FOREST FILLED WITH GAPS

EFFECTS OF GAP SIZE ON WATER AND NUTRIENT CYCLING IN TROPICAL RAIN FOREST

A STUDY IN GUYANA

TROPENBOS-GUYANA SERIES 10

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Forest filled with Gaps

Effects of Gap Size on Water and Nutrient Cycling in Tropical Rain Forest

A Study in Guyana

Bos gevuld met gaten

De effecten van de grootte van kronendakopeningen op de water- en nutriëntenkringloop in tropisch regenwoud.

Een studie in Guyana

(Met een samenvatting in het Nederlands)

Proefschrift

Ter verkrijging van de graad van doctor
aan de Universiteit Utrecht,
op gezag van de Rector Magnificus,
Prof. Dr. W.H Gispen,
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door

Oscar van Dam

geboren op 5 December 1967 te Groesbeek.

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The Utrecht Centre for Environment and Landscape dynamics *UCEL*

Utrecht University *UU*

The Netherlands Centre for Geo-Ecological research *ICG*

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"[..] een mens heeft zijn intellectuele voorsprong op de chimpansee slechts te danken aan een sterk verlengde jeugd. [..] Bij blijven is jong blijven. Tot op hoge leefdtijd."

Midas Dekkers, Het kind. In: De kip en de pinguïn, 1995.

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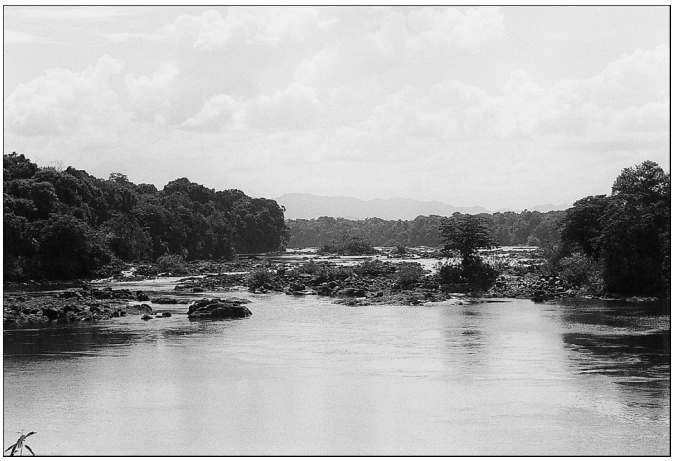


Waraputa Falls in the Essequibo River, Central Guyana

1 INTRODUCTION

GUYANA AND ITS FORESTS

> "Delight is [..] a weak term for such transports of pleasure. [..] Wandering in a Brazilian forest, [..] it is hard to say what sets of objects are most striking: the general luxuriance of the vegetation bears the victory, the elegance of the grasses, the novelty of the parasitical plants, the beauty of the flowers, the glossy green of the foliages, all tend to this end."

Charles Darwin wrote these words in his Beagle diary on 29 February 1832. Like Darwin, many authors turned poets in an attempt to describe the tropical rain forest, a term which was first introduced by Schimper (1898). His definition of an evergreen, at least 30m high forest, rich in thick-stemmed lianas and trees with herbaceous epiphytes is still maintained by many scientists, although it gives only a poor idea of what a tropical rain forest really is (*sensu* Richards 1996). Even for a casual visitor, the extravagant vegetation and abundant wildlife, if sighted, are obvious characteristics of a tropical rain forest. Less obvious, but equally important, is the heterogeneity of the soils that bear the forests, which form the base of entangled webs of competition for nutrients and water (Baillie 1989, Bernard-Reversat 1975, Brouwer and Riezebos 1998, Bruijnzeel 1989 & 1990, Douglas *et al.* 1992, Jetten 1994a). In addition, the forests themselves create a mosaic of microclimatic environments of light, temperature and humidity caused by the tumbling over of single trees (Hartshorn 1978, Orians 1982, Wayne and Bazzaz 1993, Whitmore *et al.* 1993).

The diversity of flora, fauna and the physical environment of a tropical rain forest is still poorly understood, because of the large amount of different plant species that interact with an even larger amount of animals in a whole range of environmental settings. Although research has been carried out in the tropical rain forest since the Darwinian age, these ecosystems still promise many exhilarating secrets.

Forestry in Guyana: growing awareness for sustainability

For many hundreds of years, people have used the tropical rain forest and its products, but over the past 100 years, the pressure on the tropical rain forest has increased tremendously. Whole stretches of forest are converted to pasture; trees are harvested for timber; lianas are used for furniture; fruits, seeds and other edible plant parts are collected; animals are hunted for their meat; and tropical rain forests are believed to contain many, yet still undiscovered, medicinal products. Conversion of tropical rain forest to agricultural lands traditionally occurred as shifting cultivation, although the Maya's were probably the first people to practice deforestation on a larger scale. However, the large-scale conversion of the 2nd half of the 20th century has decreased the total area of tropical forest tremendously. Conservation and sustainable use of the tropical rain forests have become hot items on international forums like Agenda 21 (UNCED 1992 chapters 11 and 15) and the global importance of tropical forest has been widely recognised. The integrity of tropical forests can be maintained through developing management techniques which promote a mix of timber and non-timber values for present and future human populations (Bruenig 1992, Dykstra and Heinrich 1992). Despite this growing awareness, the FAO (1999) estimates that 0.8% or 63 mln ha of the total area of tropical forests of 1734 mln ha worldwide are felled annually (Table 1.1). Among the countries with tropical (rain)forests, Guyana and the neighbouring countries in the Guianas – Surinam and French Guiana – have the

largest relative forest cover and lowest deforestation level in the world (FAO 1999). The FAO figures on forest cover and deforestation in Guyana give an overestimation of the actual situation, since local forestry data indicate that the country is covered for 89% with forest (Forest type map of Guyana, ter Steege 2000), including shrubs, deciduous forest, semi-deciduous forest, dry-evergreen forest and wet evergreen rain forest. But indeed, large stretches of these forests are still unspoiled.

The timber trade in Guyana dates back to the 17th century, but was limited to stretches of the main lower rivers (van der Hout 1999). More recently, forestry has become an important industry, utilizing the countries natural resources and providing work and income for thousands of peoples. In 1999, the state forest covered 13.7 mln ha (GFC 1999) of which 46% was allocated to forestry. In the last 5 years, forestry in Guyana accounted for 4 to 5 % of the country's gross domestic product (GFC 1999). Timber exports account for 1.7% of Guyana's GNP (Sizer 1995). Guyana's best-known timber species is Greenheart (*Chlorocardium rodiei*) and constitutes more than 15-20% of all exported timber. Although it amounts to only 1.5% of the standing volume of the forests of the country, locally, in Greenheart dominated forests, 20% of the standing volume has been found (Ek and van der Hout 1997). The relative importance of Greenheart declines every year, since markets are opened up for other tree species like Baromalli (*Catostemma altsonii*) (GFC 1999). However, the Greenheart bearing forests are continuously over-exploited and the Guyanese government and the forest industry desire an economic sustainable and ecological responsible forest management. Already in 1889, the need for a sustainable forest management was recognised (Crown Surveyor 1889 in van der Hout 1999). A hundred years later, in 1989, a 'National Forestry Action Plan' was designed (GNRA 1989) by the Guyana Forestry Commission, who developed a series guidelines and requirements, covering all aspects of logging: the 'Code of Practice for Forest Operations'. This 'Code of Practice' is currently being modified and is expected to become mandatory in the near future.

Table 1.1 FAO forest data of tropical forests (FAO 1999).

Country / Region	Forest Area in 1995 (×1000 ha)	Forest % of land area in 1995	Change 1990-1995 (×1000 ha)	Annual Change 1990-1995 Rate (%)	World Rank Forest 1995 (1)	World Rank Forest 1990 (1)	Tropical Countries Rank Annual Change (2)
Guyana	18,577	94.4	-43	n.s.	1	2	n.s.
Suriname	14,721	94.4	-61	-0.1	1	1	23
French Guiana	7,990	90.6	-4	n.s.	3	3	n.s.
Venezuela	43,995	49.9	-2517	-1.1	30	28	57
Brazil	551,139	65.2	-12,772	-0.5	14	13	36
South America	827,945	59.8	-23,277	-0.6			
N. & C. America	79,443	30	-5185	-1.3			
Africa	504,901	22.6	-18,475	-0.7			
Oceania	41,903	77.5	-756	-0.4			
Asia	279,766	33	-15,275	-1.1			
World	**1,733,958**	**44.6**	**-62,968**	**-0.8**			

(1): total of 203 countries, including non-tropical; (2): total of 94 countries

Research in the tropical forest in Guyana: the Tropenbos-Guyana Programme

The former Dutch Minister of Development Cooperation, Mr. J.P. Pronk, stated that: "[..] The conservation and sustainable use of the tropical rain forests is essential if we are to achieve sustainable development and maintain the world's biological diversity [..], which is vital not

only to the survival strategies of local populations, but also to the ecological balance of the entire world. [..] Research needs to focus on the ecological, social, cultural and economic significance of tropical rain forests. [..] The aim of the Dutch government is to assist developing countries in building the capacity and knowledge they need to conserve the forest and achieve sustainable forest management." (in: Tropenbos 1998). The onset to achieve this aim started in 1985, when the Dutch government initiated the Tropenbos Foundation. The main objectives of the Tropenbos Foundation are: 1) to contribute effectively to the conservation and wise use of tropical rain forest, by generating relevant knowledge, deepening insights and developing and testing methods for forest policy and management; 2) to involve local research institutions and to strengthen research capacity in tropical rain forest countries (Tropenbos 1994, 1997). Tropenbos has set up research sites in several countries with tropical rain forests, including Guyana. The objective of the Tropenbos-Guyana Programme is to achieve a sustainable forest management system in the lowland tropical rain forest of Guyana, so that timber harvesting can be economically and silviculturally sustainable, while maintaining the integrity of other forest functions (e.g. environmental services, biodiversity, resource use by the local population). Within this concept, an appropriate forest management systems is nesseccary, which includes a logging methodology that does not compromise the future value of the forest or the functioning of the forest ecosystem.

SELECTIVE LOGGING AND GAP SIZE

Selective logging

Logging in primary tropical rain forest has direct impacts on the biotic and a-biotic conditions of the forest. In Southeast Asia, clear felling is common practice and results in large-scale erosion (Malmer and Grip 1990), which completely changes the water balance and nutrient status of the soil. Forest regeneration is difficult if at all possible. Fortunately in Guyana, timber harvest proceeds through selective logging by which only those trees are felled that are commercially valuable. The overall impact on biodiversity and the forest ecosystem is small (ter Steege *et al.* 1996, ter Steege *et al.* in prep) and seen from the air, the forest appears as a vast green blanket. Nonetheless, locally, the damage to the forest can be substantial (ter Steege *et al.* 1996, van der Hout 1999, Zagt 1997). At the logging scene, there are large piles of felling debris and substantial stretches of the bare soil, created by bulldozers and skidders. But perhaps most important, the felling of mature canopy trees created many gaps in the canopy, varying in size from small holes of only a few square metres to football-field-size openings.

In pristine forests, canopy gaps are a common feature created by the natural dieback and fall of trees and branches. Actually, these tree fall gaps are essential for forest regeneration (Bazzaz 1994, Brokaw 1985a, Brown 1990, Pickett 1983) and many authors have reported on tropical rain forest gaps and their importance for the biodiversity of the forest (Denslow 1987, Poulson and Platt 1989), although recent studies have not been able to partition tree species in relation to gap size in natural tree fall gaps (Hubbell *et al.* 1999) or logging gaps with natural competition (Rose 2000).

Gaps created by logging are frequently larger than natural tree fall gaps (Table 1.2) and usually more gaps per ha can be found. Commercial tree species are often heavy seeded species that disperse their seeds near the parent tree. For example, the bulk of Greenheart seeds are found under the crown of the tree (ter Steege 1990). Although these heavy seeds can also be dispersed by mammals or roll downhill, this minimal species-induced dispersal distance creates a forest with a clumped distribution of these tree species. This is of great advantage for any tree feller, since the number of trees per ha of a desired tree species can be large. However, it is a disadvantage for the ecology of the forest, because these logging gaps are substantially larger

than would occur naturally. In these large logging gaps, microclimatic and edaphic conditions that could decrease the regeneration potential[1] of desired tree species or the forest prevail.

Table 1.2 Gap sizes (m^2) of natural tree fall gaps and felling gaps in logged forest at different intensities in central Guyana.

Intensity	No. of gaps	Average gap size (m^2)	Minimum gap size (m^2)	Maximum gap size (m^2)	Reference
natural gaps	560	91	5	942	v. Dam & Rose, 1997
natural gaps	64	64	6	372	v. Dam, unpubl.
4 trees/ha	20	152	28	361	v.d. Hout, 1996
8 trees/ha	53	234	19	775	v.d. Hout, 1996
16 trees/ha	31	277	14	1787	v.d. Hout, 1996

Microclimate, water, nutrients and regeneration performance

The growth performance of pioneer and climax species increases with increasing gap size, if light, water or nutrients are the only limiting variables (Rose 2000). Seedling and sapling growth is undoubtely steered by changes in microclimatic conditions like solar radiation and temperature and changes in water and nutrient availability. Previous research carried out in Guyana showed important changes in microclimatic conditions, water and nutrient cycling in a medium ($800m^2$) and large gap ($3400m^2$) (Brouwer 1996, Jetten 1994a). For example, the soil moisture content in gaps increased and nutrient losses increased with gap size, but on the other hand, decomposition rates were not affected. Other ecological processes also exert their influence on seedling growth in gaps, like competition, insect herbivory or chance events such as tree falls, which kill newly established plants. No matter what ecological processes influence regeneration in gaps, the vegetation in the gap is in constant need of light, water and nutrients. Understanding forest regeneration in logging gaps requires a thorough knowledge of the microclimatic and edaphic conditions in relation to gap size.

The effects of different logging intensities, expressed as canopy openings or gap size, on edaphic conditions and microclimate is not well understood. Information is scarce on how gap size affects the microclimate in gaps and in the adjacent forest, how the soil moisture dynamics are altered or how the nutrient cycle is disturbed. Such knowledge is essential in understanding the forest ecosystem and the effect of logging. At certain gap size, microclimate and edaphic conditions can be disturbed to such a degree that the ability of certain tree species or the forest in general to regenerate is strongly limited. The extent of such a ‘maximum’ gap size is not known and will be different per tree species.

The Pibiri Gap experiment

In 1996, the Tropenbos-Guyana Programme initiated the Pibiri Gap Experiment (PGE), in which biologists, ecologists and physical geographers worked in experimental forest gaps on the ecological interactions of plants, animals and the a-biotic environment (van Dam *et al.* 1999). The PGE is part of the Tropenbos-Guyana Gap Study, which encompasses all gap related studies and studied the ecological processes along a gradient of gap sizes. In a later stage of the Programme, the information on the effect of gap size on the future species composition will be used to set up guidelines for forest management and gap size could be used an indicator of good husbandry for forest managers and policy makers.

[1] The regeneration potential of a tree species is here defined as the possible growth rate a species could obtain under the prevailing environmental conditions.

Together with the other gap related studies of the Guyana-Tropenbos Programme, the study on microclimate and edaphic conditions, as presented in this thesis, aids in identifying a gap-size related parameter for the regeneration potential of selected tree species. This research only focuses on mixed Greenheart forest (see Chapter 2), because of the importance and over-exploitation of Greenheart in the forest industry of Guyana and the vast knowledge of these forests that has been gathered by the Tropenbos-Guyana Programme over the past 12 years.

MICROCLIMATE, WATER AND NUTRIENTS IN GAPS

Although it is clear that a small gap receives less light than a large gap, these distinctions are less clear for intermediate gaps. Moreover, changes in soil conditions are not readily noticeable. Changes in microclimatic and edaphic conditions can occur as gradual transitions or, where certain thresholds are exceeded, in a disrupted manner.

This study aims at identifying these changes through field measurements and numerical modelling. A model that describes the microclimate, water and nutrient cycling in gaps is useful since it:

1) helps in understanding how the microclimate and edaphic conditions interact,
2) gives insight into spatial patterns of microclimate, water and nutrient cycling in gaps and forest and
3) could predict the effect of different sized gaps on these environmental variables beyond the measurement period.

Not only does the size of the gap matter, but also transitions inside a gap: gradients from the gap edge to the gap centre. Gaps also exert their influence beyond the perimeter of the gap edge. This so called 'gap edge area' might experience disruptive microclimatic and edaphic conditions that also affect the regeneration potential of the vegetation in that area. The model that was developed had to be able to deal with these temporal and spatial processes inside a gap and in the gap edge area. In light of these objectives, intriguing research questions had to be addressed.

Gap size, microclimate and edaphic conditions: Questions

This study on microclimate, water and nutrient cycling was divided into several projects, each of which covers a section of the overall objectives. Separate research objectives, questions and hypotheses were formulated for these projects and will be discussed in the coming chapters. However, there are several focal points, which are addressed in each of these projects.

- How does the size of a gap affect the microclimatic conditions, the water balance and the nutrient cycling? Do these changes proceed proportional to gap size? Is there a certain gap size, above which these changes are no longer affected by an increase in gap size?
- Are the changes in microclimatic conditions, water and nutrient cycling of the same magnitude throughout a gap of a certain size or do these changes occur as gradients from the gap centre to the gap edge?
- Is the influence of the gap limited to the gap area itself or does a gap exert its presence beyond the perimeter of the gap edge? And if so, how far do the changes in microclimatic conditions, water and nutrient cycling extend into the forest that surrounds the gap?
- Is the size of a gap the most important factor determining the amplitude of the changes in microclimatic conditions, water and nutrient cycling or are there other factors involved as well? Which are these factors that also contribute to the way a gap affects the microclimate and water and nutrient dynamics?

