaps (Van der Meer, unpublished data).

Secondly, gap formation is often studied on relatively small areas (one to several hectares). When investigated areas are too small, it is highly probable that the results are affected by local patterns in gap formation which are not representative for the whole study area. For instance, in the forest studied in this thesis (henceforth called the Nouragues forest), gap areas differed significantly between four-hectare blocks (Chapter 4).

Thirdly, gap formation rates vary considerably between years (e.g. Chapter 4). In most studies, gap formation was measured during one year only; consequently, these gap formation rates have a limited value. Long-term data on gap formation in tropical rain forests are largely lacking. The only long-term (> 10 years) data are provided by Martinez-Ramos *et al.* (1988), who used bent palms to determine the age of gaps. They discovered that over a period of 70 years the annually opened area of a forest in Mexico varied between 0 and 10 %. Moreover, they hypothesised that different patterns in the variation in annual gap formation rates will result in differences in species diversity.

The need for clearly defined methods, longer observation periods, larger study areas, and better control of field measurements were often recognised (e.g. Bazzaz 1984; Clark 1990; Popma *et al.* 1988; Chapter 2). It is clear that canopy gap formation rates presented up to date are not precise, and that they are of limited value in helping to understand ecological processes in forests. So far however, no serious action has been taken to minimise the large errors in the measurement of gap formation rates. Obviously, these proposed measures are not easily realised.

It has become more and more clear that "tropical rain forests are no Swiss cheese" (Lieberman *et al.* 1989). The frequently mentioned gap versus non-gap dichotomy of tropical rain forests may be too simplistic a concept to explain the population dynamics and the species richness of tropical rain forests. Plants experience micro-environments which range on a wide continuum from dark (forest understorey) to light (canopy gaps). Also, light availability within gaps varies considerably, and there is no clear border between the gap and the adjacent forest (Chapter 6). The effects of canopy gaps on the seedling dynamics of species may better be understood by studying the relation between the light available to individuals and their growth. For instance, the detailed measurement of the light availability in a large gap in the Nouragues forest revealed the preferences of species (seedlings) for certain micro-habitats (Chapter 6).

Causes and consequences of falling trees and branches

In the Nouragues forest, 75% of the fallen trees and 83 % of the damaged trees were felled or damaged domino-wise by other falling trees or branches (Chapter 3). However, the causes of fallen trees that initiated treefall events (i.e. "initiators": fallen trees that were not felled by other fallen trees) could not easily be determined. Many factors determine whether or not a tree or branch falls (e.g. wind, disease, soil factors, crown shape, wood properties, existing canopy gaps, chance), and it is often hard to determine the final cause of treefalls or branchfalls.

Falling trees and branches generally create canopy openings. However, some 35% of the fallen trees and 42 % of the branchfalls in Nouragues did not create canopy gaps. Further, initiators of treefall events that resulted in a canopy gap had no larger dbh than initiators of events that did not result in a canopy gap. Neither the number of fallen trees or branches nor the size (dbh) of a fallen tree were reliable predictors of the size of a formed gap (Chapter 3).

I will now elaborate on two causes of treefalls that were found to be important in Nouragues. Firstly, local topography and differences in soils affect both the rate of gap formation as well as the size of the gaps formed (e.g. Brokaw 1985; Durrieu de Madron 1994; Jans *et al.* 1993; Kapos *et al.* 1990; Poorter *et al.* 1994). In Nouragues, we found strong evidence (high percentage of uprooted trees; small dbh of uprooted trees; large size of gaps created by uprooted trees; variation in cumulated gap area between one-hectare blocks; clustering of new gaps) that canopy gaps created by uprooted trees may cluster around specific sites associated with shallow soils, and that they may be larger at these sites than at other places in the forest (Chapter 4). Under extreme conditions, places with a permanently disturbed canopy will be formed. Examples of this are *tacotales* in Costa Rica (Sanford *et al.* 1986), or swamp areas in Indonesia (e.g. Torquebiau 1986). In Nouragues, mono-stands of the palm *Euterpe oleracea* (*Pinotière*), which are associated with swamp areas have a frequently disturbed, relatively open canopy.

Secondly, gaps are often repeatedly disturbed by new tree- or branch falls. With the ageing of gaps, canopy openness in gap centres (calculated by means of hemispherical photographs) seems to decrease less rapidly and, surprisingly, in many cases to increase (Chapter 4). One reason for this unexpected increase of canopy openness may be the renewed disturbance in older canopy gaps. Asymmetrical crowns of gap edge trees (e.g. Young & Hubbell 1991; Young & Perkocha 1994), increased turbulence around gaps (Brokaw 1985; Hubbel & Foster 1986a), and damaged trees around gaps (Putz & Chan 1986) are three important causes of the increased rate of treefalls around especially larger gaps. In addition, falling gap edge trees tend to fall more often into the gap area than in other directions (Young & Hubbel 1991). In Nouragues, treefalls occurred more often at 50 m distance from the centre of old, large gaps than at other places in the forest (Chapter 3). The observation period (one year) was obviously too short, and the method used too limited to reveal the process of repeated disturbance in gap edges. For instance, distance between fallen trees and gap edges was not studied.

Canopy gaps: hot spots of disturbance.

The forest growth cycle theory (e.g. Whitmore 1988) and sylvigenesis theory (Hallé *et al.* 1978; Oldeman 1990) suggest that when gaps are formed, the forest recovers gradually, and that it will eventually regain its high canopy stature. The formation of gaps is assumed to vary both spatially and temporally; accordingly, the forest can be regarded as a mosaic of different patches in different developmental stages. However, in many tropical rain forests, canopy disturbance is not a random process because certain areas are persistently more frequently disturbed than other areas. This may have important consequences for our understanding of how gap formation affects both the population structure of species in tropical rain forests and species richness.

It can be hypothesised that when large gaps are clustered and repeatedly disturbed, species richness in these places will decrease since the vigorous growth of light demanding species will out-compete other species. Also, the locations where light demanding pioneer species occur are more confined to fixed sites in the forest. This may have consequences for the seed dispersal and seed ecology of pioneer species. For instance, animals that mainly feed on pioneer trees and that are important agents of seed dispersal (e.g. bats: Charles-Dominique 1986) are likely to concentrate on frequently disturbed areas. When the spatial distribution of gap locations is random, animals are likely to pass more frequently through non-disturbed sites in search of new gap locations. Also, plants in large gaps may have higher risks of being damaged by falling debris than at other locations in the forest. Accordingly, traits for surviving repeated disturbances may be important for successful regeneration in gaps (Gartner 1989).

In contrast to these frequently disturbed sites, other parts of a forest may rarely be disturbed by large gaps and may remain largely intact during several centuries. In these areas, associated for instance with deep, well-drained soils, falling trees or branches will mainly create smaller gaps (Chapter 4). The large trees at these sites will not necessarily create large gaps when they die, as was reported by Jans *et al.* (1993) who found that emergent trees mainly died by gradually dropping their branches (Chapter 3). At these sites, the location and timing of gap formation is less predictable than in the regularly disturbed forest areas. Shade-tolerant species have greater chances of surviving gap formation and of taking advantage of gaps than at places with large, frequently disturbed gaps. Repeated disturbances in smaller gaps probably occurs less often than in larger gaps because in smaller gaps less space is available for crowns of gap edge trees to become asymmetrical; further, the increase in turbulence may be less important in smaller gaps than around large gaps. Also, fewer trees are damaged around small gaps than around larger gaps (Chapter 5).

Canopy gaps closure and tree seedling performance

Closure of canopy gaps

Gaps with an extended gap size smaller than 300 m^2 (after Runkle 1981; see Chapter 2) fill mainly by means of lateral growth of surrounding trees, and close within 5 to 6 years after formation (Chapter 5). In these gaps, almost no new seedlings will establish themselves: Uhl *et al.* (1988) found that four years after the formation of small gaps, advance regeneration (seedlings and saplings present before the gap was created) accounted for 97 % of all trees > 1 m tall. Canopy gaps larger than 300 m^2 will fill mainly through the growth of gap floor regeneration (both advance regeneration and new recruitment). In these larger gaps, it may take between 5 to 10 years before a canopy layer has been established which is at least 10 metres high.

The growth and survival of tree seedlings (< 1 m tall) in and around seven recently created canopy gaps (extended gap size ranged from 217 to 557 m^2) in the Nouragues forest was monitored during 36 months (Van der Meer, unpublished data). At least 90 % of the 1,470 seedlings encountered were considered to have been present before the gaps were created. The relative height growth of all seedlings differed significantly between gap zones; this growth decreased from the central to the outward gap zone, and from the outward gap zone to the adjacent forest zone (Mann-Whitney U-test; $p < 0.05$). After 36 months, the average height increment of seedlings was 20.8 cm in the central gap zone, 14.8 cm in the outward gap zone, and 7.4 cm in the adjacent forest zone. Survival rate after 36 months was 66.4 % for the central gap zone, 73.8 % for the outward gap zone, and 64.1 % for the adjacent forest zone; these differences were however not statistically significant. These findings indicate that, for many seedlings which germinate under a closed canopy, canopy gaps are advantageous for height growth, but that the growth rate of advance regeneration is generally too slow to mature in one gap episode. For instance, Clark & Clark (1992) suggest that six non-pioneer tree species require over 150 years to grow from a sapling into a mature canopy tree.

Winners and losers in canopy gaps: Can we make predictions ?

In canopy gaps, seedlings have the opportunity to establish themselves, and/or grow into larger individuals. The first years of gap regeneration constitute a crucial stage in the forest growth cycle, and define the group of plants (either pre- and post-gap seedlings; Chapter 6) from which eventually only some individuals will form the new, mature canopy. The time and place of germination and the early growth of individuals largely determine the eventual success of a plant. An important question arising when studying gap regeneration is whether we can predict which species at which location will become the new canopy trees in a gap ? Gap size or more precisely, patterns of resource availability within the gap, could be of help in answering this question.

Following the concepts of niche differentiation (Grubb 1977; Rickleff 1977) and gap partitioning (Denslow 1980), species specialise for different habitats. Competition for limited resources, and specialisation for this by species, eventually determine the species composition at a certain place. It was initially hypothesised that species or species groups specialised for different gaps sizes (Denslow 1980). Later, the environmental heterogeneity within gaps and the consequences for seedling performance were stressed (Barton 1984; Brandani *et al.* 1988; Nunez-Farfan & Dirzo 1988a; Orians 1982), indicating that gap partitioning and niche differentiation play a role at a smaller scale than was first generally thought.

Alternatively, it has been proposed that stochastic factors such as timing and location of canopy gap formation as well as the internal pattern of resource availability in gaps affect the regeneration success of most tree species. According to this view most species are generalist, and gap-filling is largely determined by the abundance and size of the seedlings and saplings already present before the gap was created (Hubbell 1979; Hubbell & Foster 1986b).

The observed regeneration of *Dicorynia* and *Pourouma* (Chapter 6) suggest that the floristic composition of seedlings in gaps may be largely determined by such incidental facts as distance from the gap to seed bearers, occurrence of seed years, and composition of seedling populations present before the gap was formed. Schulz (1960) observed that gap regeneration in the rain forest of Suriname was mainly determined by the composition of the seedling population which happened to be present at the time of gap creation and by seed that arrived and germinated after gap creation. Schulz (1960) also observed a significant difference in seedling composition between different gaps. Rollet (1983) studied the regeneration in and around 73 large gaps in 100 ha of forest near Santarem, Brazil, and suggested that differences in species composition of saplings > 1 m tall between gaps and adjacent forest were small. He concluded that the survival of advance regeneration or pre-gap seedlings is an important strategy for shade-tolerant species to reach the canopy. As mentioned earlier, Uhl *et al.* (1988) found that, four years after gap formation, advance regeneration accounted for 97 % of all trees > 1 m tall in small gaps and for 83 % of all trees in a large canopy gap. Brown & Whitmore (1992) found that the most important influence on the growth and survival of seedlings of three tree species was the seedling height at the time of gap creation, not the location in the gap or by gap size. Other studies revealed that the location of most species was independent of the canopy openness directly above individuals (saplings and trees) (e.g. Clark *et al.* 1993; Lieberman *et al.* 1995; Welden *et al.* 1991). Only pioneer species showed clear preferences for lighter places.

However, there is unmistakable evidence for the specialisation of species. It is clear that pioneer species are specialised for specific sites such as gaps (e.g. Swaine & Whitmore 1988) and for specific sites within gaps (e.g. Brandani et al. 1988; Nunez-Farfan & Dirzo 1988b). Many studies have revealed differences in the photosynthetic traits of different species (e.g. Chazdon 1986; Pearcy 1983; Poorter & Oberbauer 1993; Popma & Bongers 1991), indicating that species specialise for different light conditions. Also, plants have specialised to cope with such potential gap dangers as the increased chance of herbivory and predation (e.g. Nunez-Farfan & Dirzo 1988b; 1991; Schupp 1988; Schupp & Frost 1989), or the increased chance of physical damage through the higher rates of tree- and branchfalls in the gap area (e.g. Clark & Clark 1989; Nunez-Farfan & Dirzo 1988a). Species have developed strategies to deal with herbivory and predation: the development of tannins and lignins for instance (e.g. Coley 1988), or a symbioses with ants (e.g. Fonseca 1994). Futher, vegetative propagation, e.g. in *Piper*, makes species more suited to survive repeated disturbances (Gartner 1989; Greig 1993).