- How do the microclimatic conditions, the water and nutrient cycling change in time, when the vegetation in the gaps regenerates and do these changes increase with increasing gap size?

Most of these questions were addresses by field measurements of microclimate, soil moisture conditions and nutrient cycling studies. Questions on evapotranspiration and long-term expectations, as well as spatial patterns of microclimate, water and nutrient cycling were approached by modelling.

Gap size, microclimate and edaphic conditions: Expectations

The research questions as outlined above were formulated to test a series of hypotheses that are best explained with a figure. Figure 1.1 shows two lines that run from the undisturbed forest to the gap centre and back into the forest. These two lines represent gradients of altered microclimatic conditions, water and nutrient cycling in relation to gap size and the position inside the gap or in the gap edge area. An example of such a gradient is the amount of radiation, which is expected to increase from gap edge to the gap centre or decrease from gap edge into the forest. Relatively sharp transitions are expected at the gap edge. However, microclimatic conditions or changes in water and nutrient cycling are not expected to change continuously, but the magnitude of change will become constant above a certain gap size. Not only do these changes occur within a gap, but also differences in the magnitude of the changes are expected between gaps of different size. Radiation can serve again as an example, since the amount of radiation in a small gap is expected to be smaller than in a large gap. Moreover, the effect of a small gap on the gap edge area is likely to be smaller than in a large gap.

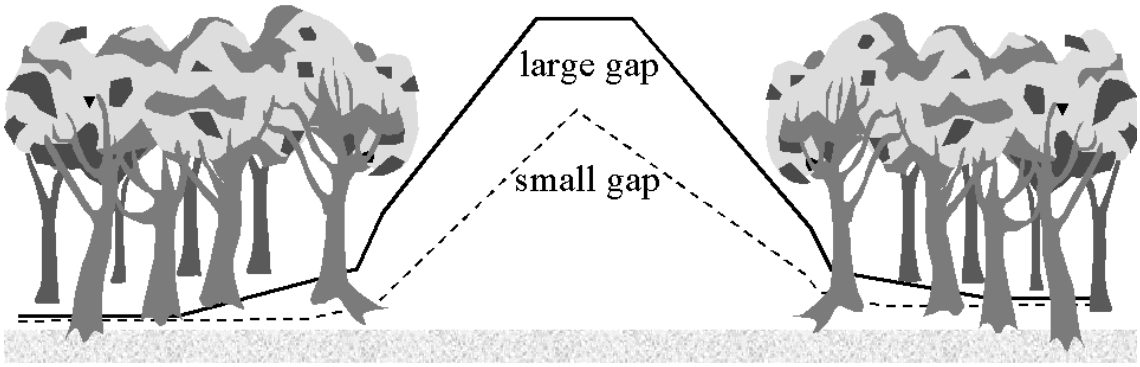


Figure 1.1 Gradients of microclimate, water dynamics and nutrient cycling from gap centre into the forest for a small and a large gap.

THESIS LAYOUT

The objectives were achieved through two methodologies of research. First, field measurements provided detailed and precise information on specific environmental settings as present in the different experimental gaps and forest. Interactions or dependency between different aspects of microclimate, water and nutrients were studied simultaneously under similar environmental conditions. Unfortunately, this high level of detail made the application on the research results in slightly different environments difficult. Moreover, information is lacking of these processes at other locations in the gaps or gap edge area or for other periods of time than the locations and periods of the field measurement campaign. Extrapolation of the research results outside the boundaries of the data collection is hardly possible. This problem has been solved by the second research approach: modelling the processes under study. These two research methodologies can be found throughout this thesis.

The major work of the thesis is divided into two parts: one part covers the microclimate and water balance and one part is concerned with the nutrient cycle. These two main research topics dealing with field data are interlinked through modelling (Figure 1.2).

Chapter 2 gives a review of previous work on tropical rainforest microclimate, water balance and nutrient cycling. The physical environment of the study area is described and the Pibiri Gap Experiment is explained.

Chapter 3 tackles the problem of microclimate and soil moisture in gaps and surrounding forest as measured over a period of 3 years.

Only a few measurements on the water balance have been carried out. Instead, the water balance has been modelled with the PCRaster model FORGAP, which is explained in Chapter 4 and the results of the model are given in Chapter 5.

Studies on the nutrient cycle include: litterfall (Chapter 6), decomposition (Chapter 7), mineralisation (Chapter 8) and nutrient leaching (Chapter 9).

Data on microclimate and soil moisture, as presented in Chapter 3, is used in the chapters on the nutrient cycling. In turn, litterfall and decomposition modelling is incorporated in the FORGAP model. FORGAP is used to calculate the nutrient fluxes as presented in Chapter 9.

This research is summarized in Chapter 10, where the conclusions on the effects of gap size on microclimate, water and nutrient cycling are.

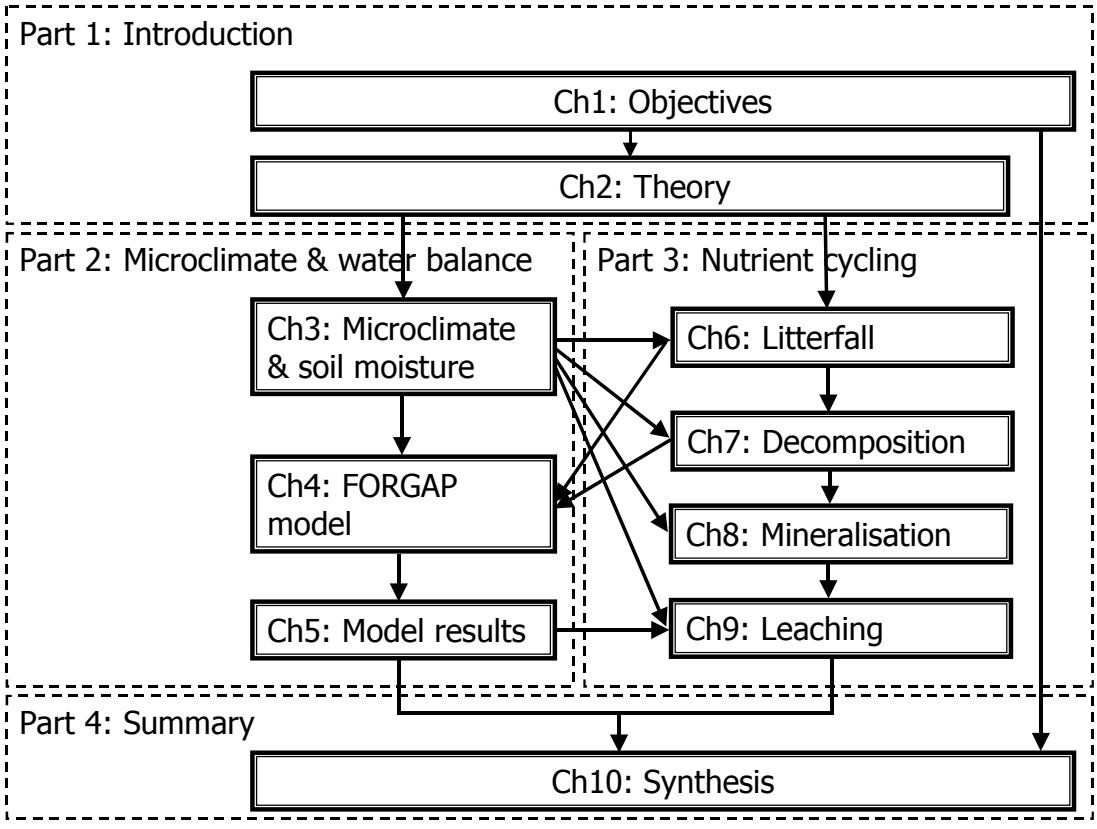


Figure 1.2 Thesis layout.

Creating experimental gaps

2 STUDY AREA, THE PIBIRI GAP EXPERIMENT AND ASPECTS OF MICROCIMATE, WATER AND NUTRIENT CYCLING IN TROPICAL RAIN FOREST LOGGING GAPS

Abstract.
This chapter describes the set-up of the Pibiri Gap Experiment and provides background information on the physical environment, vegetation and climate of the study area. Some theoretical aspects of microclimatic conditions, hydrology and nutrient cycling of the tropical rain forest of the region and of logging gaps in particular are discussed.

THE PIBIRI GAP EXPERIMENT

Objectives

As was explained in the introduction chapter, there is a lack of knowledge as to the effects of logging gaps of different size on edaphic conditions, microclimate and regeneration in the gap and the forest surrounding the gap. The question concerning what form of inevitable disturbance that accompanies forest exploitation is most conducive to a desired regeneration of the forest is addressed in a broad range of projects of the Tropenbos-Guyana programme. The Pibiri Gap Experiment (PGE) forms the nucleus of this research topic.

One of the main timber species of Guyana is *Chlorocardium rodiei* (Greenheart). Greenheart is a heavy seeded tree species with a limited dispersal distance from the parent tree, usually within the crown zone (ter Steege 1990). Notably, Greenheart dominated forest has a clumped spatial distribution. Exploitation of this species ultimately results in areas of variable sizes being opened up. Both light demanding and shade tolerant species are thereby exposed to a multitude of environmental conditions. The ecological constraints of these various gap sizes on the regeneration potential of the forest in general and commercial tree species in particular is not well understood.

The PGE aims at generating knowledge about the ecological interactions in logging gaps that can contribute to the definition of a maximal or optimal gap size for the regeneration of the forest in general and of desired tree species in particular. This information can be used for policy makers and forest managers to set-up guidelines for forest management. The PGE is part of the Gap Study programme of Tropenbos-Guyana, which encompasses a range of gap related studies (see Brouwer 1996: nutrient cycling, Ek 1997: botanical diversity, Jetten 1996a: hydrology, Thomas 1999: forest productivity, van der Hout 1999: reduced impact logging, Zagt 1997: tree demography). The study presented in this thesis forms an integral part of the PGE. Other studies within the PGE are: plant population biology (Rose 2000), plant ecophysiology (Houter *in prep*) and plant-animal relations (Hammond *in prep*). The set-up of the Pibiri Gap Experiment is summarized below, but additional information can be found in a Tropenbos-Guyana Interim report (van Dam *et al.* 1999).

Research area

The study as presented in this thesis was carried out in three study areas, which were located within the Demerara Timbers Ltd. forest concession, approximately 250 km south of the capital

Georgetown (Figure 2.1). The main research activities took place in the Tropenbos Pibiri reserve, located 50 km South of the Mabura Hill township (5°17'N, 58°42'W). The PGE took place in this reserve (5°02'N, 58°38'W) and the study area was located between the study areas of van der Hout (1999) and Ek (1997). The area contained 200 ha of undisturbed mixed Greenheart forest (*Chlorocardium rodiei*) on one soil type and an almost flat topography. Furthermore, the area had the logistical advantages of the Pibiri field camp of previous researches. The second study area was located in the Forest Reserve Mabura Hill (FRMH), which was located at 15 km south of Mabura (5°09'N, 58°42'W). The research activities in the FRMH area took place in two experimental gaps, where previous research on nutrient cycling had taken place (Brouwer 1996). A third study area called 2K, was located at 3 km south of Mabura Hill (5°16'N, 58°42'W). At 2K, two logging gaps were selected with known age and their original size (Ek 1997).

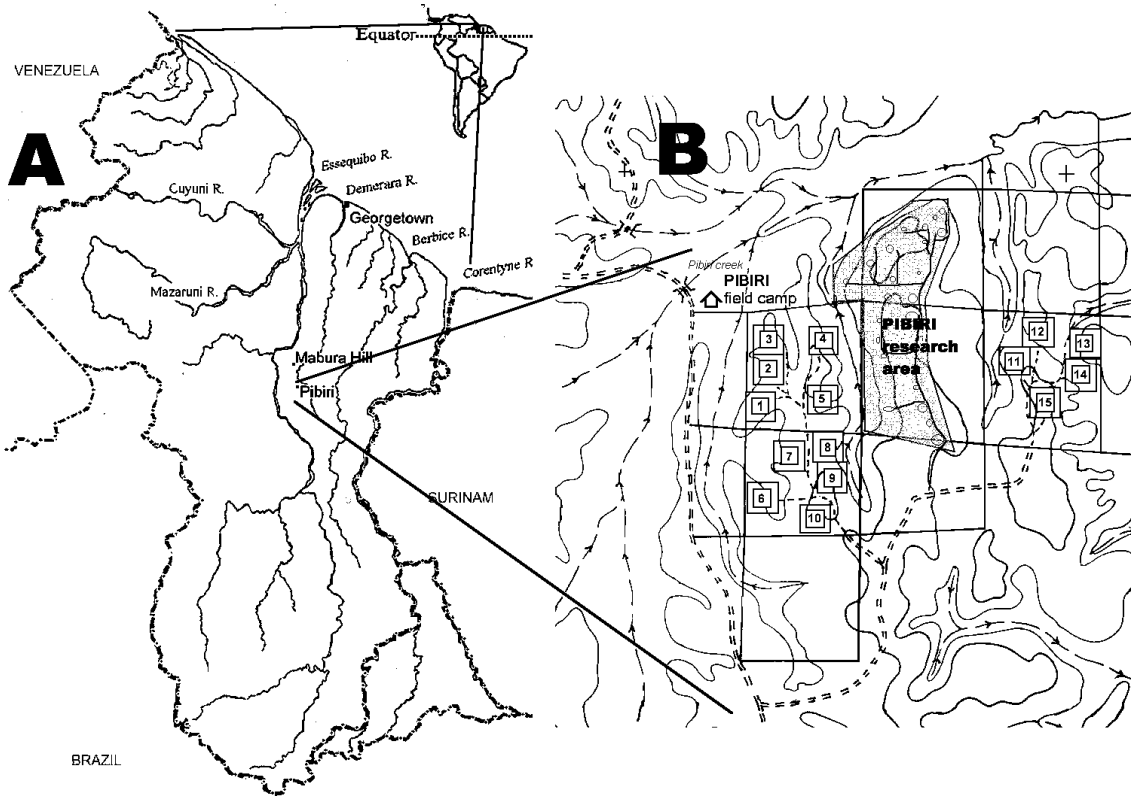


Figure 2.1 Location of the research area in Guyana (A) and in the Pibiri research site (B). Numbers in map B refer to the research sites of van der Hout (1999) & Ek (1997).

PGE methodology: selection of gap sizes and gap definition

The effect of gap size on the regeneration potential of selected tree species was addressed in an experimental set-up in which a gradient of gap sizes was created in undisturbed mixed Greenheart forest. Gap size ranged from small single tree fall gaps to large multiple tree fall gaps. In logging gaps, conditions are very variable due to remaining trees and saplings, localised skidder operation and crown zones of the felled trees, tree stems and stumps. Since the number of gaps that could be created was limited, it was decided to create a situation in which variability in growth conditions and species composition between gaps was reduced as much as possible except for the gap size variable. The selection of the gap sizes for the experiment was based upon calculations of potential radiation in the centre of perfect circular gaps that were surrounding by trees of 30m height. For these calculations, a simplified above-canopy solar

projection at the equinox was used, with standard solar equations (Kreith and Kreider, 1975; Gates, 1980 see also Chapter 4). The variation in radiation showed a sigmoidal relation with a logarithmic change in canopy gap size (Figure 2.2). The largest increase in radiation occurs between 50 and 5000m^2. The size of experimental gaps was selected within this range, namely 50, 100, 200, 400, 800, 1600 and 3200m^2. This logarithmic increase of gap size gave an almost linear increase of 1.8 MJ.m^{-2}.d^{-1} (or 4.3 mol.m^{-2}.d^{-1} in Photosynthetic Photon Flux Density PPFD units) in the centre of the gaps. The range of gap sizes also covers the full range of gap sizes from natural tree fall gaps to gaps created during normal felling operations. In the initial set-up, each gap size was replicated three times. It was foreseen that this would be difficult to achieve in practice and a continuum in sizes would be the result. However, after measuring the actual gap sizes, gaps could still be grouped together within a certain range.

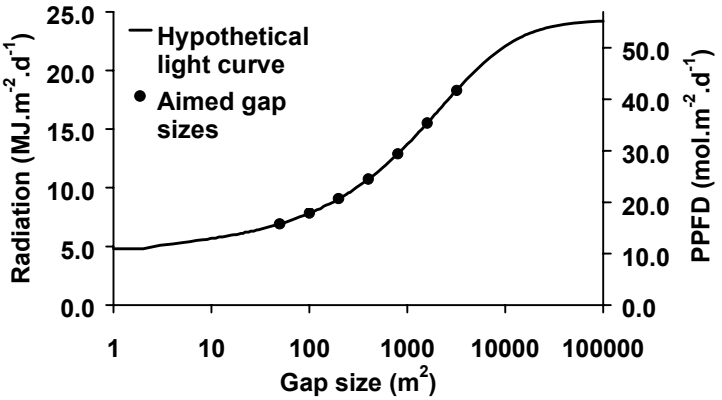


Figure 2.2 Hypothetical light curve in increasing circular gaps (potential radiation on 1 April at 5°latitude and 50m altitude).