Results presented in chapter 6 indicated that seedlings of the pioneer species *Cecropia* specialised for a specific range of light availability and for germination on top of dead wood. Also, the shade-tolerant species *Dicorynia* clearly specialised for a specific range of light availability. A micro-habitat differentiation which is more detailed than the division in light availability classes we used (e.g. more precise light quantity and light quality measurements, sunflecks, abundance of dead wood and litter, local topography, soil factors etc.) is likely to reveal (1) more narrowly circumscribed ranges of micro-habitats for species and (2) micro-habitat specialisation for more species. The incorporation of the factor time (c.f. Brown & Whitmore 1992) may be also important, as recruitment opportunities for species may change in ageing gaps: for instance, both *Cecropia* and *Dicorynia* recruit more abundantly in new gaps than in older gaps.

The specialisation concept and the generalisation concept are not mutually exclusive (e.g. Hubbell & Foster 1990). There is a wide continuum between highly specialised species and generalist species, although for most species in tropical rain forest, exact requirements and levels of specialisation are unknown. However, as mentioned by Hubbell & Foster (1986b), stochastic factors (e.g. new tree- and branchfalls, predation or trampling by animals) greatly affect the probability of eventual success of individuals.

Canopy gap research and forest management

In several parts of the world efforts have been made to manage natural tropical rain forests (for reviews see Lamprecht 1986; Poore *et al.* 1989; Schmidt 1991). Ecological understanding of forests will provide the reference information that is needed to design ecologically sound management practices and to evaluate their consequences (e.g. Anderson 1990; Attiwill 1994; Bertault *et al.* 1995; Gomez-Pompa *et al.* 1991). Especially knowledge about the processes of natural disturbance in tropical rain forest is important (e.g. Attiwill 1994; Skorupa & Kasene 1984; Uhl *et al.* 1990). Some existing forest management systems which are based on natural processes will now be discussed, followed by some potential applications of the findings presented in this thesis.

Canopy gaps and forest management systems

In the Peruvian Amazon rain forest of Palcazu, concepts of gap dynamics were used in an attempt to manage the forest in a sustainable way (Hartshorn 1989; 1990). The key to the management system, that harvested forest is renewed through gap-phases regeneration, is based on the observations that (1) between 50-60 % of the tree species need gaps to mature (Hartshorn 1978; cited in Hartshorn 1990), and (2) that the median life span of trees > 10 cm dbh is only 34 years (Lieberman *et al.* 1985; cited in Hartshorn 1990). Timber exploitation is limited to long (200-500 m), narrow (30-40 m) strips, where all trees are harvested (clear cut). Each strip is bordered by intact forest which is the source of new seeds for regeneration. Distances between strips exceed 100 m, and the strips are logged every 30-40 years. Prelimary results indicate that 27 months after clear cut, there was abundant regeneration, with 155 tree species > 1 m tall, more than double the number of tree species initially harvested from the 0.15 ha strip.

In South Kalimantan, Indonesia, a so called "gap cutting" system was introduced in the 1980's (Sagala 1994). The exploitation area is divided into 35 permanent compartments (forest blocks of several thousand ha) of more or less equal size. In year one, 25 % of the forest area in the first block is harvested in clear-cut gaps of 1,000-2,000 m^2. In subsequent years, subsequent blocks are harvested. After 35 years, 25 % of the first block will again be harvested, and in the years 36-70, subsequent blocks will be harvested for the second time. In each block, 50 % of the forest will be left undisturbed as an ecological conservation area. In the clear-cut gaps, advance regeneration of valuable species are repeatedly liberated (3, 5, 8, and 15 year after clear cut) from competing neighbours of undesirable species.

Several remarks can be made with regard to the ecological sustainability of both systems. Firstly, both clear-cut strips and gaps are generally larger, and more intensively disturbed areas than naturally formed canopy gaps. A large proportion of the advance regeneration of shade tolerant species is likely to be killed during the clear-cut measures, and surviving advance regeneration will experience heavy competition from the abundant, fast growing pioneers. Observations over longer periods of time have to show whether or not the regeneration will mainly consist of (low value) pioneer species, and whether shade-tolerant species will have enough time to mature. Secondly, the repeated clearcut on the strips, and perhaps also in the gaps, is likely to cause an impoverishment of the nutrient status of the soil, which will eventually (after several rotations) result in lower growth rates and lower species diversity. Thirdly, it is questionable whether the buffer capacity of the surrounding forest is large enough to prevent a species change in the whole area. Fourthly, falling edge trees as a result of crown damage or asymmetric growth of crowns may eventually cause a substantial mortality of the regeneration.

A system which probably has a lower impact on the forest structure and species diversity than the two gap based approaches is the Celos Management System. This system, which is strictly speaking not a gap-cutting system, was developed during 20 years of research in Suriname (De Graaf 1990; De Graaf & Poels 1990). The ecological basis for the system was provided through restrictive measures, followed by a close observation of the effects of the measures and comparison with other, non-disturbed forests. It is based on (1) controlled, selective logging of valuable species, aiming at reduced damage and costs, followed by (2) repeated refinement, at 8-year intervals, in which non-commercial species are killed to favour the growth of the valuable species (De Graaf 1986; Hendrison 1990; Jonkers 1987). Unfortunately, observations were discontinued in the early eighties, but new measurements of the forest plots are planned in the near future. New experiments near Manuas (Brazil) are also underway.

Application of canopy gap research in forest management practices

Gap formation rates, when correctly measured over longer periods of time and on large areas, provide a guideline for the amount of disturbance allowed by forest manipulations (e.g. selective logging of valuable species) (Chapter 4). On a smaller scale, the total area covered by logging roads, loading ramps, and canopy gaps created by both naturally fallen and selectively felled trees is larger than the area affected by the natural disturbance regime (e.g. Bertault *et al.* 1995). It is also likely that most logging will take place in areas which normally experience the lowest rate of disturbance, as these areas are likely to contain the largest trees (Chapter 4). It is therefore important to minimise the gap sizes at these locations. However, when large areas around the logged forest are left unmanaged, the additional disturbance caused by logging may be buffered on a larger scale. Large-scale disturbances have always been a natural phenomenon of rain forests (e.g. Nelson *et al.* 1994; Uhl *et al.* 1990), and tropical rain forests have many responses (e.g. buried seeds, seed dispersal by many vectors, resprouting, advance regeneration) to ensure that the forest will persist.

Falling trees fell and damage many other trees (Chapter 3). In logging the selected trees, felling procedures should aim at minimising the number of domino-wise felled and damaged trees. Further, the damage to advance regeneration should be minimised to ensure the natural pathway of gap regeneration (Chapter 6). Ultimately, it may be necessary to replant saplings of the valuable species at the disturbed sites ("enrichment planting", e.g. Bartault *et al.* 1995) to compensate for the loss of seeds (and seedlings) through the harvesting of seed trees of these species. Knowledge about the species' various micro-habitat requirements and about the micro-habitat distribution in man-made gaps would enable the planting of these desired species at right locations in gaps where chances of success are largest (Chapter 6). Liberating of the pre-gap seedlings of valuable species may also be advantageous, especially when the canopy is not too disturbed (Boot 1994).

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Summary

Canopy dynamics of a tropical rain forest in French Guiana

The canopy of tropical rain forests is dynamic. On average, around 1 % of the forest canopy is annually opened by treefalls and branchfalls. In these so called canopy gaps ("an opening in the forest canopy extending through all height levels") new patches of forest start to grow which eventually will form a new mature forest. The formation of canopy gaps in tropical rain forests affects the population dynamics (e.g. recruitment, growth, survival) of many tree species. In this thesis, the canopy dynamics (i.e. the formation and closure of canopy gaps) of a tropical rain forest in French Guiana are studied. More specifically, the study presented in this thesis aims to reveal (1) how, and how often canopy gaps are formed by means of treefalls and branchfalls, (2) how, and how fast canopy gaps close; and (3) how canopy gaps affect the population dynamics of tree seedlings.

Chapter 1 starts with a general introduction on canopy dynamics in tropical rain forests. The formation of canopy gaps, and the effect of canopy gaps on the availability of plant resources such as light and nutrients are described. Different routes of vegetation development in gaps are described and the response of seedlings to canopy gaps are further discussed. The aims of the study are formulated and are followed by a description of the rain forest at Nouragues, French Guiana, where the fieldwork for this research was carried out.

Chapter 2 deals with the question how three currently used gap definitions result in different measures of gap size, and how the use of different gap definitions affects the calculation of turnover time (the time needed to cover a unit area of forest with gaps, using the mean area annually affected by gaps) of a forest. Gap sizes of 18 canopy gaps were measured using three different gap definitions. Gap sizes measures differed significantly between the three gap definitions. One of the gap definitions gave a reasonable estimate of the area of the forest canopy in a gap, while another gap definition was representative for the area at the forest floor which was affected by a canopy gap. The calculated turnover time was clearly affected by the choice of gap definition: the turnover time at the forest floor was 4 to 8 times shorter than the turnover time in the forest canopy. It is concluded that gap- and turnover time studies which have been carried out so far can only be compared when the same gap definitions are used.

In Chapter 3 patterns of treefall and branchfall in 12 ha of forest are described and discussed. Of 6314 trees (diameter > 10 cm) initially present in the 12 ha of forest 1.5% had fallen and 1.3% had lost at least one major branch after one year. Some 75% of the fallen and 83% of the damaged trees were "domino-wise" felled or damaged (i.e. by other falling trees or branches). Of the "initiating treefalls" (treefalls not caused by other falling trees or branches), 38% were uprooted and 62% were snapped-off above the ground. The presence of canopy gaps did not increase the chance of surrounding trees to initiate a treefall or branchfall. However, initiating tree- and branchfalls were found clustered at around 50m from large gaps, while few initiating tree- and branchfalls occurred at around 25m from old gaps. Some 35% of all fallen trees did not create canopy gaps and 42% of the damaged trees were not involved in the creation of a canopy gap. Initiating treefalls that resulted in a canopy gap had no larger diameter than initiating treefalls not resulting in a canopy gap. In contrast, trees that dropped branches that created a canopy gap had a larger diameter than trees that dropped branches which did not form a canopy gap. Gap size increased with the number and basal area of the trees involved. Both the forest turnover rate based on the number of fallen trees and the turnover rate based on the area of canopy gaps underestimate the actual disturbance regime of the forest, as branchfalls cause considerable disturbance too.

In Chapter 4 the formation and closure of canopy gaps in the Nouragues forest is investigated. In April 1991, 74 canopy gaps > 4 m^2 were located in 12 ha of forest of which 60 gaps were formed before January 1990. Between January 1990 and December 1993, 5 to 15 gaps were annually formed, opening 0.64 - 1.33 % of the forest canopy each year. Of all gaps, 41 % were created by falling, snapped trees, 34 % by falling, uprooted trees, 22 % by falling branches, and 3 % by falling dead stems. A refined nearest neighbour analysis showed that gaps formed after January 1990 were clustered. The clustering of new gaps most probably is associated with the abundant shallow soils at Nouragues. Uprooting of trees is related to shallow soils, and relatively many other trees were felled when a tree uprooted, independently of the diameter of the uprooting tree. Canopy openness (percentage of un-obstructed sky) in the gap centre was monitored over three years and is expected to decrease with the ageing of the gap. In 54 % of the gaps however canopy openness increased with gap ageing. It is argued that edges of especially large gaps may frequently be re-disturbed by falling trees or branches. Results suggest that on average gaps have become indistinguishable from closed forest after around 15 years.

Chapter 5 focuses on vegetation development in canopy gaps, and how this varies between large and small gaps. The percentage of space occupied by vegetation ("vegetation occupation") was determined at intervals of one metre in and around three large and three small gaps. Vegetation occupation above each inventory point was determined in three height ranges in different vertical intervals: 0 - > 30 m (5 m intervals); 0 - 10 m (1 m intervals), and 0 - 2 m (0.25 m intervals). Inventories were made 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, while large gaps fill mainly by seedling and sapling growth in the gap. It is estimated that on average small gaps "disappear" within 5 to 6 years after formation, while it may take between 5 to 10 years before a canopy layer of at least 10 m high has been established in large gaps. The data did not warrant a further extrapolation to estimate the time needed for the vegetation in large gaps to form a canopy layer of at least 20 m high, which is regarded as the minimum height of closed forest.

In Chapter 6 the effect of canopy gaps and light availability on seedling performance is studied. The recruitment, height growth and mortality of naturally occurring seedling populations of the tree species *Cecropia obtusa*, *Dicorynia guianensis* and *Pourouma bicolor* were studied in canopy gaps and under closed forest. Density of all three species was significantly higher in gaps than under closed forest. *Pourouma* seedlings grew faster in gaps than under closed forest, whereas height growth of *Dicorynia* seedlings did not differ between gaps and closed forest. *Cecropia* seedlings grew only in the largest gap, and not under closed forest. In one large canopy gap we found significant differences between the densities of seedlings established before ("pre-gap" seedlings), and seedlings established after gap formation ("post-gap" seedlings). Pre-gap *Dicorynia* seedlings grew slower than post-gap seedlings and did not adapt to the gap environment. In contrast, post-gap *Pourouma* seedlings grew faster during the second year than during the first year after gap formation. *Cecropia* seedlings that germinated on dead wood had higher survival and growth rates than those germinated on the ground. *Cecropia* seedlings germinated in the lightest spots of the gap, whereas post-gap *Dicorynia* seedlings had a clear preference for the darker places. Pre-gap *Pourouma* seedlings were more abundant at the darker places of the gap. Height growth of post-gap *Dicorynia* and *Cecropia* seedlings and of pre-gap *Pourouma* seedlings showed a modest positive correlation with light availability.