Gap definitions

In an undisturbed forest, falling trees or branches create gaps in the canopy. The occurrence and size of these natural gaps is referred to as gap dynamics. As was explained in the previous chapter, these gaps trigger the regeneration of the forest (Bazzaz 1991, Brokaw 1985b, Brown 1990, Pickett 1983). A widely tested hypothesis states that different tree species partition different light climates and thus occur in different sized gaps (Denslow 1987, Poulson and Platt 1989). This hypothesis assumes that climax species perform better in the low light environment of small gaps (approximately < 100m^2) and pioneer species have the highest grow rate in large gaps (approximately > 250m^2). Recent studies however did not find a correlation between gap size and species dominance, but suggest that regeneration is a stochastic process and that the simple presence of a species at the time of gap creation (Hubbell *et al.* 1999) or the height of the seedlings and saplings (Rose 2000) is more important. Knowledge about the variation of the amount and size of naturally created gaps is needed, when the effects of loggings are to be assessed. Unfortunately, 'a gap' is not clearly defined and consequently, many definitions can be found in literature (Table 2.1). In most studies however, the definition by Brokaw (1982a) is applied.

A slightly adapted gap definition of Brokaw (1982a) has been used in this study (see also van Dam and Rose 1997; van Dam *et al*. 1999):

> A gap is a hole in the canopy extending through the layer of the crowns of the trees that form the canopy. A gap is not limited by a minimum area, but for practical reasons canopy openings smaller than 5m^2 are within the natural variation of a closed canopy and are not considered a gap. A gap is not limited by maximum seedling height, but it is assumed that when the crowns of the trees within the original canopy opening reach a height by which they are becoming part of the main canopy layer, the gap is closed.

Table 2.1 Definitions of a 'Gap'.

Reference	Definition	Addition constraints
Oldeman 1978	"Chablis": the fallen tree and the resulting destruction.	
Runkle 1981	Canopy gap expanded to the bases of the canopy trees surrounding the gap.	
Brokaw 1982a	Hole in the forest extending through all levels	Maximum average height vegetation in gap 2m.
Brandani *et el.* 1988	Perpendicular projection of opening or disturbance.	Including zone where tree crown fell, even if this zone lies under closed canopy.
Popma *et al.* 1988	Projected canopy opening: *sensu* Brokaw 1982a	Total gap effected area: projected canopy opening including the area with young pioneer over 0.5m.

In the gap definition a of this study, the height constraint of the vegetation in the gap (2m) by Brokaw (1982a) was dropped. Changes in edaphic conditions after gap creation can continue to occur for several years (Brouwer, 1996; Jetten, 1994a). Since the purpose of the study was to measure the effects of gap formation on edaphic conditions, it was important to ensure that the changes in edaphic conditions that were measured in a newly created gap were not a result of older gaps that were already present before the creation of the experimental gaps. Regenerating saplings in gaps easily attain heights over two meters in one or two years and, according to the definition of Brokaw (1982a), there would have been no more gap. Therefore, this definition was adjusted.

PGE gap creation

Prior to gap creation, the future location of the experimental gaps was determined thereby restricting the future gaps to one soil type (section 2.2.2) and not in the vicinity of natural tree fall gaps (section 2.2.4). A total of 22 gaps were created between 18 June and 4 July 1996. Trees were felled using directional felling techniques (see van der Hout 1996). This enables most trees to be felled in a pre-determined direction. Felling started from the smallest gap size moving up to the larger ones. To obtain circular gaps, trees on the edge of the gaps were felled towards the gap centre, thus creating a large pile of crown debris in the gap centre. Felled trees were identified and the diameter at breast height recorded. Gap sizes were measured according to the Octangular Gap Size and the Contour Gap Size methods (Appendix 2.1). The smallest gap measured 40m^2 and the largest gap 3200m^2 (Figure 2.3). An overview of the basic data per gap is given in Appendix 2.2 and a detailed map of PGE study area is shown in Appendix 2.3. Hemispherical photographs were taken in the centre of the gaps and canopy openness[1] was calculated with the program WINPHOT 5.0 (ter Steege 1997). The smallest gap had a canopy openness of 5.01% and the largest gap of 41.31%.

Gap preparation

An important part of the PGE studied the demography (Rose 2000) and ecophysiology (Houter *in prep.*) of experimental plants. To facilitate space for the growth experiment and to exclude competition for light, nutrients and water between the experimental seedlings and plants that survived the logging operation, all established seedlings, saplings and sprouts were killed. In the centre of the gaps, every felled tree-stem and crown was removed. This was done manually for

[1] Canopy openness is defined as the openness of open sky of the gap plus the openness of the surrounding "closed canopy", compared with the total hemisphere. Gap openness is the percentage of open sky of the gap, compared with the total hemisphere (see Appendix 2.1).

all gaps up to 800m^2 and a skidder helped clear the 1600 and 3200m^2 gaps, although no skidder activities were allowed in a demarcated area of 17 by 14m in the centres of the gaps. Also, no skidding activities were allowed between the cleaned centre square and the western gap edge, so there was no soil disturbance for the soil hydrological and nutrient related measurements. In the centre of all gaps, no experimental seedlings were planted in an area of 4 by 4m, which was reserved for the measurements of this thesis. The skidder was also used to clear roads for easy access by car.

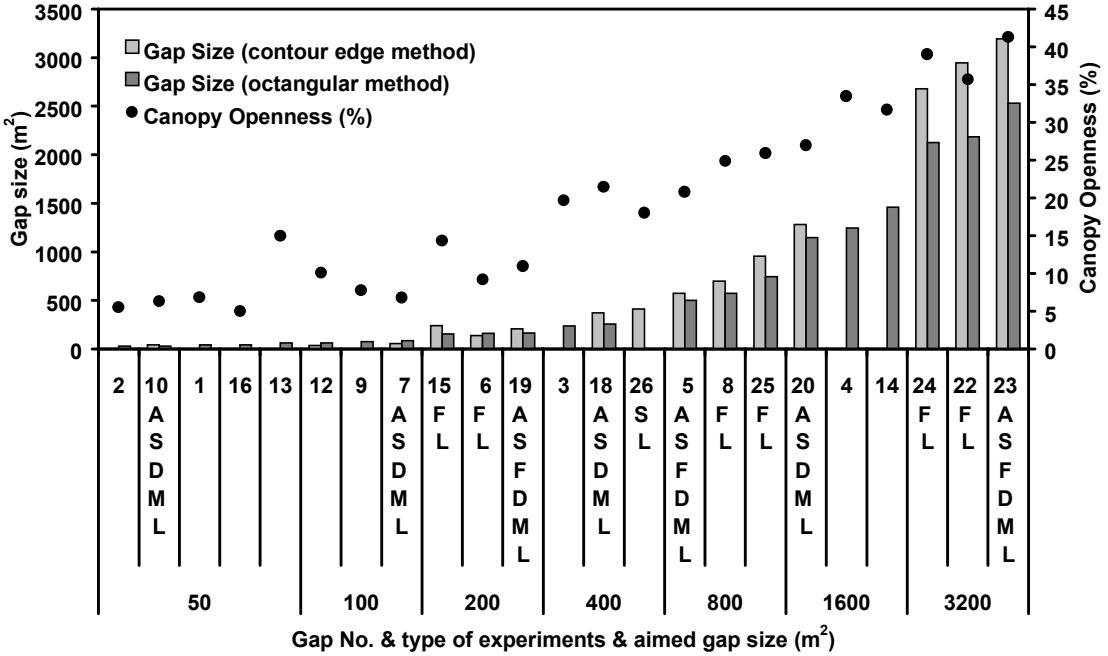


Figure 2.3 Gap size and canopy openness of the PGE experimental gaps. The letters indicate the type of experiments that were carried out in the gaps: A: microclimate, B: soil moisture, F: litterfall, D: decomposition, M: mineralisation and L: leaching. Eperimental plants were present in all gaps. (see for gap size methods Appendix 2.1 and detailed information of the gaps Appendix 2.2).

Experimental plants

After felling and clearing, eight common tree species were introduced in the centres of the gaps. These species were selected based on experiences of previous studies on their regeneration behaviour in relation to gap size and on a range of seed sizes (Rose 2000). Commercial, potentially commercial and non-commercial species were included. The following species were included: *Chlorocardium rodiei* (Schomb.) Rohwer (Greenheart), *Goupia glabra* Aubl. (Kabukalli), *Catostemma fragrans Benth* (Sand Baromalli), *Laetia procera* (Poeppig) Eichler (Warakairo), *Cecropia obtusa Trecul*. (Congo Pump), *Ormosia coccinea* (Aubl.) (Barakaro), *Pentaclethra macroloba* (Willd.) Kuntze (Trysil) and *Sclerolobium guianense* Benth. Var (Kaditiri).

Research activities in the gaps

The research as presented in this thesis was carried out in 14 of the 25 PGE gaps. Litterfall was measured in all 200, 800 and 3200m^2 gaps (200m^2: no. 6, 15 & 19, 800m^2: no. 5, 8 & 25, 3200m^2: no. 22, 23 & 24) and the other experiments were carried out in a range of gap sizes from 50 to 3200m^2 (no. 5, 7, 10, 18, 19, 20 & 23).

PHYSICAL ENVIRONMENT AND VEGETATION

Geology and geomorphology

The geological history of the study area dates back to the Precambrian, when the oldest rocks in Guyana – consisting of metamorphized schists, amphibolites, granites and sandstones (Akaiwanna and Muruwa Formation) – were formed. This "crystalline basement complex" belongs to the Guyana Shield, which extents from Colombia to French Guiana and the Amazon River. After tectonic activities, these rocks were deposited (Roraima Formation) and partly metamorphized by huge basic intrusions, later followed in Mesozoic times by minor dolorite dykes. Several tectonic uplifts, sedimentary deposits, volcanic intrusions and peneplanations took place until the Tertiary, during which ironstone was formed in the metamorphic and intrusive rocks. In Plio-Pleistocene times, the crust was subsiding and large sandy deposits were laid down known as the White Sands Formation or Berbice Formation. These sandy deposits can be traced into Surinam (Zanderij Formation) and French Guiana (Sables Blanc). A new period of uplifting and tilting of the area towards the coast removed large parts of the White Sands Formation. Many erosive streams were formed that cut through the sandy deposits, exposing the underlying crystalline rocks. (see also Jetten 1996a, ter Steege *et al.* 1996, van Kekem *et al.* 1996).

The Mabura Hill area is located on the White Sands Plateau, on the transition to the Precambrian Plateau. The parent material consists of basic, igneous dolerite and metamorphic rocks, locally with ironstone (Laterite) that are overlain by unconsolidated or alluvial sediments of the White Sands Formation, mainly (white) sands and (brown) sandy loams. The area is gently undulating, locally penetrated by Laterite-covered dolerite dykes, which forms ridges and hills. Where the white sand layer is thin, streams may have cut through, exposing the underlying brown (loamy) sand and sandy clay loams. The three study areas are all located within these brown sandy soils. The study areas are flat (0-2%), but very steep (35%) slopes usually demarcate the extent of the study site. Micro-relief is present in the form of soil mounts around up-rooted trees, elevations due to roots and buttresses and 1-1.5m high ant mounts.

Soils of the three study sites

General soil description

The soil of the study areas belongs to the Brown Sands Series (Khan et al. 1980; van Kekem et al. 1996). The soils are very deep and well drained. They have a yellowish brown to strong brown colour. The topsoil is moderately thick with a loamy sand to sandy clay loam texture. The sub-soil has a sandy loam to clayey texture. Three different soil types are distinguished in the research areas:

- *Tabela loamy sand* (Guyana soil classification); *ferralic Arenosol* (FAO)
  Excessively drained soil in upland topographic positions with a dark brown to dark greyish brown sand topsoil underlain by a yellowish or reddish-brown loose sand or very friable loamy sand subsoil (van Kekem *et al.* 1996). These soils are often found adjacent to albic Arenosols, with a very sharp boundary. Acidity is high (pH 4-4.5) and total bases and CEC are about 6 meq/100g in the topsoil and less than 2 meq/100g in the subsoil (Jetten 1996a). This soil type is present in the PGE area, where it borders albic Arenosols, and in the FRMH study area.
- *Kasarama sandy loams* (Guyana soil classification); *haplic Ferralsols* (FAO)
  Well drained soil in sediments of the Berbice Formation with a dark brown to brown sand or loamy sand topsoil overlying a strong brown or yellowish red, very friable sandy clay loam subsoil, with a higher clay content than the Tabela sand, which increases with depth (van Kekem *et al.* 1996). Where streams have cut into the loose sand, the underlying crystalline basement is exposed, usually within 5 to 10m from the top of the slope. Acidity is very high

(pH < 4) and because of the higher clay content, total bases and CEC can be between 2 and 6 meq/100 g throughout the profile (Jetten 1996a). This is the main soil type of the PGE study area.

– *Ebini sandy clay loams* (Guyana soil classification); *haplic Acrisols* (FAO)
Well drained soil in sediments of the Berbice Formation with a dark brown to brown sandy loam surface that is underlain by a strong brown to yellowish red sandy clay to clay subsoil (van Kekem *et al.* 1996). This soil type occurs in small patches in the PGE area and in the 2K study area.

Two other soil types occur in the PGE study area, namely a gleyic Arenosol and albic Arenosol, but no experiments were carried out on these soils and no further description is given here. For a general description of these soils, the reader is referred to Driesen and Dudal (1989) or more specific in the Mabura Hill area to Brouwer (1996), Jetten (1994a), Khan *et al.* (1980) or van Kekem *et al.* (1996).

Soil surveys of the study areas

In the PGE area, a soil survey was carried out from May 6 to May 17, 1996. Auger observations were made at 100m intervals on N-S orientated lines, which were 50m apart. Soil colour, soil texture, slope and occasionally field pH were recorded. Transitions between brown sand and white sand were easy to identify and some extra observations were made to determine the exact borders. The resulting soil map of the PGE area is given in Appendix 2.4. Two soil profile descriptions were made in the PGE area and one in the 2K area (van Dam 1998, Appendix 2.5). Soil profile descriptions of the FRMH area were used of Brouwer (1996) and Jetten (1994a). The soils in the three study areas have different chemical properties (Table 2.2). The 2K soil is the most fertile one, but also has the highest content of toxic Al. Soil physical properties are comparable, although the 2K soil has the highest available water content (AWC) (Table 2.3).

Table 2.2 Soil chemical properties ($mg.kg^{-1}$) per study area (values between brackets in $t.ha^{-1}$).

Location	Soil type	N	Al	Ca	K	Mg	Na	P	Mn	Fe
PGE	Haplic Ferralsol	783	4980	50.7	166.6	17.7				
		(10.9)	(69.2)	(0.7)	(2.3)	(0.2)				
FRMH(1)	Ferralic Arenosol	443	14667	21.9	77.1	58.6	24.9	63	5	4233
		(6.4)	(213)	(0.3)	(1.1)	(0.8)	(0.4)	(0.9)	(0.1)	(61.4)
2K	Haplic Acrisol	1508	73810	36	72.6	178.9	42.9	266	130.6	26080
		(21.7)	(1063)	(0.5)	(1.0)	(2.6)	(0.6)	(3.8)	(1.9)	(376)

Note (1): Source Brouwer 1996.

Table 2.3 Soil physical properties per study area.

Location	Bulk density $kg.dm^{-3}$	Porosity %	Stones %	Sand %	Silt %	Clay %	Texture USDA	AWC(1) (0-20cm) %	Root mass (0-20cm) $t.ha^{-1}$
PGE	1.39	41.5	0.3	83.0	2.1	14.5	SL	15.5	31.7
FRMH(2)	1.45	57.6		66.5	14.2	19.4	SL		28.6
2K	1.44	45.2	3.2	72.1	5.1	19.6	SL	41.8	46.0

Note (1): AWC: Available water content = θ pF2.0 – θ pF4.2;
Note (2): Topsoil 0-20cm, Source: Jetten 1996a.

Roots in forest and gaps

Roots are concentrated in the top 20cm of the soil (Brouwer 1996, Klinge and Herrera 1978, Prinssen and Straatsma 1992), where they compete with each other for the scarce nutrients in

the poor soils of the study area. This so called 'root mat' serves as a nutrient conserving mechanism (Jordan and Herrera 1981), since nutrients are extracted from the soil solution, either by the roots themselves or through mycorrhiza associations, which prevents nutrient loss. Nutrients that flush past this root mat into deeper soil layers are likely to be lost from the forest ecosystem. In the soils of the study area, more than 70% of the root content in the top 100cm is located in the top 20cm of the soil (Figure 2.4A: Prinssen and Straatsma 1992) and only 10% of the root content is located below 1m depth (Figure 2.4B: Eernisse 1993). Approximately 50% of the roots were located in the top 20cm in the soil of the PGE study area, but this could also be a result of the limited amount of replicates (n=2) compared to the root study in the FRMH area (n=14).

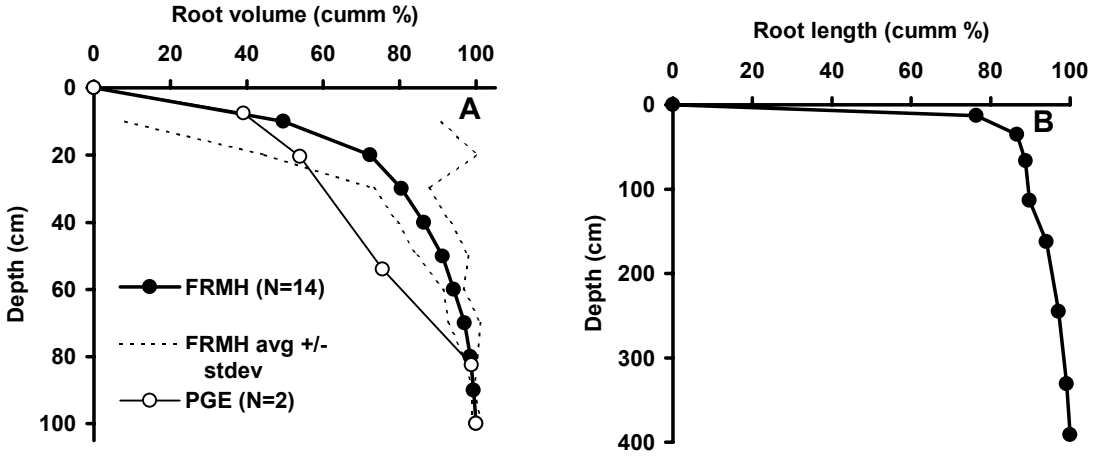


Figure 2.4 Relative cumulative root content in the Brown Sand soils of the study area. A) Measured as root volume ($g.dm^{-3}$), FRMH data from Prinssen & Straatsma (1992). B) Measured as root length ($cm.dm^{-3}$), after Eernisse (1993).