Finally, in Chapter 7, the major findings of this study are discussed. Firstly, the formation of canopy gaps in tropical rain forests is considered. The difficulties with gap size measurements indicate that reliable measures of gap formation rates can only be obtained by using a clearly defined gap definition, a long observation period, a large study area and well-controlled field measurements. The causes and consequences of treefalls and branchfalls are examined and it is concluded that canopy gap location is not random. Soil factors may make some areas in the forest hot spots of disturbances, whereas other areas are less frequently disturbed. Secondly, the closure of canopy gaps and tree seedling performance in gaps are discussed. The growth of pre-gap seedlings is enhanced in gaps, but most seedlings need more than one gap-episode to become mature canopy trees. It is argued that chance plays an important role in gap regeneration. Recruitment in gaps is largely determined by the fortuitous occurrence of seedlings and sapling that were present before the gap was formed. Specialisation of species is discussed and its concluded that detailed information on micro-habitat availability (in gaps) and on micro-habitat needs of species may indicate which

individuals at which location have the highest chance of survival. Thirdly, the potential application of these findings for application in forest practices are examined. Some management systems which try to follow natural disturbance regimes are briefly discussed and potential applications of the findings of this thesis are given.

Samenvatting

De kronendak-dynamiek van een tropisch regenbos in Frans Guyana

Het kronendak van tropisch regenbos is dynamisch. Gemiddeld vallen jaarlijks in 1 % van het kronendak gaten door vallende bomen en takken. Op de hierdoor ontstane open plekken begint een stuk jong bos te groeien dat op den duur weer een volwassen, gesloten bos zal vormen. Het ontstaan van open plekken in een tropisch regenbos beïnvloedt de vestiging, groei en mortaliteit (populatie-dynamiek) van veel boomsoorten. In dit proefschrift wordt het ontstaan en dichtgroeien van open plekken (de kronendak-dynamiek) in een tropisch regenbos in Frans Guiana bestudeerd. De hierin gepresenteerde studie heeft als doel antwoord te geven op de volgende vragen: (1) hoe, en hoe vaak ontstaan open plekken door het vallen van bomen of takken; (2) hoe, en hoe snel sluiten open plekken; en (3) hoe beïnvloeden open plekken de populatie-dynamiek van boomzaailingen.

Hoofdstuk 1 begint met een algemene introductie over de dynamiek van het kronendak van tropische regenbossen. Het ontstaan van open plekken en de gevolgen hiervan voor de beschikbaarheid van hulpbronnen voor planten, zoals licht en nutriënten, worden besproken. Verschillende manieren van vegetatiegroei in open plekken worden besproken en de effecten van open plekken op zaailingen wordt verder uitgewerkt. De doelstellingen van dit proefschrift worden geformuleerd, gevolgd door een beschrijving van het regenbos in Nouragues, Frans Guyana, waar het veldwerk voor dit onderzoek werd verricht.

In Hoofdstuk 2 worden drie regelmatig gebruikte methoden om open plekken te definiëren beschreven en met elkaar vergeleken. Verder wordt het effect bestudeerd van verschillende open plek definities op het berekenen van de benodigde tijd om een stuk bos in zijn geheel met open plekken te bedekken, gebruik makend van het oppervlak van de gaten die gemiddeld jaarlijks in het kronendak ontstaan ("turnover-rate"). De grootte van 18 open plekken werd gemeten gebruikmakend van de drie verschillende definities. De oppervlakten die volgens de verschillende definities werden gemeten verschilden significant van elkaar. Eén van definities gaf een redelijke schatting van het oppervlak van de open plek dat in het kronendak was gemaakt, terwijl een andere definitie een goede schatting was voor het oppervlak van de bosbodem dat door de open plek beïnvloed werd. De berekende turnover-rate van het bos werd duidelijk beïnvloed door het hanteren van verschillende definities om open plekken af te bakenen: de turnover-rate op de bosbodem was 4 tot 8 keer korter dan de turnover-rate in het kronendak. Studies naar open plekken en turnover-rates van tropische bossen kunnen alleen met elkaar vergeleken worden als dezelfde definities gebruikt zijn.

In Hoofdstuk 3 wordt het vallen van bomen en takken nader bestudeerd. Van de 6.314 aanwezige bomen (> 10 cm diameter) in 12 hectare regenbos waren er na 1 jaar 96 (1.5 %)

bomen omgevallen, en hadden 84 (1.3%) bomen een tak van minstens 10 cm diameter laten vallen. Verder werd 75 % van de gevallen bomen en 83 % van de beschadigde bomen op de "domino-manier" geveld of beschadigd (d.w.z. door andere vallende bomen of takken). Van de gevallen bomen die niet door anderen werden geveld ("initiërende boomval") was 38 % ontworteld en was 62 % boven de grond afgebroken. Initiërende boom- en takvallen leken vaker voor te komen op 50 meter afstand van het centrum van open plekken, terwijl er relatief weinig initiërende boom- en takvallen werden gevonden op 25 meter van open plekken. Ongeveer 35 % van de gevallen bomen en 42 % van de bomen die een tak hadden laten vallen resulteerde niet in een open plek. Initiërende boomvallen die een open plek creëerden verschilden niet in diameter met vallende bomen die géén open plek veroorzaakten. Echter, vallende takken die een open plek veroorzaakten vielen uit bomen met een grotere diameter dan vallende takken die geen open plek veroorzaakten. De grootte van de open plek nam toe met een toename van het aantal betrokken bomen en het grondvlak van de betrokken bomen. De turnover-rate berekend op basis van zowel (1) het aantal gevallen bomen als (2) het aantal open plekken van een bos geeft een onderschatting van de werkelijke verstoring van een bos omdat (1) gevallen takken ook aanzienlijke verstoringen opleveren en (2) niet alle gevallen bomen open plekken creëren.

In Hoofdstuk 4 wordt het ontstaan en dichtgroeien van open plekken onderzocht. In april 1991 werden alle open plekken > 4 m^2 in 12 hectare bos gelokaliseerd en opgemeten: 60 van de in totaal 74 open plekken waren ontstaan vóór januari 1990. Tussen januari 1990 en december 1993 ontstonden jaarlijks tussen de 5 en 15 nieuwe open plekken, die 0.6- 1.3 % van het kronendak openden. Van alle open plekken werd 41 % gevormd door gevallen bomen die boven de grond geknakt waren, 34 % door gevallen ontwortelde bomen, 22 % door gevallen takken en 3 % door gevallen dode stammen. Een "nearest neighbour" analyse gaf aan dat open plekken, ontstaan na januari 1990, geclusterd voorkwamen. Deze clustering hangt vermoedelijk samen met de veel voorkomende ondiepe bodems in Nouragues. Uit andere studies blijkt dat het ontwortelen van bomen gerelateerd is aan bodemfactoren. In Nouragues velden ontwortelde bomen relatief veel andere bomen, ongeacht hun diameter. De openheid van het kronendak (percentage onbedekte hemel) in het centrum van open plekken werd gedurende 3 jaar gemeten, en was verondersteld af te nemen met het ouder worden en dichtgroeien van de open plekken. Echter, de kronendak openheid nam in 54 % van de open plekken toe met de leeftijd van de open plek. Randen van met name grote open plekken werden waarschijnlijk regelmatig verstoord door nieuwe vallende takken en bomen. De resultaten geven verder aan dat het gemiddeld ongeveer 15 jaar duurt voordat open plekken niet meer te onderscheiden zijn van het omringend gesloten bos.

Hoofdstuk 5 richt zich op vegetatieontwikkeling in open plekken, en met name op de verschillen tussen grote en kleine open plekken. Het percentage van de ruimte waarin vegetatie voorkomt (de vegetatiedichtheid) werd boven iedere meter bepaald op lijn-transecten door 3 grote en 3 kleine open plekken. De vegetatiedichtheid werd gemeten in 3 verschillende hoogteklassen, in verschillende intervallen: 0 > 30 m (in 5 m intervallen); 0 - 10 m (in 1 m intervallen); en 0 - 2 m (in 0.25 m intervallen). Metingen werden verricht in oktober 1991 en november 1993. In het midden van kleine open plekken waren de netto verschillen in vegetatie dichtheid het grootst in de 0 - > 30 m klasse, terwijl de netto verschillen in vegetatie dichtheid in het midden van grote open plekken het grootst waren in de lagere hoogteklassen (0-2 en 0-10 m). Kleine open plekken lijken dus voornamelijk te sluiten door middel van de ingroei van takken van omringende bomen, terwijl grotere open plekken voornamelijk sluiten door middel van de groei van zaailingen, struiken en jonge bomen. Naar schatting groeien kleinere open plekken dicht na ongeveer 5-6 jaar, terwijl grotere open plekken tussen de 5 - 10 jaar nodig hebben voordat er zich een kronendak van tenminste 10 m hoogte heeft ontwikkeld. De gegevens waren niet geschikt voor een verdere extrapolatie om de snelheid van het dichtgroeien van grote open plekken tot een hoogte van 20 meter (minimale hoogte van gesloten bos) te kunnen voorspellen.

In Hoofdstuk 6 wordt het effect bestudeerd van open plekken en de beschikbaarheid van licht op zaailingen. De vestiging, hoogte groei en mortaliteit van populaties zaailingen van de boomsoorten *Cecropia obtusa*, *Dicorynia guianesis*, en *Pourouma bicolor* werden bestudeerd in zowel open plekken als onder gesloten bos. De dichtheid van alle drie de soorten was hoger in open plekken dan onder gesloten bos. *Pourouma* zaailingen groeiden sneller in open plekken, terwijl de hoogtegroei van *Dicorynia* niet verschilde tussen open plekken en gesloten bos. *Cecropia* zaailingen groeiden alleen in de grootste open plek, en niet onder gesloten bos. In een grote open plek werden significante verschillen gevonden in dichtheid van zaailingen die aanwezig waren voordat de open plek ontstond (pré-open-plek zaailingen), en zaailingen die zich vestigden nadat de open plek ontstaan was (post-open-plek zaailingen). Pré-open-plek *Dicorynia* zaalingen groeiden langzamer dan post-open-plek zaailingen, en vertoonden geen duidelijke aanpassing aan de nieuwe omstandigheden in de open plek. Post-open-plek *Pourouma* zaailingen groeiden sneller in het tweede dan in het eerste jaar na het ontstaan van de open plek. *Cecropia* zaailingen die ontkiemden op dood hout hadden een hogere overlevingskans en groeiden sneller dan andere *Cecropia* zaailingen. *Cecropia* zaailingen kiemden met name in de lichtere gedeelten van de open plek, terwijl post-open-plek *Dicorynia* zaailingen een duidelijke voorkeur hadden voor de donkere plaatsen van de open plek. Pré-open-plek *Pourouma* zaailingen kwamen in hogere dichtheid voor in de donkere plaatsen van de open plek. De hoogtegroei van post-open-plek *Cecropia* en *Dicorynia*, en pré-open-plek *Pourouma* zaailingen was matig gecorreleerd met de lichtbeschikbaarheid.

In Hoofdstuk 7 worden tenslotte de voornaamste resultaten van deze studie bediscussiëerd. Ten eerste wordt het ontstaan van open plekken behandeld. De moeilijkheden met het bepalen van het oppervlak van open plekken geven aan dat betrouwbare gegevens omtrent de turnover-rate van een bos moeilijk te verkrijgen zijn. Alleen wanneer één duidelijk definitie wordt gebruikt, observaties over een langere termijn en op een groot oppervlak worden verricht en veldmetingen goed worden gecontroleerd kan de turnover-rate van een bos betrouwbaar worden vastgesteld. De oorzaken en gevolgen van het vallen bomen en takken worden verder besproken en er wordt geconcludeerd dat open plekken niet willekeurig voorkomen. Bodemfactoren kunnen er de oorzaak van zijn dat bepaalde plaatsen in het bos zogenaamde "hot spots" van verstoringen zijn, terwijl op andere plaatsen minder frequent open plekken ontstaan. Ten tweede wordt het dichtgroeien van open plekken en het succes van zaailingen in open plekken bediscusiëerd. De groei van zaailingen neemt over het algemeen toe in open plekken, maar de meeste zaailingen hebben meer dan één open plek episode nodig om een volwassen boom te worden. Toeval speelt een belangrijke rol bij het dichtgroeien van open plekken. De samenstelling van zaailingen in open plekken wordt met name bepaald door de op die plaats toevallig voorkomende pré-open-plek zaailingen. De specialisatie van soorten wordt besproken. Er wordt gesuggereerd dat, met behulp van gedetailleerde informatie over de micro-habitat beschikbaarheid en de micro-habitat behoefte van de planten, de plaatsen bepaald kunnen worden waar bepaalde soorten de hoogste overlevingskansen hebben en de beste groei zullen vertonen. Ten derde wordt de potentiële toepassing van de gevonden resultaten bij het ontwerpen en verbeteren van bosteeltsystemen besproken. Een aantal bestaande bosteeltsystemen die het natuurlijke verstoringsregime van het bos proberen na te bootsen wordt behandeld en getoetst aan de hand van de resultaten van dit proefschrift. Verder worden enkele suggesties gedaan voor het toepassen van de resultaten van dit onderzoek bij het opzetten van bosteeltsystemen.