Simple quantities of roots, either in root weight or root length per soil volume or soil dry weight, would not give adequate information on the amount of roots involved in the extraction of water or nutrients or de amount of roots available for decomposition. A distinction must be made between dead and living roots (Table 2.4). Although the total root content in the FRMH area was 18% higher than in the PGE and 2K areas, the living small root content at FRMH, responsible for most of the nutrient extraction, was almost equal the living root content at 2K. The PGE soil had fewer living small roots, but more dead roots.

Table 2.4 Content of living and dead roots[2] ($t.ha^{-1}$) per study area in the top 20cm of the soil.

Location	no.	Living	σ	Large living	σ	Dead	σ	Large dead	σ	Total	σ
2K	9	34.0	9.73	3.8	8.29	2.2	1.28	0.0	0.00	40.0	9.85
FRMH	10	34.3	6.90	11.8	18.41	1.5	1.03	0.0	0.00	47.7	22.44
PGE	27	25.4	9.90	9.4	21.11	2.6	2.90	1.9	5.90	39.3	24.44

Large roots: diameter > 1cm.

[2] Soil samples were taken with a 20cm long metal tube with a diameter of 5cm. Roots were separated from the soil by washing the soil sample over a fine sieve. The distinction between dead and living roots was based upon criteria like brittleness, discolouration and signs of decompsition. After sorting, the roots were over-dried (48 hours at 70° C) and weighed.

There are large differences between undisturbed forest and gaps in the total amount of living and dead roots, both in initial content as in root growth[3] (Figure 2.5). The living root content in the PGE undisturbed forest was 88.4% (13.9%) of the total root content, while at 2 years after gap creation in the 3200m^2 gap, the living root content was only 20.3% (12.4%) of the total root content. Despite the large difference in initial living and dead root content between the forest and the gap, there were no significant differences (Mann-Whitney test, $p<0.05$) in root growth between the sites for each harvest.

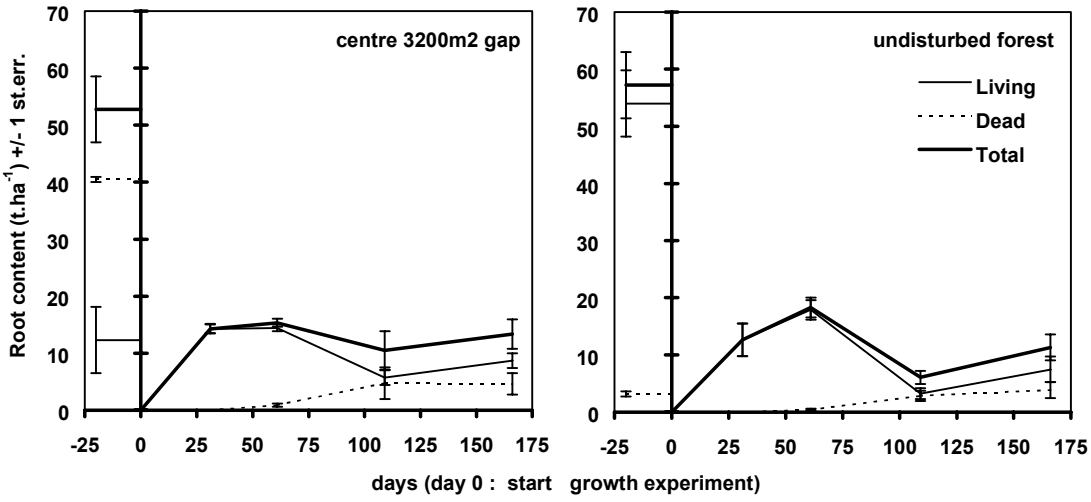


Figure 2.5 Root growth in the centre of a 3200m^2 gap and in the undisturbed forest in the top 20cm of the soil.

Vegetation and gap dynamics

Large parts of the forests in Guyana are dominated by one or a few tree species (Davis & Richards 1934, Fanshaw 1952, ter Steege *et al.* 1993). Most of these clearly identifiable forest patches are usually associated with particular soil types or soil conditions. In the study area *Chlorocardium rodiei* (Greenheart), *Lecythis confertiflora* (Wirimiri Kakaralli) and *Catostemma fragrans* (Sand Baromalli) are the dominant tree species. *Mora gonggrijpii* (Morabukea), *Carapa guianensis* (Crabwood), *Licania spp.* and *Swartzia leiocalycina* (Wamara) occur as co-dominants. *Paypayrola longifolia*, *Oxandra asbeckii* and *Tapura guianensis* are the most common understory species whilst *Peltogyne venosa* and *Hymenaea courbaril* are amongst the most common emergents (van der Hout 1996, 1999).

The forest type in the FRMH research area was classified as mixed Greenheart forest on well drained soils according to the classification given by ter Steege (1993). In this forest, *Chlorocardium rodiei* (Greenheart), *Eschweilera sagotiana* (Black Kakeralli) and other Lecythidaceae, and *Dicymbe altsonii* (Clump Wallaba) are dominant tree species. No forest inventory was made of the 2K study area, but the forest can also be classified as mixed Greenheart forest on well drained soils, although locally, poorly drained soils are present due to the higher clay content of the soil (pers. obs.).

[3] Root growth was determined in 20cm deep and 5cm wide holes, that were filled with sand from which all roots had been removed. Location of the holes were tagged in the field to ensure the sampling of the exact location during harvest.

Gap dynamics: natural tree fall gaps in the PGE study area
The locations of the experimental gaps were not allowed to coincide with the presence of a natural gap. In natural gaps, soil conditions could prevail that reflected past changes in water and nutrient cycling and not the active ones caused by the newly formed gap. Therefore, each opening in the canopy – a gap according to the definition given above – was recorded between 6 May 6 and 14 June 1996 (van Dam & Rose 1997). During this survey, information was recorded on the cause of the gap formation; single or multiple tree fall, crown fall, branch fall and ill formed canopy. In total 560 gaps were measured with an average elliptical gap size of 90m^2 (range 5-940m^2). The study area of 82.58 ha had a total gap area of 5.21 ha, resulting in a percentage of forest in a gap phase of 6.13%. About 75% of all gaps were smaller than 100m^2, with the highest frequency between 25 and 50m^2 (Figure 2.6). Branch fall and crown fall produced gaps of approximately the same size, although there were only 4 recordings of branch fall. Multiple tree fall gaps had the largest occurrence and were on average twice as large as single tree fall gaps (van Dam & Rose 1997).

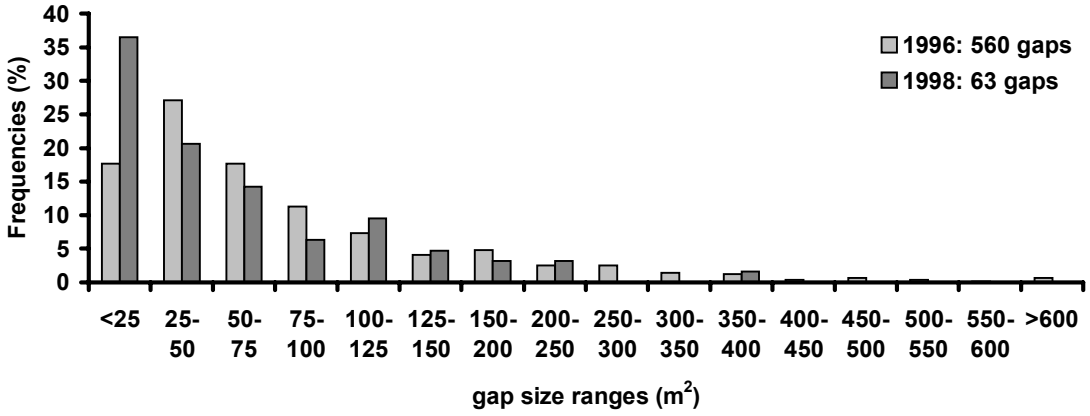


Figure 2.6 Natural tree fall gaps in the whole PGE study area (82.6 ha) in 1996 and in the PGE reference area (6.0 ha) in 1998. Note that only in 1996 were gaps recorded above 400m^2.

In general, 1 – 2% of a tropical rain forest canopy is opened by gaps per year (Hartshorn 1990). To study the gap dynamics of the PGE area in more detail, the natural gaps in the PGE reference area (see map Appendix 2.2) were remeasured from 4 to 7 August 1998. During this survey, 63 gaps were found with an average gap size of 65m^2 (range 5-370m^2). The study area was 6.00 ha with a total gap area of 0.09 ha (1.42%). About 78% of all gaps were smaller than 100m^2, with the highest frequency below 25m^2 (Figure 2.6). In 1996, this same area had only 36 gaps with a total gap area of 0.19 ha (average gap size 50m^2, range 5-200m^2). A canopy closure rate of 0.05 ha.yr^{-1} is highly unlikely, especially since almost twice as many gaps were recorded in 1998 than in 1996. It is more likely that these results reflect the subjectivity of the two different research groups of 1996 and 1998 in determining the perpendicular projection of the gap edge. No unambiguous conclusions can be drawn from the results of these surveys.

CLIMATE AND EL NIÑO

According to Köppen's classification, most parts of Guyana can be classified as tropical rain forest (Af), with a mean temperature throughout the year of more than 18°C and continuous rainfall with no month having less than 60mm. The seasonal changes in the climate of Guyana is characterised by the north-south movement of the Inter Tropical Convergence Zone (ITCZ)

(Nieuwolt 1977). A long wet season occurs from May to August and a short wet season from December to February. Two dryer seasons occur from March to April and September to November, the latter being the driest (Jetten 1996a). The total annual rainfall in Mabura ranges between 2500 and 3400mm and the daily average temperature is approximately 25°C. The Penman potential evaporation ranges between 1350 to 1500mm (Jetten 1996a).

The Pibiri climate station 1996 – 2000

From April 1996 to April 2000, meteorological measurements were made in the Pibiri field camp and in the PGE research area, either by hand or with a fully automated weather station. The PGE climate station consisted of an automated, solar powered, Campbell CR10X data logger with a Vaisala temperature/humidity probe (installation height 10m, one measurement per hour), a Campbell cup anemometer (installation height 10m, hourly average of 4 sec interval measurements), a Druck air pressure device (installation height 2m, one measurement per hour), a Kipp pyranometer (300-3000 □m, installation height 10m, hourly average of 4 sec interval measurements) and a Campbell AAR10 tipping bucket (0.2mm per tip, installation height 1m) (see van Dam 1999). The climate station was located in a 3200m^2 gap, which was surrounded by trees of on average 28m.

Radiation & cloudiness

Global radiation varied during the year with a noticeable peak in September and a less clear peak in April (Table 2.6 of Appendix 2.6). In 1997, the yearly daily average radiation was 14.48 MJ.m^{-2}.d^{-1} and in 1998 13.99 MJ.m^{-2}.d^{-1}. At 5° latitude there was little variation in sunrise (5:30-6:00h) and sunset (18:00-18:30h). The maximum incoming radiation was around 13h (Figure 2.7) and could be as high as 1037 W.m^{-2}, while the lowest recorded radiation at 13h was 63 W.m^{-2}. The cloud factor, defined here as the actual radiation divided by the potential radiation, was 65.5% in 1997 and 64.6% in 1996. This is much higher than the 30 to 40% transmissivity levels as measured by Jetten (1994a), but well within the range of 50 to 80% as reported by ter Steege and Persaud (1991). The daily fluctuation of the cloudiness showed two distinct peaks, one in the morning around 7 am due to night fog and one around 5 pm due to afternoon rain showers (Figure 2.7).

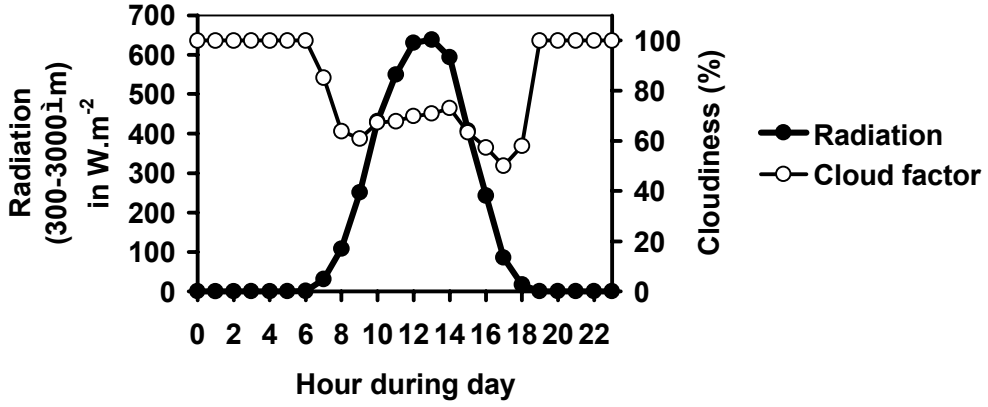


Figure 2.7 Daily average fluctuation of radiation and cloud factor (= actual radiation / potential radiation) in 1996 – 1999 at the Pibiri climate station.

Temperature and humidity

The highest mean monthly air temperature occurred in October (27°C) and a weak second peak was observed in March, while the lowest mean monthly temperature was found in January (24.5°C). The highest observed air temperature was 36.0°C (30 Sep '96, 3 pm) and the lowest

temperature was 19.1°C (several days at 4 am). The daily course of air temperature and humidity is shown in Figure 2.8 and the monthly average of air temperature and humidity are given in Table 2.7 and Table 2.8 of Appendix 2.6. In September and October 1997 and February and March 1998, during the ENSO event, temperature was higher and humidity was lower than normal. The annual average temperature in 1997 was 25.5°C and in 1998 26.3°C. The annual average relative humidity in 1997 was 87.7% and in 1998 89.4%. At night, air temperature dropped to 22-23°C and relative humidity fluctuated between 97 to 100%. In 1997, the lowest relative humidity during mid-day was 38.9% and in 1998 read 40.5%.

Air pressure and wind

Air pressure was between 1000 and 1008 mbar and on average 1004.6 mbar. Air pressure showed little variation during the research period and there was no noticeable yearly fluctuation. Usually, the air pressure dropped 2-3 mbar during the day due to rainstorms at the end of the day. In the research area, wind was strongly correlated with approaching rainstorms. Heavy gusts of wind were noticed just minutes before the onset of rain. The PGE climate station did not record these strong winds, but measured only hourly average wind speed. The highest recorded average hourly wind speed was 1.21 $m.s^{-1}$, but often no wind was recorded at all. During the research period, the average wind speed was 0.22 $m.s^{-1}$. Monthly average wind speed is presented in Table 2.9 of Appendix 2.6.

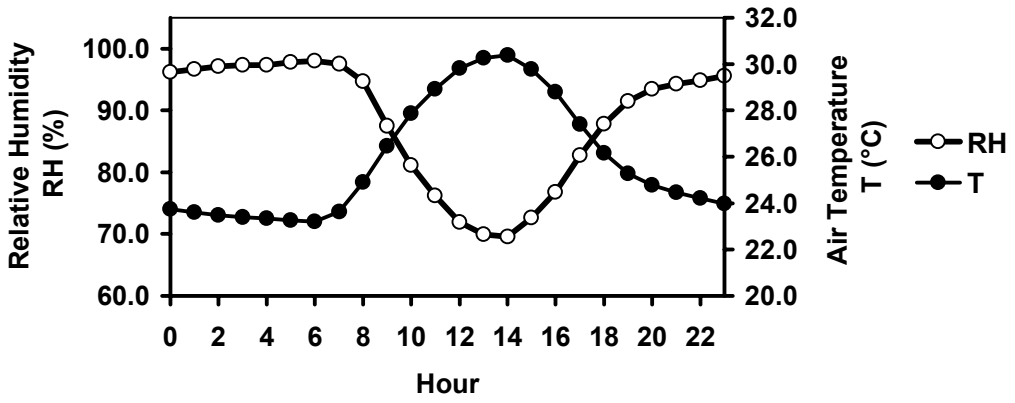


Figure 2.8 Daily course of air temperature and relative humidity in the Pibiri climate station.

Rainfall

The total annual rainfall in Mabura in 1996 – 2000 was between 2362 and 2779mm (average 2772mm, which includes incomplete year data of 1996 and 2000, see Table 2.10 of Appendix 2.6 and Figure 2.9). Due to the '97/'98 El Nino Southern Oscillation (ENSO) event, 1997 and 1998 had lower rainfall amounts of on average 88mm (excluding Nov. and Dec. 1997). The long wet season of 1996, 1998 and 1999 were wetter then the average long wet season in Georgetown.

During the '97/'98 ENSO, which lasted from June 1997 to March 1998, rainfall was on average 27% lower than the 9-years-average as measured at Great Falls (Table 2.10 of Appendix 2.6), but compared to the Georgetown record, only the dry period in 1998 was much drier (Table 2.5). The largest amount of rainfall ever recorded in the region was 601mm in August 1999. Rainfall intensity ranged from 0.2 $mm.min^{-1}$, which accounts for 67% of the measured rainfall intensities, to 4.2 $mm.min^{-1}$. The highest amount of rainfall in one hour was 20.1mm and in one day more than 170mm (measured in April 1996).

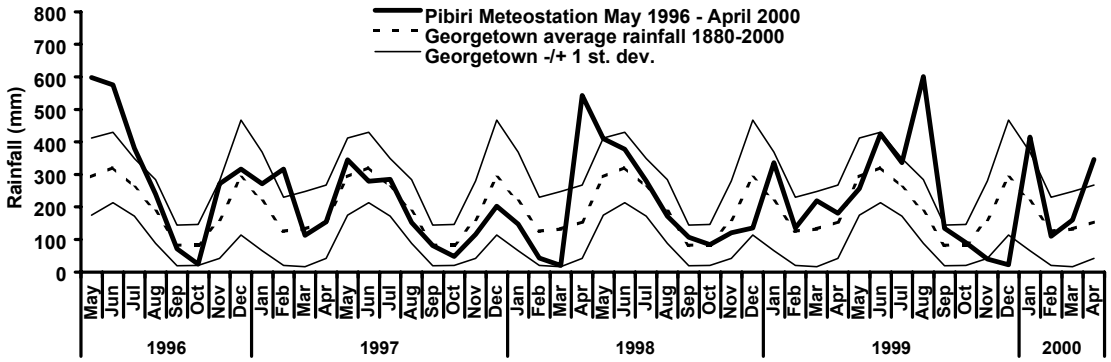


Figure 2.9 Rainfall in Pibiri (1996-2000) and average monthly rainfall in Georgetown (1880-2000, source HYDROMET, Ministry of Agriculture, station 06858104 Botanical Gardens, Georgetown, Guyana).

The El Niño event of 1997 – 1998

Peruvian fishermen have known about the El Niño or "the Christ Child" for centuries and it referred to the occacional occurance of large amounts of fish around Christmas. They also noted that the fish yield off the coast of Peru would mysteriously disappear every three to five years. Since scientist found the explanation for this phenomenon of a reduction in fish yield and the phenomenon is now known as the El Niño event, which is somewhat inconsistant with the original meaning of the event. El Niño is a warm, nutrient poor, ocean current that flows southward along the coast of northern Peru. El Niño is actually the result of a Pacific Ocean oriented cycle that lasts from three to five years. The event itself lasts about 12 to 18 months. This cycle is collectively referred to as the El Niño Southern Oscillation (ENSO), where 'El Niño' refers to the oscillation in temperature in the south eastern Pacific, and 'Southern Oscillation' refers to the "flip-flop" in pressure between the east Pacific and west Pacific. The cycle is accompanied by an oscillation in sea surface temperature (SST). The Southern Oscillation Index (SOI) is a measure of sea-level differences in atmospheric pressure between Tahiti and Darwin, Australia. Large negative values of the SOI indicate a warm event or El Niño, and large positive values indicate a cold event (also referred to as La Niña). There is no one-to-one correspondence between the occurrence of Southern Oscillation events and El Niño events, using the spatially restrictive original definition of El Niño.

In Guyana, rainfall has been recorded since 1880 and although the amount of rain in 1997 and 1998 was small, these small amounts have been recorded before (Table 2.5). During the past 120 years, 25 of El Niño events have been recorded, the worst drought occurred in 1997-1998 (Figure 2.10). Previous to this, the El Niño event in 1982-1983 was the strongest SOI and STT peaks. A typical El Niño year in Guyana starts in June-July and continues to April the following year, although some El Niño events persisted for more than one year. As can be seen in Figure 2.10, El Niño years result in rainfall less than average ($\chi^2 = 11.56$, $P = 0.0007$). Only four out of 25 showed higher rainfall than expected. In all these years the El Niño effect was negated by a warm SST in front of the coast of Guyana, which forms part of the North South Atlantic Dipole. Another phenomenon that causes a super-annual fluctuation of rainfall in coastal NE South America with a periodicity of c. 10 year (Carton 1997, Chang *et al.* 1997).

Table 2.5 Georgetown rainfall records 1880-2000: month and year average (Avg), standard deviation (St Dev), minimum (Min) and maximum (Max) rainfall (mm).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Avg	217	125	132	154	293	322	260	186	82	83	161	291	**2305**
St Dev	151	105	115	112	119	108	89	97	62	63	119	177	**477**
Min	24	12	1	8	32	131	47	16	0	0	0	34	**1268**
Max	823	526	577	542	645	822	532	655	377	348	589	1024	**3748**

Source: Min. of Agriculture, Georgetown, Guyana.

Due to the drought of the '97/'98 ENSO, fires occurred in large parts of the Rupununi savanna in southern Guyana as well as in small patches of forest (< 1 ha) near the research areas. Fortunately, no fire damage was made to the research area, but drought effects on the vegetation, like increased litterfall (see Chapter 6) and dying of small plants, were noticed. The effects of the ENSO event could have been even more dramatic if December 1997 and January 1998 had not received a 'normal' amount of rainfall.

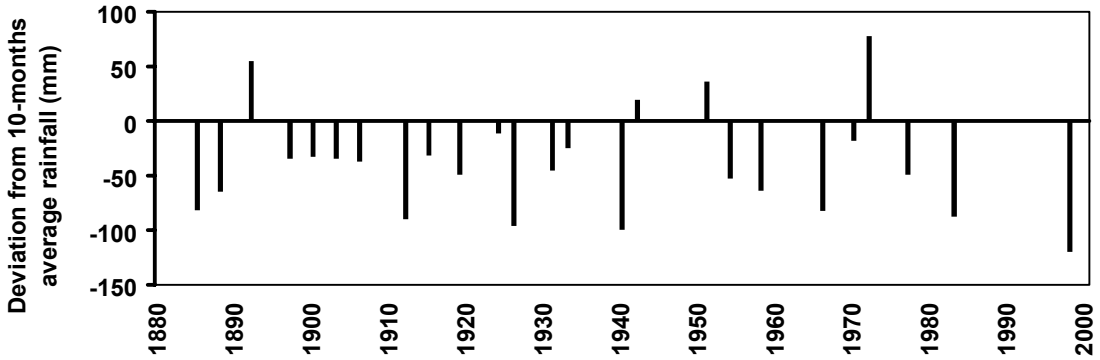


Figure 2.10 El Niño events in Georgetown in the past 120 years. The data on the y-axis displays a 10-months-moving average rainfall of a year minus the average of all 10-months-moving averages (186mm) (after Ropelewski and Halpert 1996). A negative value indicates a drier than normal year and a positive values indicates a wetter than normal year, but only the El Niño years with a low Southern Oscillation index are displayed (Ropelewski and Halpert 1996, Rasmusson and Carpenter 1983).

MICROCLIMATE AND HYDROLOGY IN FOREST AND GAPS

Spatial scales of microclimate, water cycling and logging

Microclimatic conditions and the water balance of tropical rain forests have been described at various spatial scales: single tree (Schuttleworth *et al*. 1984a & 1998b, Jetten 1996a), catchment (De Beer and Bacchus 1992, Lesack 1993, Schellekens 2000) or regional (Leopoldo *et al.* 1987). These differences in spatial scales generate a variety of approaches to field studies and water balance modelling. Water balance studies at regional scales generally work with bulk vegetation, climate and soil data and are often incorporated into a geographical information system (GIS). Catchment studies usually work with average values of the vegetation, microclimate and soil, but additional data on groundwater discharge and run-off are necessary. Single tree or forest stand studies require a detailed data set of the vegetation, microclimate at various levels inside and above the forest and a thorough analysis of the underlying soil physical parameters. Logging induces changes to the water cycle of the forest. Depending on the extent

of the logging activities, the changes in the water cycle can also be expressed at various spatial scales. At a regional scale, logging can increase the frequency and duration of flooding. Clear-felling operations accompanied by slash-and-burn practice when, at least parts, of the original forest are removed are best studied at a catchment scale (Bruijnzeel 1990, Malmer & Grip 1990). Selective logging only removes one or a few trees (10 - 20) per ha. The gaps that are created by selective logging are within a range of 10 to approximately a maximum of 5000m^2. At this scale, the effects of logging on the microclimate and the water cycle are studied at the single tree or forest stand scale. Also, changes in the water balance on a catchment scale due to selective logging cannot be noticed, due to the buffering effects of the surrounding forest and soil (Jetten 1996a). Therefore, the effects of logging gaps on the microclimate and hydrological cycle was studied at the single tree or forest stand scale. The qualitative effects of logging on the microclimate and the water balance are discussed in the coming sections.

The forest hydrological cycle in a nutshell

The forest hydrological cycle is shown in Figure 2.11, in which the left part represents the undisturbed forest and the right part a gap. Although the pathways of water in both systems are similar, the magnitudes of the fluxes are different. The emphasis of this study lies on these differences between forest and gap and the spatial variability inside a gap. The major fluxes of water can be summarized as follows (the fluxes as displayed in Figure 2.11 are given in italic).

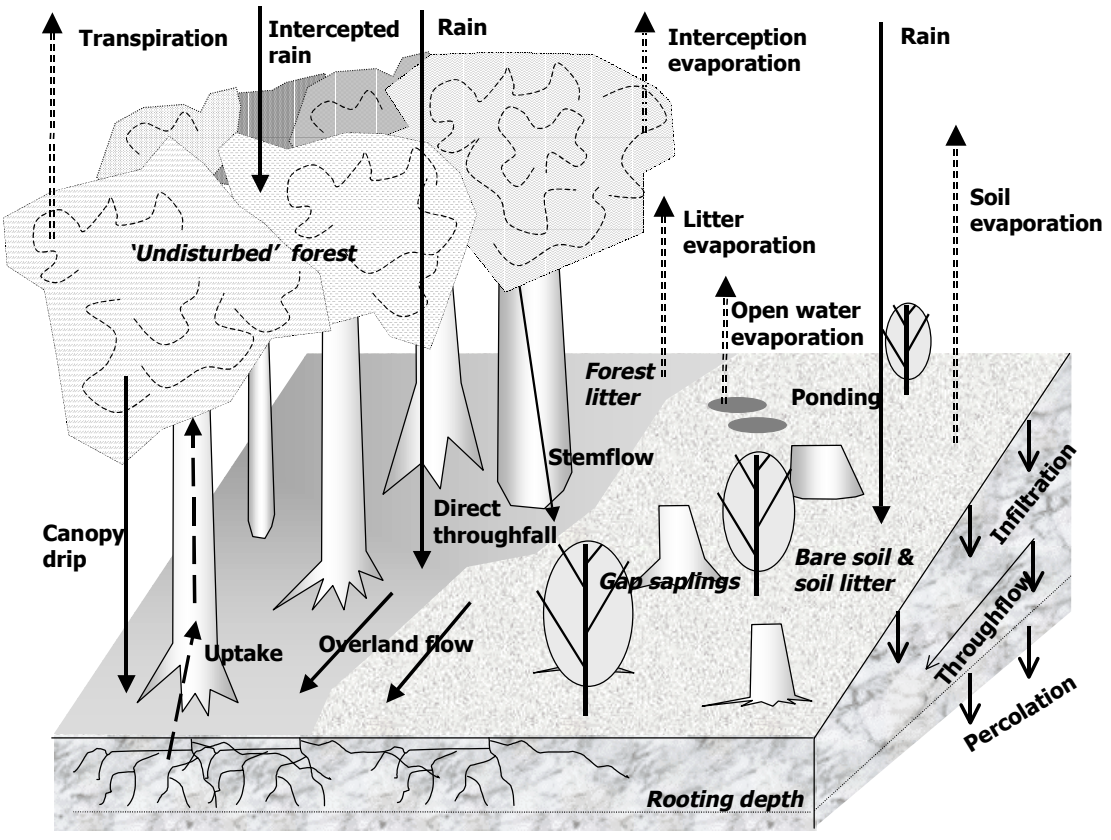


Figure 2.11 Schematic representation of the main water fluxes in a forest – gap environment.

Rain enters the forest/gap system and is intercepted by the mature canopy trees or on the smaller vegetation in the gaps (*intercepted rain*) or falls directly on the soil litter or soil (*direct throughfall*). Most intercepted water on the vegetation drips through to the soil litter (throughfall = *canopy drip* + *direct throughfall*) or drains to the soil via the stems of the trees or

saplings (*stemflow*). Water that remains behind on the leaves evaporates (*interception evaporation*). The part of the throughfall that remains behind on the soil litter also evaporates (e.g. *litter evaporation*) and the remainder infiltrates into the soil (*infiltration*). *Ponding* will occur when rainfall or throughfall intensities exceeds the infiltration rate. When the ponding capacity is exceeded and the topography of the terrain is not flat, the excess water is transported downhill to streams and creeks as *overland flow*. In flat terrain, most ponded water will form small puddles from where the water slowly drains into the unsaturated zone of the soil or evaporates (*open water evaporation*). Water in the unsaturated zone of the soil either flows through to deeper soil layers (*through flow*) or is lost from the topsoil trough direct *soil evaporation*. The vegetation extracts water from the soil through their roots (*uptake*) after which it is transpired (*transpiration*). Water leaves the forest/gap system through *percolation* below the rooting depth of the vegetation and will drain to the groundwater.

The main differences between 'undisturbed' forest and a logging gap are:
1) The interception capacity of the vegetation that influences the amount of throughfall and interception evaporation. Immediately after gap creation, the remaining vegetation in a gap, like small seedlings and saplings, defines the interception area in a gap. The interception area in a gap will be much smaller than that of the surrounding forest. In time, when the vegetation in the gap regenerates, the interception area will increase until the original interception area of the forest is reached, both in terms of the storage capacity of the individual plants and in terms of the area covered. The rate of the recovery of the interception area depends on the type of regenerating vegetation and magnitude of the disturbance (Figure 2.12).

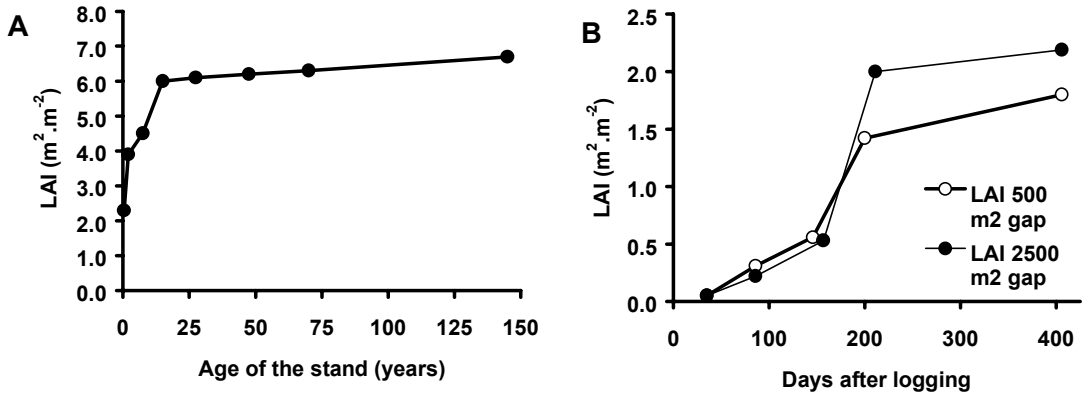


Figure 2.12 Recovery of the leaf area in A) abandoned slash-and-burn agricultural fields in Columbia (The fitted line is a logarithmic function. Source: Saldarriaga 1994) and B) natural tree fall gaps in Costa Rica (Source: Parker 1985).

2) The area of bare soil influences the amount of soil evaporation. The felling activities in the gap, e.g. skidder movements or dragging/pushing of the crown of the felled tree, removes much of the litter layer, thereby exposing the soil. Modelling the evaporation loss from bare soil in a logging gap in Guyana showed that soil evaporation loss could increase 25 times compared to the undisturbed forest (Jetten 1996a).
3) The uptake from the soil by the vegetation and successive transpiration is less in a gap than in the undisturbed forest. The mature trees of the undisturbed forest have a larger leaf area available to transpiration and a better developed root system for uptake than the smaller vegetation in the gaps. If in a gap all vegetation is removed, transpiration is even absent. Over time, the regenerating vegetation in the gap will changes the water fluxes towards the level of the undisturbed forest.

Complex edge effects can be expected at the gap edge, where the trees on the edge extract water from the gap and where an increase in growth of the vegetation in the gap edge extracts additional water.

Spatial variability of microclimate and water cycling in gaps

The spatial and temporal variations of microclimatic conditions are regulated by solar radiation and rainfall patterns. Rainfall has a highly irregular and unpredictable yearly pattern, whereas the spatial pattern of the amount of rain that is available for infiltration is determined by the interception capacity of the vegetation overhead (see section above). The spatial and temporal patterns of microclimatic conditions in a gap – excluding rainfall – are regulated by the diurnal patterns of solar radiation and the total amount of radiation that enters a gap (Figure 2.13). The direct light on a clear day that enters a gap is concentrated around mid-day in a small gap and is present almost throughout the whole day in a large gap (Figure 2.13A). In general, light input in a gap increases with increasing gap size and decreasing canopy height (Orians 1982). Also, light input in gaps decreases with time since gap formation, because of lateral growth of canopy trees adjacent to the gap (Gysel 1951, Trimble & Tyron 1966).