Résumé

La dynamique de la canopée dans une forêt tropicale humide en Guyane française

La canopée de la forêt tropicale humide est dynamique. En moyenne, des trouées se forment annuellement dans 1 % de la canopée, en raison de la chute d'arbres et de branches. Sur les chablis ainsi créés, une forêt jeune commence à pousser, qui redeviendra à long terme une forêt adulte, dense. L'apparition de chablis dans une forêt tropicale humide influence l'implantation, la croissance et la mortalité (dynamique de peuplement) de nombreuses espèces d'arbres. Dans cette thèse, on a étudié comment apparaissent et se densifient les chablis (la dynamique de la canopée) dans une forêt tropicale humide en Guyane française. L'étude ici présentée a pour but de répondre aux questions suivantes : (1) comment, et à quelle fréquence apparaissent des chablis par la chute d'arbres ou de branches ; (2) comment et à quelle vitesse se ferment les chablis ; et (3) comment les chablis influencent-ils la dynamique de peuplement des plantules d'arbres.

Le chapitre 1 commence par une introduction générale sur la dynamique de la canopée des forêts tropicales humides. L'apparition de chablis et ses conséquences sur la disponibilité de ressources pour les plantes, comme la lumière et les éléments nutritifs, sont traités. Différents modes de croissance de végétation dans les chablis sont étudiés et les effets des chablis sur les plantules sont développés en détail. Les objectifs de cette thèse sont formulés, suivis d'une description de la forêt tropicale à Nouragues, Guyane française, où a été effectué le travail sur le terrain pour cette enquête.

Dans le chapitre 2, trois méthodes régulièrement utilisées pour définir les chablis sont décrites et comparées les unes aux autres. Par ailleurs, on étudie l'effet de différentes définitions de chablis sur le calcul du temps nécessaire pour recouvrir entièrement une forêt avec des chablis, en utilisant la surface des trouées qui apparaissent en moyenne annuellement dans la canopée (taux de renouvellement). La taille de 18 chablis a été mesurée en utilisant les trois différentes définitions. Les surfaces mesurées selon les différentes définitions présentaient des différences significatives. L'une des définitions donnait une évaluation raisonnable de la surface du chablis créé dans la canopée, tandis qu'une autre constituait une bonne estimation de la surface du sol forestier qui était influencé par le chablis. Le taux de renouvellement calculé de la forêt était influencé de façon évidente par l'application de différentes définitions pour délimiter les chablis : le taux de renouvellement sur le sol forestier était de 4 à 8 fois inférieur au taux de renouvellement dans la canopée. Les études sur les chablis et les taux de renouvellement des forêts tropicales ne peuvent être comparées les unes aux autres que si les mêmes définitions sont utilisées.

Dans le chapitre 3, la chute d'arbres et de branches est étudiée plus précisément. Après 1 an, sur 6.314 arbres présents (diamètre > 10 cm) sur 12 hectares de forêt tropicale, 96 arbres (1,5 %) étaient tombés et 84 arbres (1,3 %) avaient perdu une branche d'au moins 10 cm de diamètre. En outre, 75 % des arbres tombés et 83 % des arbres abîmés étaient abattus ou endommagés par "effet domino" (c'est-à-dire par la chute d'autres arbres ou de branches). Parmi les arbres qui n'avaient pas été abattus par d'autres ("chute initiatrice d'arbre"), 38 % étaient déracinés et 62 % étaient cassés au-dessus du sol. Les chutes initiatrices d'arbres et de branches semblaient se produire plus fréquemment à une distance de 50 m du centre des chablis, alors que relativement peu de chutes initiatrices d'arbres et de branches se produisaient à une distance de 25 mètres des chablis. Environ 35 % des arbres tombés et 42 % des arbres ayant perdu une branche n'avaient pas entraîné de chablis. Les chutes initiatrices d'arbres qui avaient créé un chablis ne présentaient pas un diamètre différent de celui des arbres tombés qui n'avaient pas entraîné de chablis. Toutefois, les chutes de branches qui entraînaient un chablis provenaient d'arbres ayant un diamètre supérieur à celui d'arbres dont la chute des branches n'entraînait pas de chablis. La taille des chablis augmentait au fur et à mesure de l'augmentation du nombre d'arbres concernés et de la base des arbres concernés. Le taux de renouvellement calculé sur la base (1) du nombre d'arbres tombés aussi bien que sur la base (2) du nombre de chablis d'une forêt représente une sous-estimation de la perturbation réelle d'une forêt parce que (1) les branches tombées engendrent également des perturbations considérables et (2) les arbres tombés ne créent pas tous des chablis.

Dans le chapitre 4, on étudie comment apparaissent et se densifient les chablis. En avril 1991, tous les chablis > 4 m² ont été localisés et mesurés sur 12 hectares de forêt : sur le nombre total de 74 chablis, 60 sont apparus avant janvier 1990. Entre janvier 1990 et décembre 1993, de 5 à 15 nouveaux chablis sont apparus chaque année, qui ouvraient 0,6 à 1,3 % de la canopée. Sur l'ensemble des chablis, 41 % étaient formés par des arbres tombés qui étaient cassés au-dessus du sol, 34 % par des arbres tombés déracinés, 22 % par des branches tombées et 3 % par des troncs morts tombés. Une analyse du "plus proche voisin" indiquait que les chablis apparus après janvier 1990 se présentaient de façon groupée. Ce "regroupement" est probablement lié au fait que les sols peu profonds sont fréquents à Nouragues. D'autres études ont montré que le déracinement d'arbres était en rapport avec des facteurs liés au sol. A Nouragues, les arbres déracinés entraînaient la chute d'un nombre relativement important d'autres arbres, quel que soit leur diamètre. L'ouverture de la canopée (pourcentage de ciel non couvert) au centre des chablis a été mesurée pendant 3 ans et on supposait qu'elle diminuerait avec l'âge et la densification des chablis. Toutefois, l'ouverture de la canopée a augmenté dans 54 % des chablis avec l'âge du chablis. Les bords des grands chablis, notamment, étaient certainement régulièrement perturbés par de nouvelles chutes de branches et d'arbres. Par ailleurs, les résultats indiquent qu'il faut en moyenne une quinzaine d'années pour que les chablis ne se distinguent plus de la forêt dense environnante.