The location of a seedling in a gap determines the maximum amount of radiation it can receive. The incident of solar radiation (θ in Figure 2.13B) for a seedling in a gap decreases from gap centre (θ_{-c}) to gap edge (θ_{-e}) and from a large gap (θ_{l-}) to a small gap (θ_{s-}). A centrally located seedling always receives more sunlight than a peripherically located one (Orians 1982). This creates a spatial distribution of solar radiation in a gap and thus a spatial distribution of soil and air temperature, humidity and evapo(transpi)ration. In turn, the spatial gradients of evapo-(transpi)ration create spatial gradients of soil moisture distribution and thus the hydrological fluxes in the soil.

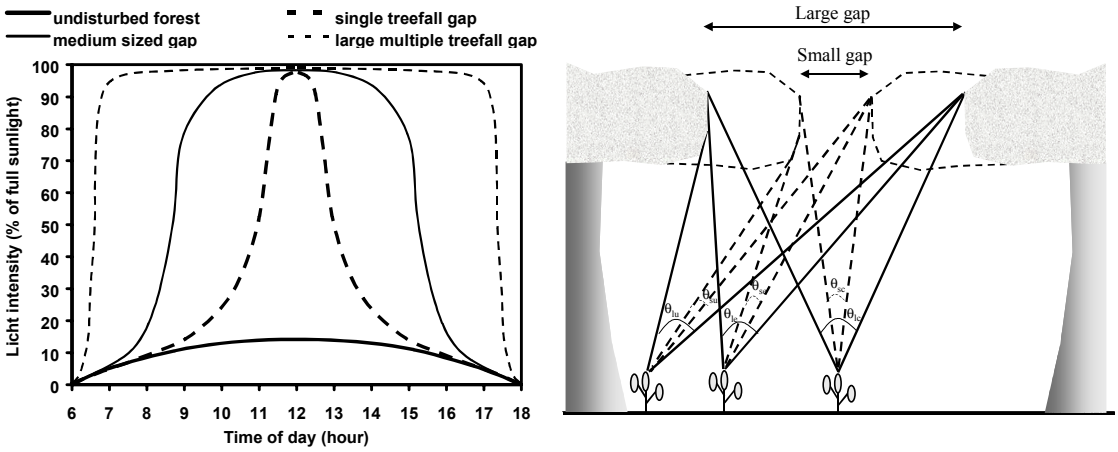


Figure 2.13 Spatial and temporal patterns of sunlight in gaps. A) Probable diurnal pattern of light intensity in undisturbed forest and three gaps of different size on a clear day. B) Direction (θ) of incident radiation in two gaps of different size and at different location in the gaps (subscripts of θ: l: large, s: small, c: centre, e: edge & u: understory) Source: Orians 1982.

Which factors influence the microclimate and water cycling?

As explained above, most microclimatic factors in a gap and the surrounding area of a gap are directly influenced by the radiation in the gap or more specific by differences in sunlight due to differences in the size and shape of the gap and it's orientation to the sun. On the other hand, the

amount of radiation in a gap is also influenced by the amount of vegetation in a gap. There is a relation between the amount of leaves and the extinction of the radiation through these leaves (Monsi & Saeki 1953 but see Chapter 4). Therefore, the vegetation in a gap also determines the amount of radiation that reaches the soil. Moreover, the amount of radiation on the soil will decrease in time, when the amount of leaves on the vegetation in the gap increases.

Beside this 'vegetation growth' – 'radiation on the soil' relation, there are other, microclimate-independent, factors that influence the microclimate and water cycling in gaps. For example, soil temperature and the amount of soil evaporation also depend on the amount of litter on the soil. Soil physical parameters, like texture, bulk density, water retention, hydraulic conductivity and infiltration capacity influence the soil moisture fluxes. Soil physical characteristics can be influenced by logging due to the activity of the skidder and the dragging of the log (Hendrison 1990, Jetten *et al*. 1993). However, the hydrological properties of the Haplic Ferralsol have a large spatial variability (Jetten 1996a), which may obscure the impact of logging. Infiltration rate, sorptivity and saturated hydraulic conductivity of the brown sands of the research area had a standard deviation which was equal to 70–110% of its mean value and at least 30% of the variance was found within 2m and more than 80% of the variance was found within 20m (Jetten 1996a). This high spatial variability may obscure the difference in water balance between gaps.

NUTRIENT CYCLING IN FOREST AND GAP

What do we want to know about the nutrient cycle?

Nutrient cycling in ecosystems is extremely complex. Some chemical components cycle predominantly between living organisms and the atmosphere, while others cycle only between living organisms and the soil. Some chemicals follow both pathways. Furthermore, internal cycles within plants or animals can be recognised. Based on these differences, Kimmins (1997) recognized three mayor chemical cycles: 1) the geochemical cycle, in which exchanges of chemicals occur between ecosystems, 2) biogeochemical cycles, in which exchanges of chemicals are present within ecosystems and 3) biochemical or internal cycles, which describe the redistribution of chemicals within individual organisms (Figure 2.14).

Spatial and temporal scales

The study of the nutrient cycle in tropical rain forest ecosystem involves the study of the three cycles of Figure 2.14 or at least parts of them. Since it is impossible to study all aspects of the nutrient cycle in a tropical rain forest in one lifetime, a selection was made, which addressed the problems at hand adequately. In this study, the spatial and temporal variation of the nutrient fluxes had to act at a similar scale and rate as the expected effects of logging. The choice of the spatial and temporal scales was based on previous research on the nutrient cycle in pristine and logged forest (Brouwer 1996, Bruijnzeel 1990, Burghouts 1993, Cogdon & Herborn 1993, Cuevas & Medina 1986, Golley *et al.* 1980a & 1980b, Jordan 1985). In logging gaps at the FRMH study site, Brouwer (1996) found the bulk of the changes in nutrient leaching within 1 year after logging. These results delimited the temporal scale of months up to few years. Other fluxes in the nutrient cycle have either a highly irregular temporal pattern (e.g. rainfall) or their change is so slow that they do not contribute to the changes created by logging (e.g. weathering). The spatial scale of the nutrient cycle was limited by the same constraints as the hydrological cycle: the size of the gaps and the surrounding areas. Also, structural differences in the amount of atmospheric input are not likely to occur within these gaps and adjacent forest.

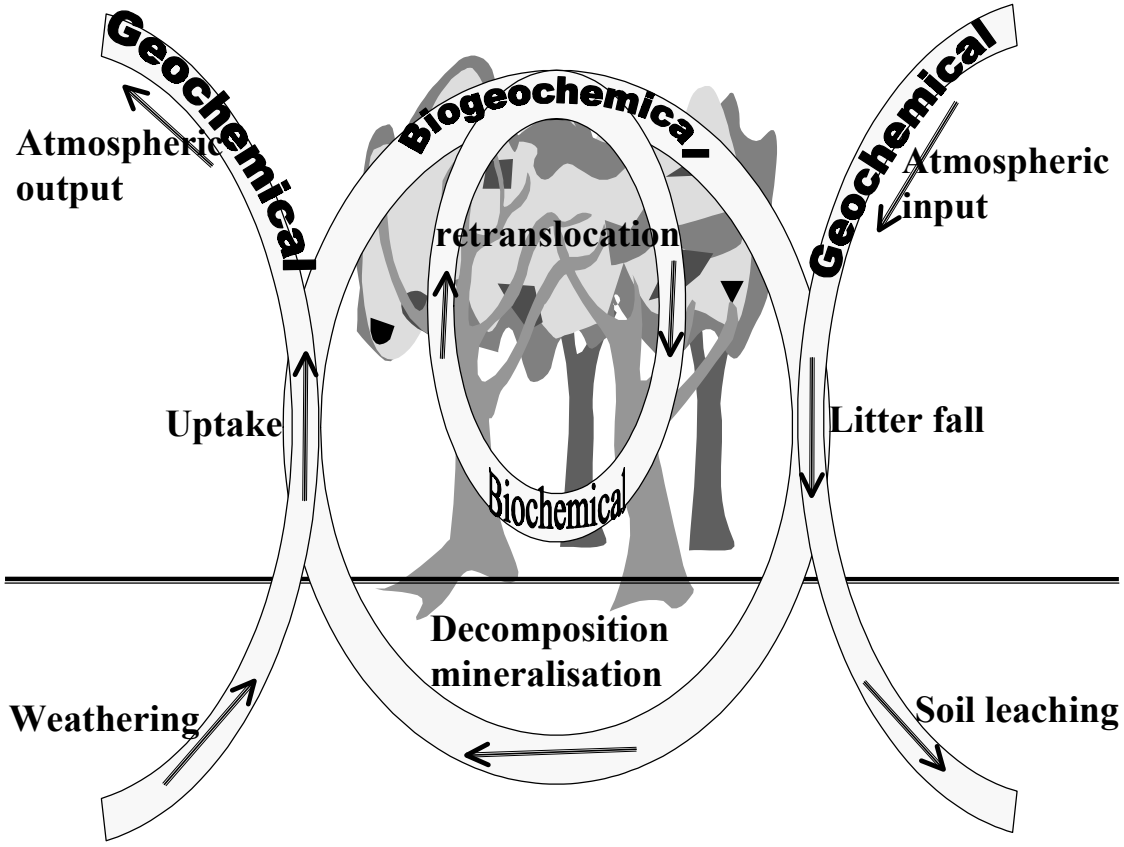


Figure 2.14 The three mayor nutrient cycles in a forest ecosystem (Source: Kimmins 1997).

The major components of the forest nutrient cycle
There are almost as many different pathways as there are nutrients to study. Although the macronutrients (N, P, K) are essential for plant performance and growth, other chemical elements, even though they may only occur as trace elements, can play an important role in the metabolism in plants (e.g. Mb in N-fixation). Likewise, there are many chemicals that are toxic for plants or special adaptations are necessary (e.g. Al). Each chemical element has it's own different cycle in soil or plants. Figure 2.15 gives an overview of the nitrogen cycle. Although some aspects of the nitrogen cycle are unique to N, the main pathways are similar for all elements. Since nitrogen is one of the major components of plant material and parts of the nitrogen cycle have been studied more intensively in this study, the nitrogen cycle is explained in more detail in the following section (with the fluxes of Figure 2.15 in italic).

The bulk of the ecosystem's external nutrients enter the forest through *atmospheric input* and only a very small amount through soil *weathering*. Some tree species have a symbiotic biological *N_2-fixation* between their leaves or roots and nitrogen-fixing bacteria. Roggy *et al.* (1999) estimated that 7.5% of the tree species in French Guiana is capable of N_2-fixation. Rainfall is enriched with nutrients if it drips through the canopy to the soil (*throughfall*), because dust particles that accumulated on the leaves of the vegetation are washed down with rainfall water and the vegetation itself excretes cetrain chemicals. Throughfall is especially enriched with K and SO_4 (> 3 times) and to a lesser extent with PO_4, Mg, Na, NH_4 and NO_3 (> 2 times) (Table 2.6).

The largest source of nutrients in the ecosystem is present in living plant tissue, either above ground or below ground in roots. The bulk of the nutrients that are added to the soil arrive in

through *litterfall*. Brouwer (1996) estimates that 11% of the aboveground biomass in mixed forest on brown sand in Guyana returns to the forest floor in one year. The bulk of the litter that falls continuously to the ground consists of leaves, flowers, seeds, fruits and small twigs or branches. Large branches, whole tree crowns or stems are another, but temporal irregular, source of nutrients. Before shedding its leaves, plants translocate chemicals from their leaves into the plant. Therefore, there is a difference in chemical composition of 'green leaves' that were attached to the crown of a felled tree and naturally shed 'brown leaves'.

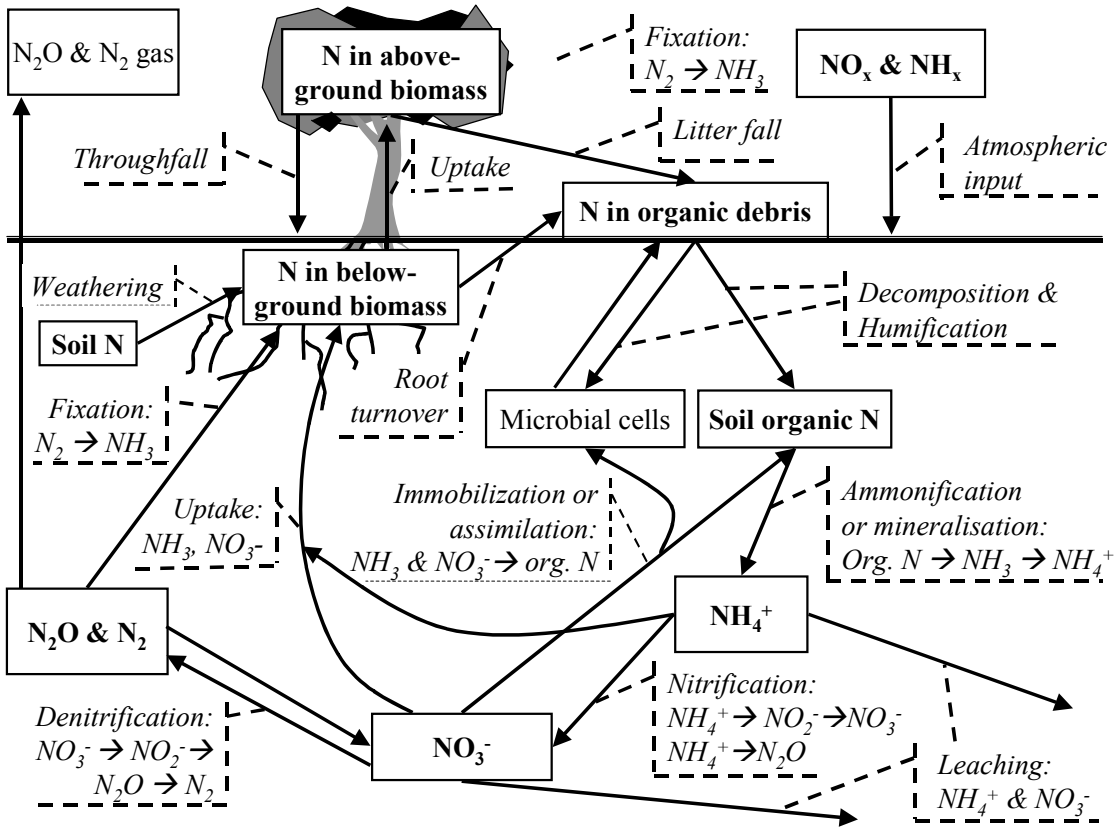


Figure 2.15 Nitrogen cycle in forest soil. Note that the arrows do not signify the importance of a process. Compiled from Nikiforoff (1938), Paul & Clark (1996) and Tietema (1992).

Table 2.6 Average electrical conductivity (□S.cm^{-1}), acidity (pH units) and concentrations of chemicals (mg.l^{-1}) in rainfall (R), throughfall (Th) and groundwater discharge to creeks (Cr) of the PGE research area (1 1996-1999) and the FRMH (2 1992-1995).

	EC	pH	NO3	NH4	PO4	K	Ca	Mg	Na	Cl	SO4	Al	Source
R	6.05	5.88	0.34	0.19	0.18	0.28	0.09	0.04	0.42	1.11	0.39	0.02	1
R	5.15	5.27	0.23	0.10	0.01	0.16	0.11	0.05	0.59	0.87	0.30	0.02	2
Th	14.09	5.65	0.42	0.34	0.19	0.93	0.18	0.19	1.11	1.63	0.74	0.04	1
Th	11.53	5.61	0.65	0.22	0.04	0.59	0.17	0.15	1.28	1.52	1.01	0.03	2
Cr	27.10	4.40	0.46	0.30	0.26	0.23	0.05	0.16	1.39	2.85	0.44	0.26	1
Cr	34.00	4.00	0.56	0.17	0.01	0.25	0.22	0.45	1.53	2.60	0.80	0.41	2

Source: 1) this study, 2) Brouwer 1996.

The difference in composition of the plant material in gaps – brown or green leaves, leaves or woody parts, species type – is of importance in the next step in the nutrient cycle: *decomposition*. The plant litter on the soil and the *dead roots* in the soil are decomposed.

Decomposition is the break-down of organic debris into finer fractions. The finest fractions are broken-down by the microbial soil community into lignin and lipids (slow conversion to soil organic matter), and carbohydrates and proteins (fast conversion to soil organic matter). Turnover rates of forest floor litter in mixed forest on brown sand in Guyana are approximately half a year (Brouwer 1996).

During the break-down of plant material, several processes act simultaneously or shortly after one another. The macromolecules of plant debris are first broken down into polymers and than into dimers and finally into monomers. Micro-organisms use these monomers for the construction of their cells. These micro-organisms are taken up into the break-down and humification processes after they die. *Humification* is the formation of the end-products of the metabolism of these micro-organisms. These end-products are difficult to break-down and are the basic constituents of humus molecules.

The monomers can also be completely mineralised. *Mineralisation* (*ammonification* and *nitrification* in the N-cycle in Figure 2.15) is the transformation of organically bound elements to inorganic elements by micro-organisms. Contrasting to mineralisation is *immobilisation*, which is the use of inorganic elements by micro-organisms for their metabolism. Furthermore, the nitrogen cycle includes *denitrification*, which is the transformation of nitrate to nitrogen gas. After decomposition and mineralisation, the inorganic elements can either be lost from the ecosystem through *leaching* or are being removed from the soil by plants or mycorrhiza (*uptake*) or used by micro-organisms in their metabolism (immobilisation). After redistribution of the nutrients in the plants, they are returned to the soil through litterfall again. For a more complete and extended overview of the nutrient cycle in tropical rain forests, the reader is referred to Brouwer (1996), Bruijnzeel (1990), Kimmins (1997), Locher en de Bakker (1990), Proctor (1987) or Vitousek & Sandford (1986).

Which factors influence the nutrient cycle in the soil?

Soil chemical characteristics and soil pH Nitrogen mineralisation is probably related to the overall soil fertility or available soil N (Lamb 1980), total soil N (Motavalli *et al.* 1995) or the C:N ratio. Jordan *et al.* (1979) studied the activity of nitrifying bacteria on laterite and sandy soils in Amazonian rain forests and found that their activity is low due to a low soil pH. They suggested that a low pH could act as an N conservation mechanism. Many enzymes in bacterial cells involved with nitrification are pH depended (Paul and Clark 1996). In tropical rain forest gaps, pH levels can drop to pH(H_2O) 3.5 in leachate water (Brouwer 1996). The precise effect of soil pH is not clear, since soil pH as explanatory variable for mineralisation is reported as negatively correlated (Marrs *et al* 1988) or not correlated (Strong *et al* 1999a).

Soil physical characteristics and soil moisture Texture, bulk density, presence and amount of micro- and macro pores and the actual soil moisture content determine the mobility of the micro-organisms involved in the mineralisation process (Clark 1990; Strong *et al*. 1999c). Higher amount of organic-N can be found in very small pores (< 0.6 μm), which act as a physical barrier against microbial attack, and in larger pores (10-30 μm), because these pores are infrequent water filled (Strong *et al.* 1999b). Water in the soil acts as a transport medium for micro-organisms. At low moisture levels, the matrix pores are not connected, which limits the free mobility of these organisms, but large soil moisture levels cause anoxic conditions that increase nitrogen immobilisation and denitrification. Cavelier *et al.* (2000) reported an increase in mineralisation with a decrease in soil moisture from field capacity (35%) to drier conditions (25%). Soil moisture and N content explain most variation in N-mineralisation and nitrification (Strong *et al.* 1999a).

Microclimate The optimal temperature for nitrification lies in the range 25 to 35°C, although for some bacteria, the optimal growth lies around 40°C (Prosser & Cox 1982). High temperatures in open areas like a large gap could limit micro bacterial activity, but these high

temperatures (over 40°C) only occurred in the top litter layer and topsoil temperatures rapidly decreased with depth (van Brunschot and de Lange 1992). No significant differences at 23°C or 35°C were present for nitrification or net mineralisation (Cavelier *et al.* 2000). Concluding, temperature in tropical rain forest is near optimal for the functioning of micro-organisms and temperature fluctuations in gaps is not likely to have a significant influence on the mineralisation process. Air humidity is more likely to affect mineralisation, since air humidity in large gaps decreases during the day to a minimum of 40%. Unfortunately, little has been reported in literature on the effects of air humidity on mineralisation.

Micro flora and fauna The presence and activity of soil micro-flora and fauna are key factors in the rate of decomposition and mineralisation. For many plants, the infections of their roots with mycorrhizas are essential in the extraction of nutrients from the soil, since these mycorrhizas associations enhance nutrient uptake, especially N and P (Alexandre 1989). Two main groups of mycorrhizas are distinguished: ecto-mycorrhizas and endo-mycorrhizas. The vesicular-arbuscular mycorrhizas, belonging to the endo-mycorrhiza group, are the most common fungi in tropical forest soils, while ecto-mycorrhizas are often found with tree species that are dominant in a forest (Alexandre 1989). The trade-off of nutrients between roots and mycorrhizas goes at a loss of photosynthate. Not much is known about the type and function of the micro-flora and fauna in tropical forest soils and differences in their behaviour in forest or gap. A bacteriological or mycological study is beyond the scope of this research.

Roots Living roots extract inorganic forms of nitrogen, while dead roots are a source of organic-N. Live roots have been known to stimulate ammonification rates, while dead roots increased extractable N (Ehrenfeld *et al*. 1997). The interrelation between microbial activity and root dynamics works both ways. Roy & Singh (1995) reported that in dry tropical forest in India, fine root development was facilitated by larger amounts of mineral-N, irrespective of the form in which N was present. On the other hand, Gower (1987) in a study in Costa Rica found no relation between fine root biomass and N availability.

How do gaps alter the nutrient cycle?

Removal or destruction of the vegetation in nutrient-deficient ecosystems will result in rapid loss of the nutrient capital, and can convert tropical forests to wet deserts (Kimmins 1997). The erosion associated with logging can considerably drain the nutrient stock of the forest (Richards 1996). Sixteen years after disturbance of soils in the Brazilian Amazon, nutrient concentrations of N, P, K and C decreased with increasing disturbance intensity, while concentrations of Ca and Mg increased (McNabb *et al.* 1997). Gaps in the forest alter the nutrient cycle by:

1) Nutrient extraction in logs. Brouwer (1996) estimated that logging removed at least 3.1 kg $N.m^{-3}$ wood, 0.04 kg $P.m^{-3}$, 0.4 kg $Ca.m^{-3}$, 0.3 kg $K.m^{-3}$ and 0.1 kg $Mg.m^{-3}$.

2) Less nutrient input due to less litterfall. Litterfall, whether it is leaf litter, flower parts, small branches or whole trees, has a limited dispersal. Obviously, the heaviest woody parts will only drop down vertically, while lighter leaves can drift several tens of meters from their source. The bulk of the litterfall at a site will come from the vegetation overhead. Removal of this vegetation therefore, immediately changes the amount of litterfall.

3) Decomposition and mineralisation rates are effected by altered microclimatic and soil moisture conditions. Decomposition and mineralisation are influenced by: 1) the resource quantity and quality, usually plant debris and dead roots; 2) the quantity of living roots; 3) the quantity of bacteria involved in the mineralisation process and their decomposition efficiency; 4) soil chemical characteristics, like N content, nutrient retention capacity and soil pH; 5) soil

physical characteristics, like texture, water retention capacity and bulk density; 6) the soil moisture content and; 7) the microclimatic conditions. Resource quantity or the amount of organic matter that is available for mineralisation depends on the amount of litter on the soil and the amount of dead roots. The forest litter layer mass is a combined function of litterfall and decomposition rates and the quality of the litter varies between plants and plant parts. The bulk of the roots in the gap were dead and were a potential source of nutrients for the regeneration vegetation in the gaps. The amount and type of bacteria are responsible for the transformation of organic matter to inorganic elements. Changes in soil chemical properties and soil physical properties can occur after gap creation as well as the moisture content of the soil. These all affect the decomposition and mineralisation of soil organic matter.

4) Nutrient loss through leaching (Brouwer and Riezebos 1998). The removal of the vegetation also kills the roots and associated mycorrhiza infections. This reduces or completely stops the extraction of nutrients from the soil solution. As a consequence, nutrients are likely to be lost from the forest ecosystem, when they have travelled past the bulk of the root mat. Brouwer (in ter Steege *et al.* 1996) estimated a 800% increase in $N\text{-}NH_4^+$ loss one year after logging.

5) Low pH levels (pH<4, Brouwer and Riezebos 1998) liberate aluminium from the soil complex, which is toxic for most plants (Alexandre 1999).

Which aspects of the nutrient cycling in gaps are studied?

The overview above clearly highlights some of the aspects of the nutrient cycle that need to be studied in order to gain insight into the major effects of gaps and gap size on the changes in fluxes of nutrients. In short, the major nutrient fluxes have been studied: litterfall (Chapter 6), decomposition (Chapter 7), N-mineralisation (Chapter 8) and leaching (Chapter 9). Plant uptake was not measured, since the experimental plants could not be harvested. During the coming years, their growth will be monitored. Values on the nutrient pools were taken from literature, as well as other fluxes from the nutrient cycle. Atmospheric input was measured regularly and the results were given in Table 2.6. It was assumed that weathering of soil minerals was negligible (*sensu* Brouwer 1996).

Appendix 2.1 Gap size, gap openness and canopy openness

Measuring gap size

There are three commonly used methods to measure gap size. The simplest one assumes an elliptical shaped gap, which is based upon the longest axis of the gap and the perpendicular axis to that longest axis. The "elliptical gap size" (EGS in m^2) is calculated with:

$$EGS = \left[(r_1 \cdot r_2 \cdot \pi) + (r_2 \cdot r_3 \cdot \pi) + (r_3 \cdot r_4 \cdot \pi) + (r_4 \cdot r_1 \cdot \pi)\right] / 4 \quad (1)$$

where r_1 to r_4 represent the distances in m of the 4 axes from the gap centre to the gap edge. The second method is the "octangular gap size" (OGS). For this method, the distances from the centre to the edge of the gap are measured in 8 compass directions (intervals of 45°). The co-ordinates of these 8 gap edge locations are calculated, assuming a co-ordinate system with the gap centre as the origin. The OGS (m^2) is calculated using:

$$OGS = \left| \sum_{i=1}^{i=n} [(x_{i+1} - x_i) \cdot (y_{i+1} + y_i)] / 2 \right| \quad (2)$$

where x_i and y_i (in m) are the co-ordinates of the edges of the gap and the last point (n+1) being equal to the first point, as they are physically actually the same (ter Steege 1997). The last method is the most laborious one, since it involves the exact mapping of the gap edge. Changes in the shape of the edge of the gap are surveyed and the points are given a co-ordinate. Equation 2 can be used again to calculate the "contour gap size" CGS (m^2).

Measuring canopy openness

Canopy openness is defined as the openness of open sky of the gap plus the openness of the surrounding "closed canopy", compared with the total hemisphere. Gap openness is here defined as the percentage of open sky of the gap, compared with the total hemisphere. For the same gap, canopy openness is larger than gap openness. Canopy openness was estimated with hemispherical photographs taken in the centre of the gaps at 1.5 m height with a Nikon/Fujix digital camera and a Sigma 8 mm fish-eye lens. Photographs were taken either in the early mornings or late in the afternoon. The colour images were split into a red, green and blue channel and the image with the highest contrast (usually the blue channel) was used for further analyses. The contrast of the image was enhanced and the images were analysed with the program WINPHOT 5.0 (ter Steege 1997).

Measuring gap openness

Gap openness was estimated in the field from inclination measurements from the centre of the gap to the top of the closed canopy at the gap edge in eight compass directions. The gap openness (%) was estimated with the equation:

$$GapOpenness = 100 - \left[\left(\sum_{i=1}^{i=8} \sin \alpha_i \right) / 8 \right] \cdot 100\% \quad (3)$$

where α_i the inclination of one compass direction. This method does not compensate for the measuring height (usually at eye-height), but this only introduces an error of approximately 3 % with an average tree height of 35 m. The results can be regarded as an estimate of the actual gap openness and a crude underestimation of canopy openness. With decreasing gap size, the error in the estimated canopy openness increases due to the increased component of the openness of the surrounding vegetation.

Appendix 2.2 Felling date, gap size and canopy openness of the experimental gaps.

Gap	Felling Date	Aimed Gap Size (m^2)	Octangular Gap Size (m^2)[1,2]	Contour Gap Size (m^2)[1,2]	Canopy Openness Winphot (%)[2,3]	Gap Openness field (%)[2]	No. of felled trees	Total Basal Area (m^2)[4]
1	18-06-96	50	40		6.86	1.9	2	0.11
2	18-06-96	50	30		5.54	1.1	3	0.09
3	18-06-96	400	240		19.71	14.0	5	0.35
4	18/19-06-96	1600	1250		33.46	22.2	33	3.57
5	19-06-96	800	500	570	20.78	25.3	6	0.75
6	19-06-96	200	160	140	9.22	4.3	9	0.31
7	20-06-96	100	90	60	6.77	8.8	2	0.15
8	20-06-96	800	580	700	24.9	22.3	13	1.15
9	21-06-96	100	80		7.78	3.0	8	0.09
10	21-06-96	50	30	40	6.34	1.4	2	0.14
12	21-06-96	100	60	40	10.11	1.7	2	0.16
13	21-06-96	50	60		14.97	1.6	4	0.11
14	21/22-06-96	1600	1460		31.66	24.4	39	2.57
15	22-06-96	200	160	240	14.35	7.6	3	0.35
16	22-06-96	50	50		5.01	2.1	2	0.09
17	24/25-06-96	400	340		19.56	11.1	11	0.81
18	24-06-96	400	260	370	21.47	10.1	5	0.33
19	24-06-96	200	170	210	10.95	5.2	28	2.63
20	25-06-96	1600	1150	1280	26.96	26.1	48	5.65
21	25-06-96	400	330		20.49	11.9	47	4.26
22	27/28-06-96	3200	2190	2950	35.70	26.4	50	4.59
23	1/2-07-1996	3200	2530	3200	41.31	35.8	12	1.44
24	3/4-07-96	3200	2130	2680	39.01	33.8	2	0.11
25	5-07-96	800	750	960	25.90	14.7	3	0.09
26	29-6-98	400		410	18.02			

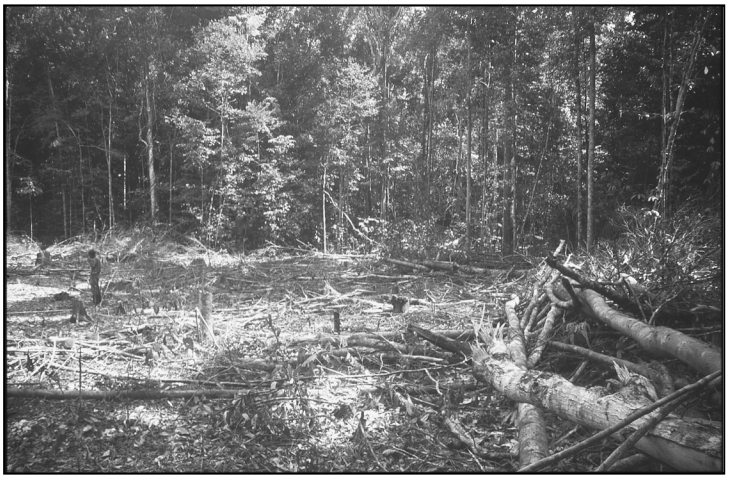
Notes

(1) Gap sizes are rounded off to the nearest $10m^2$.

(2) Octangular gap size, contour gap size, canopy openness and gap openness are explained in App. 2.1.

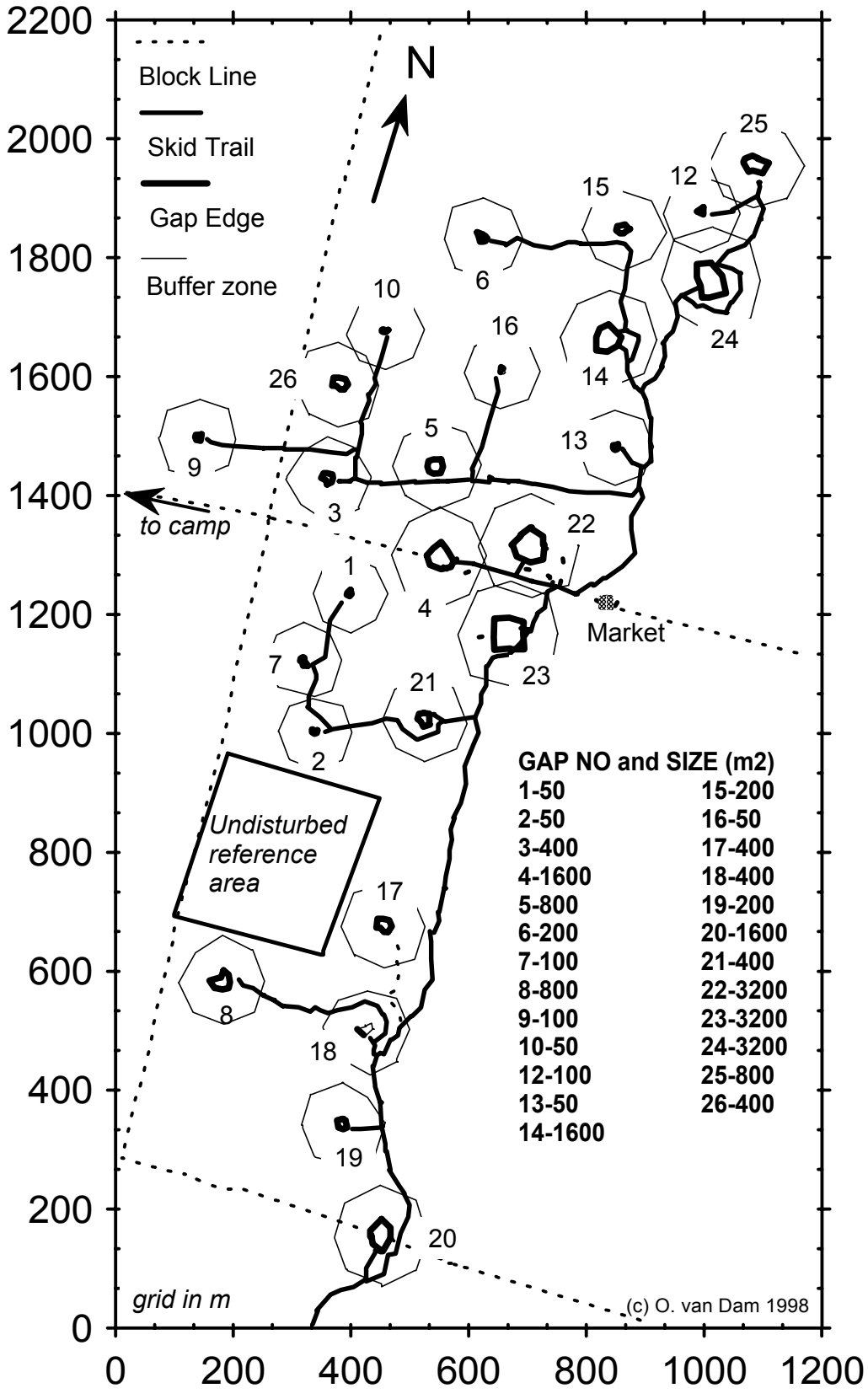
(3) Canopy openness by N. Houter.