Le chapitre 5 est axé sur l'évolution de la végétation dans les chablis, et notamment sur les différences entre les petits et grands chablis. Le pourcentage d'espace dans lequel apparaît une végétation (la densité de végétation) a été déterminé au-dessus de chaque mètre sur des bandes par 3 grands et 3 petits chablis. Le degré de végétation a été mesuré dans 3 classes de hauteur différentes, à différents intervalles : 0 > 30 m (à intervalles de 5 m) ; 0 - 10 m (à intervalles de 1 m) ; et 0 - 2 m (à intervalles de 0,25 m). Les mesures ont été effectuées en octobre 1991 et novembre 1993. Les différences nettes de densité de végétation étaient les plus importantes au milieu des petits chablis pour la classe 0 > 30 m, tandis que les différences nettes de densité de végétation étaient les plus importantes au milieu des grands chablis pour les classes de hauteur inférieures (0 - 2 et 0 - 10 m). Les petits chablis semblent donc se fermer essentiellement par la pousse de branches d'arbres environnants, tandis que les chablis plus importants se ferment surtout par la croissance de plantules, d'arbustes et de jeunes arbres. On estime que les petits chablis sont denses après environ 5 à 6 ans, tandis que les plus grands chablis ont besoin de 5 à 10 ans pour qu'une canopée d'au moins 10 mètres se soit développée. Les données n'étaient pas appropriées pour une extrapolation ultérieure permettant de prévoir la vitesse de densification des grands chablis jusqu'à une hauteur de 20 mètres (hauteur minimale d'une forêt dense).

Dans le chapitre 6, l'effet des chablis et la disponibilité de la lumière sur les plantules sont étudiés. L'implantation, la croissance en hauteur et la mortalité des peuplements de plantules des espèces d'arbres *Cecropia obtusa, Dicorynia guianesis* et *Pourouma bicolor* ont été étudiées aussi bien dans des chablis qu'en forêt dense. La densité des trois espèces dans les chablis était supérieure à celle de la forêt dense. Les plantules de *Pourouma* poussaient plus rapidement dans les chablis, tandis que la croissance en hauteur de *Dicorynia* ne présentait pas de différence entre les chablis et la forêt dense. Les plantules de *Cecropia* ne poussaient que dans le plus grand chablis et non en forêt dense. Dans un grand chablis, des différences significatives ont été trouvées entre la densité des plantules qui étaient présentes avant l'apparition du chablis (plantules pré-chablis) et celle des plantules qui se sont implantées après l'apparition du chablis (plantules post-chablis). Les plantules pré-chablis de *Dicorynia* poussaient moins vite que les plantules post-chablis et ne présentaient pas d'adaptation évidente aux nouvelles conditions du chablis. Les plantules post-chablis de *Pourouma* poussaient plus vite en deuxième année qu'en première, après apparition du chablis. Les plantules de *Cecropia* qui germaient sur du bois mort avaient une chance de survie supérieure à celle des autres plantules de *Cecropia* et poussaient plus rapidement. Les plantules de *Cecropia* germaient notamment dans les parties plus claires du chablis, tandis que les plantules post-chablis de *Dicorynia* avaient une nette préférence pour les endroits plus sombres du

chablis. La densité des plantules pré-chablis de *Pourouma* était supérieure dans les endroits plus sombres du chablis. La croissance en hauteur des plantules post-chablis de *Cecropia* et *Dicorynia* et des plantules pré-chablis de *Pourouma* avait un rapport modéré avec la disponibilité de lumière.

Enfin, dans le chapitre 7, les principaux résultats de cette étude font l'objet d'une discussion. Premièrement, il est traité de l'apparition des chablis. Les difficultés de détermination de la superficie des chablis indiquent qu'il est difficile d'obtenir des données fiables en ce qui concerne le taux de renouvellement d'une forêt. Le taux de renouvellement d'une forêt ne peut être établi de façon fiable que si une seule définition claire est utilisée, si les observations sont effectuées à long terme et sur une grande surface et si les mesures sur le terrain sont bien contrôlées. Il est plus amplement traité des causes et conséquences de la chute d'arbres et de branches et on conclut que les chablis n'apparaissent pas de façon arbitraire. Des facteurs liés au sol peuvent avoir pour effet que certains endroits de la forêt sont des "points chauds" de perturbations, tandis que les chablis apparaissent moins fréquemment à d'autres endroits. Deuxièmement, la densification des chablis et la réussite des plantules dans les chablis sont portées à discussion. La croissance des plantules augmente en général dans les chablis, mais pour la plupart des plantules, un seul épisode "chablis" ne suffit pas pour devenir un arbre adulte. Le hasard joue un rôle important dans la densification des chablis. La composition des plantules dans les chablis est notamment déterminée par les plantules pré-chablis qui sont apparues par hasard à cet endroit. Il est traité de la spécialisation des espèces. Il est suggéré que, à l'aide d'informations détaillées sur la disponibilité du micro-habitat et sur les besoins des plantes en micro-habitat, il est possible de déterminer les endroits où certaines espèces ont les plus grandes chances de survie et présenteront la meilleure croissance. Troisièmement, il est traité de l'application potentielle des résultats trouvés pour la conception et l'amélioration des systèmes de sylviculture. Un certain nombre de systèmes de sylviculture existants, qui tentent de reproduire le régime naturel de perturbation de la forêt, sont développés et testés au moyen des résultats de cette thèse. Par ailleurs, quelques suggestions sont apportées en ce qui concerne l'application des résultats de cette étude pour la mise en place de systèmes de sylviculture.

Curriculum Vitae

Petrus Jacobus van der Meer werd op 15 februari 1962 geboren te Renkum. In 1981 behaalde hij het Atheneum-B diploma aan het Katholiek Gelders Lyceum te Arnhem. Na zijn militaire dienstplicht begon hij in 1982 met de studie bosbouw (oriëntatie tropisch) aan de toenmalige Landbouw Hogeschool in Wageningen. Voor één afstudeervak werd onderzoek gedaan naar de bos-dynamiek van een savanne-bos in Zuid-Oost Australië. Een beurs van het Australian-European Award Program stelde hem in staat om hiervoor 10 maanden aan het Department of Forestry van de Australian National University, Canberra, Australië, te studeren. Verder verbleef hij bijna 4 maanden in Ivoorkust, West Afrika, voor een onderzoek naar lijnbeplantingen in een gedegradeerd stuk regenbos. Tevens werd een afstudeervak gedaan bij de vakgroep Landmeetkunde van de Landbouw Universiteit Wageningen wat zich bezighield met het modelleren van gegevens ten behoeve van een erosie model. In Juni 1988 werd de studie bosbouw succesvol afgerond.

Aansluitend op zijn studie onderzocht hij (als toegevoegd onderzoeker bij de vakgroep Bosbouw) de gevolgen van uitkap systemen op de regenbossen van Noord-Oost Australië. Verder nam hij deel aan een expeditie met het kronendak-vlot in Frans Guyana in november 1989. In augustus 1990 volgde een aanstelling voor vier jaar als assistent in opleiding (AIO) bij de vakgroep Bosbouw, gefinancierd door de stichting "Het Kronendak". Gedurende deze periode werd in totaal 16 maanden veldwerk verricht in het regenbos van Frans Guyana. Van september 1994 tot october 1995 was hij gastmedewerker bij de vakgroep Bosbouw en werd zijn proefschrift afgeschreven alsmede enkele artikelen. Vanaf november 1995 gaat hij werken als onderzoeker bij het Department of Nature Conservation & Natural Resources in Victoria, Australië.