(4) Basal area by S. Rose.

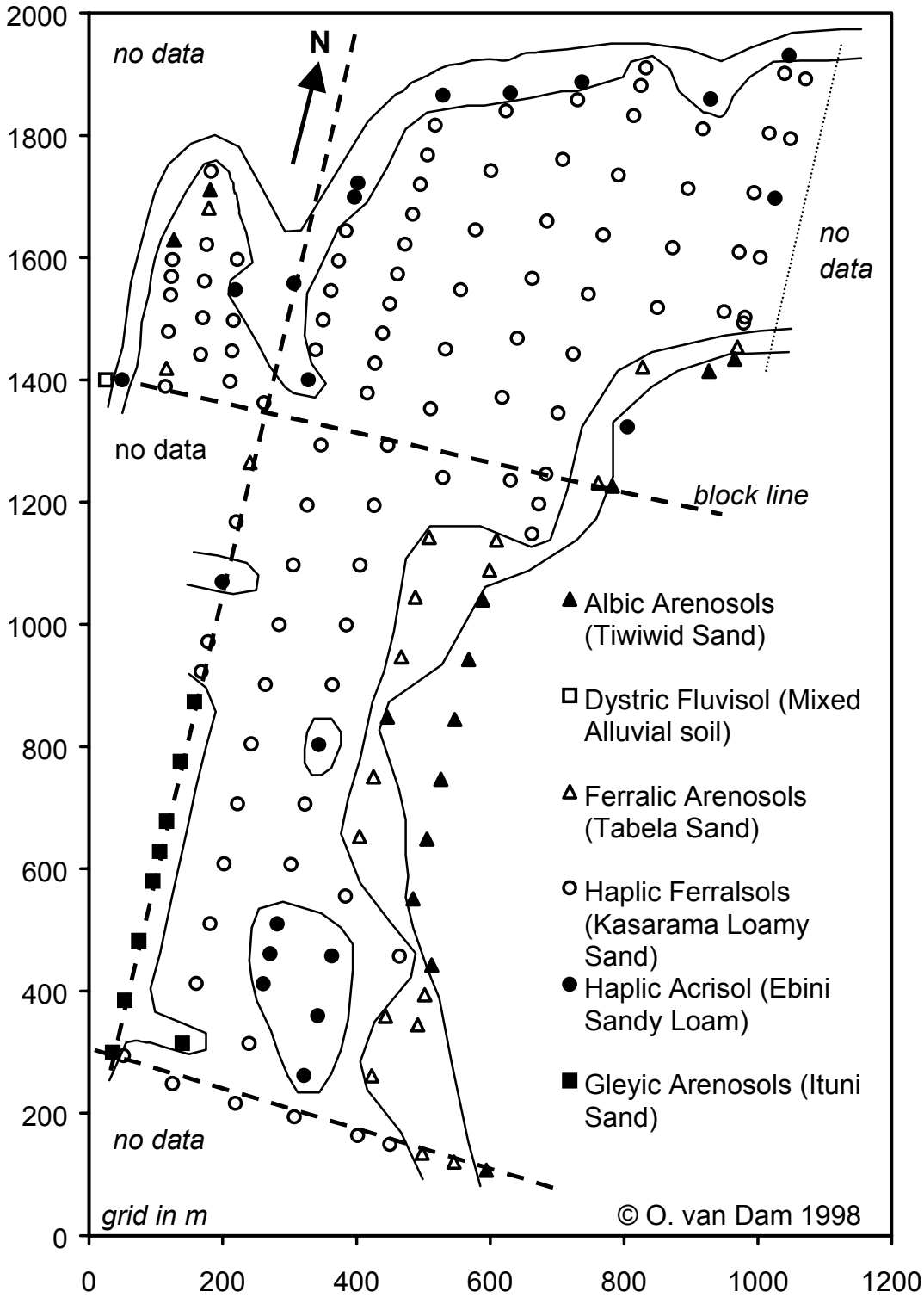


An experimental gap after cleaning.

Appendix 2.3 Map of the Pibiri Gap Experiment.



Appendix 2.4 Soil map of the Pibiri Gap Experiment study area



Appendix 2.5 Soil profile descriptions of PGE study area

PGE soil profile 1

Soil name:	FAO: haplic Ferralsol USDA: Oxisol Guyanese: Kasarama sandy loam
Author:	O.van Dam, 24-6-1997.
Location:	West Pibiri compartment of Demerara Timbers Ltd., 50 km South of Mabura Hill 10m East of skidtrial to Gap 16, 150m North on skidtrial.
Site description:	Flat topography with micro relief up to 20 cm around trees and highly decomposed logs. The site has an approximate elevation of 70m. The soil is developed in the White Sand Formation, which consists of highly weathered pre-cambrium shield. The parent material consists of sand on which a mixed greenheart (Chlorocardium rodiei) forest is present. The area has a warm tropical climate, with average yearly rainfall of 2700mm and average daily temperature of 26 ºC.
General characteristics:	The soil profile is moist throughout and is a well to somewhat excessively drained (class 4-5), no information on the depth of the groundwater table. There are no surface stones or and no erosion can be seen.
Weather of past 14 days:	Sunny, but usually some rain in the afternoon.

Horizon	Description
1A 0-6 cm	Dark brown (7.5YR3/4) loamy coarse sand, single grains, many very fine pores, loose consistence when moist, non sticky and non plastic when wet. Many very fine, fine and medium sized roots, large roots commonly present. Field pH 4.5. Gradual and smoothly changing into;
1AC 6-17 cm	Dark yellowish brown (10YR4/6) loamy sand, single grains, many very fine pores, very friable when moist, non sticky and non plastic when wet. Many very fine, fine and medium sized roots, no large roots. Field pH 4.5. Gradual and smoothly changing into;
1C1 17-40 cm	Yellowish brown (10YR5/4) sandy loam, weak sub-angular blocky, many very fine pores, loose consistence when moist, non sticky and non plastic when wet. Very few very fine, fine and medium sized roots, few large roots. Field pH 4.5. Clearly but irregular changing into;
1C2 40-44 cm	Yellowish brown (10YR5/4) sandy clay loam, weak sub-angular blocky, many very fine pores, loose consistence when moist, non sticky and non plastic when wet. Few very fine, fine and medium sized roots, many large roots. Field pH 5.0. Clearly but irregular changing into;
1C3 44-57 cm	Yellowish brown (10YR5/6) sandy clay loam, weak sub-angular blocky, many very fine discontinuous vesicular random pores, loose consistence when moist, non sticky and non plastic when wet. Only a few medium sized roots. Field pH 4.5. Diffuse and smoothly changing into;
1C4 57-120 cm	Yellowish brown (10YR5/6) sandy clay loam, weak sub-angular blocky, many very fine discontinuous vesicular random pores, loose consistence when moist, non sticky and non plastic when wet. Only very few medium sized roots. Field pH 4.5.

Brown sand soil profile

Soil physical analysis 1 (θ_i: initial soil moisture, BD: bulk density, W: weight, V: volume)

sample	θ_i %	BD kg.m^{-3}	Root W g.kg^{-1}	Root V g.dm^{-3}	Porosity %	Stones %	Sand %	Silt %	Clay %	Texture
1A	12.6	1.29	3.74	4.84	44.2	0.1	96.6	0.4	2.8	S
1AC	24.9	1.44	1.98	2.84	46.8	0.2	86.8	1.6	11.3	LS
1C1	25.7	1.54	2.21	3.40	38.8	0.1	81.5	2.2	16.2	SL
1C2						0.8	76.6	2.3	20.2	SCL
1C3	21.4	1.44	0.18	0.26	40.7	0.2	75.9	2.2	21.7	SCL
1C4	18.8	1.34	4.34	5.80	39.7	0.1	77.0	2.1	20.8	SCL
1C5	16.0	1.45	0.12	0.18		0.2	76.4	1.8	21.6	SCL

Water retention characteristics 1 (AWC: available water content)

sample (cm suction)	PF0.4 -3	PF1.0 -10	PF1.5 -32	PF2.0 -100	PF2.3 -200	PF2.5 -316	PF2.7 -501	PF3.5 -3162	PF 4.2 -15,849	AWC PF2 – PF4.2
1A	43.7	41.7	15.3	11.6	11.1	10.5	9.6	2.6	1.2	10.3
1AC	43.2	39.1	28.9	25.2	23.6	22.5	21.3	5.0	3.4	21.8
1C1	39.1	37.2	30.8	24.0	22.4	20.9	20.0	5.3	4.3	19.7
1C3	40.3	37.0	27.6	21.8	19.9	18.9	18.1	6.3	5.0	16.8
1C4	41.1	37.7	27.1	20.6	18.9	17.9	17.1	6.5	5.2	15.4

Soil chemical analysis 1 (in mg X.kg^{-1} dry soil)

sample	N	P-tot	K	Ca	Mg	Na	Al
1A	771	0.0	0.2	0.1	0.1	0.0	4.0
1AC	891	0.0	0.2	0.1	0.0	0.0	5.0
1C1	324	0.0	0.2	0.0	0.0	0.0	0.7
1C2	750	0.0	0.2	0.1	0.0	0.0	6.4
1C3	671	0.0	0.2	0.1	0.0	0.0	7.1
1C4	1015	0.0	0.2	0.1	0.1	0.0	9.2
1C5	304	0.0	0.2	0.0	0.0	0.0	5.9

PGE soil profile 2

Soil name:	FAO: haplic Ferralsol USDA: Oxisol Guyanese: Kasarama
Author:	O.van Dam, 25-6-1997.
Location:	West Pibiri compartment of Demerara Timbers Ltd., 50 km South of Mabura Hill between gap 19 and gap 18, 25 m West of main skid trail.
Site description:	Flat topography with micro relief up to 20 cm around trees and highly decomposed logs. At 50m West of the soil pit a 1.3 m high ant burrow is present. The site has an approximate elevation of 70m. The soil is developed in the White Sand Formation, which consists of highly weathered pre-cambrium shield. The parent material consists of sand on which a mixed greenheart (Chlorocardium rodiei) forest is present. The area has a warm tropical climate, with average yearly rainfall of 2700mm and average daily temperature of 26 ºC.
General characteristics:	The soil profile is moist throughout and is a well to somewhat excessively drained (class 4-5), no information on the depth of the groundwater table. There are no surface stones or and no erosion can be seen.
Weather of past 14 days:	Sunny, but usually some rain in the afternoon.

Horizon	Description
2A1 0-9 cm	Dark brown (7.5YR3/2) coarse sand, single grains, many very fine pores, loose consistence when moist, non sticky and non plastic when wet. Many very fine, fine and medium sized roots, few large roots. Field pH 4. Clear and smoothly changing into;
2A2 9-24 cm	Dark yellowish brown (10YR4/3) sandy loam, weak sub-angular blocky , many very fine pores, friable when moist, non sticky and non plastic when wet. Many very fine, fine and medium sized roots, very few large roots. Field pH 4. Gradual and smoothly changing into;
2A3 24-65 cm	Yellowish brown (10YR5/3) sandy clay loam, weak sub-angular blocky, many very fine pores, friable when moist, slightly sticky and slightly plastic when wet. Few very fine and fine sized roots, common medium and very few large roots. Field pH 4. Layer with increasing charcoal contents with depth, highest concentration between 55 and 65 cm. Clearly but wavy changing into;
2C 65-120 cm	Yellowish brown (10YR5/6) loam, weak sub-angular blocky, many very fine pores, friable when moist, slightly sticky and slightly plastic when wet. Only very few medium sized roots. Field pH 5.0.

Soil physical analysis 2 (θ_i: initial soil moisture, BD: bulk density, W: weight, V: volume)

Horizon	θ_i	BD	Root W	Root V	Porosity	Stones	Sand	Silt	Clay	Texture
	%	$kg.m^{-3}$	$g.kg^{-1}$	$g.dm^{-3}$	%	%	%	%	%	
2A1	15.3	1.213	6.189	7.51		0.3	95.1	1.4	3.2	S
2A2	23.2	1.353	1.478	2.00	44.4	0.2	87.2	3.2	9.4	LS
2A3	26.7	1.415	3.555	5.03	39.6	0.7	81.4	3.2	14.7	SL
2C1	17.4	1.440	0.153	0.22		0.2	81.1	2.5	16.2	SL
2C2	14.7	1.388	0.159	0.22	37.6	1.0	80.8	2.2	16.0	SL

Water retention characteristics 2 (AWC: available water content)

	PF0.4	PF1.0	PF1.5	PF2.0	PF2.3	PF2.5	PF2.7	PF3.5	PF 4.2	AWC
	-3	-10	-32	-100	-200	-316	-501	-3162	-15,849	PF2 – PF4.2
2A1	46.0	41.8	16.5	13.6	12.5	12.0	11.4	2.6	1.8	11.8
2A2	45.6	40.6	27.8	21.4	19.5	18.3	17.4	5.0	3.4	18.0
2A3	40.2	38.5	31.9	25.9	24.9	24.4	22.2	6.1	5.2	20.7
2C1	40.8	38.9	25.8	17.6	16.0	15.1	14.4	5.5	5.0	12.7
2C2	38.4	36.0	25.9	16.5	16.1	15.6	14.0	5.3	4.7	11.8

Soil chemical analysis 2 (in mg $X.kg^{-1}$ dry soil)

	N	P-tot	K	Ca	Mg	Na	Al
2A1	715	0.0	0.1	0.1	0.0	0.0	1.9
2A2	1027	0.0	0.1	0.1	0.0	0.0	3.5
2A3	2065	0.0	0.1	0.0	0.0	0.0	1.6
2C1	453	0.0	0.1	0.0	0.0	0.0	6.7
2C2	409	0.0	0.2	0.1	0.0	0.0	7.8

Appendix 2.6 Radiation, temperature, humidity, wind and rainfall observations from 1996 – 2000 of the Pibiri climate Station.

Table 2.7 Monthly average daily radiation sum ($MJ.m^{-2}.d^{-1}$) in 1996 – 2000 in the Pibiri climate station compared to the average in 1991 – 1993 in the FRMH area[(1)].

	Jan	Feb	March	April	May	June	July	Aug	Sep	Oct	Nov	Dec	Year
1996								14.13	16.76	17.72		11.97	
1997	11.88	12.38	14.26	15.01	12.55	14.55	*15.87*	*17.62*	*18.39*	*15.58*	*14.36*	*11.36*	**14.48**
1998	*12.38*	*12.78*	*12.26*	12.24	13.66	15.33	12.02	16.93	17.48	16.26	13.75	12.78	**13.99**
1999	12.34	13.21											
PGE avg	12.2	12.79	13.26	13.63	13.1	14.94	13.95	16.23	17.54	16.52	14.05	12.04	**14.28**
FRMH	12.16	12.18	12.94	12.9	13.54	12.71	13.6	13.46	13.06	13.99	12.78	12.12	**12.95**

Note: the ENSO event is shown in italic. (1) Source: Jetten (1994a) made radiation recordings from October 1991 to December 1993 in the Forest Reserve Mabura Hill, approximately 15 km South of Mabura Hill.

Table 2.8 Monthly temperature (°C) in 1996 – 2000 in the Pibiri climate station compared to the average in 1991 – 1993 in the FRMH area[(1)].

	Jan	Feb	March	April	May	June	July	Aug	Sep	Oct	Nov	Dec	Year
1996							25.4	26	26.6	27.0		25.8	
1997	24.5	24.8	24.8	25.8	25.4	25.1	*25.1*	*25.8*	*26.6*	*26.9*	*26.4*	*25*	**25.5**
1998	*24.9*	*26.3*	*26.6*	26.4	26.6	26.4	26.2	26.5	26.6	26.5	26.3	26.2	**26.3**
1999	24.9	25.0											
PGE avg	24.8	25.3	25.7	26.1	26.0	25.7	25.5	26.1	26.6	26.8	26.3	25.7	**25.9**
FRMH	24.3	23.9	24.7	24.9	25.1	25.5	25.4	25.6	26.0	25.9	25.8	25.1	**25.2**

Note: the ENSO event is shown in italic. (1) Source: Jetten (1994a) made temperature recordings from October 1991 to December 1993 in the Forest Reserve Mabura Hill, approximately 15 km South of Mabura Hill.

Table 2.9 Monthly humidity (%) in 1996 – 2000 in the Pibiri climate station compared to the average in 1991 – 1993 in the FRMH area[(1)].

	Jan	Feb	March	April	May	June	July	Aug	Sep	Oct	Nov	Dec	Year
1996							90.9	86.8	84.8	82.6		87.5	
1997	92.5	91	87	87.1	91.9	90.8	88	85.3	81.5	82.3	83.4	91.5	**87.7**
1998	90.1	83.4	78	93.5	93	92.6	90.5	89.9	88	88.7	90.9	93.8	**89.4**
1999	86.9	91.8											
PGE avg	89.8	88.7	82.5	90.3	92.5	91.7	89.8	87.3	84.8	84.5	87.2	90.9	**88.3**
FRMH	88.4	88.5	85.8	87	88.1	90	90	89.4	88.3	85	88.2	89.8	**88.2**

Note: the ENSO event is shown in italic. (1) Source: Jetten (1994a) made humidity recordings from October 1991 to December 1993 in the Forest Reserve Mabura Hill, approximately 15 km South of Mabura Hill.

Table 2.10 Monthly windspeed ($m.s^{-1}$) in 1996 – 2000 in the Pibiri climate station compared to the average in 1991 – 1993 in the FRMH area[(1)].

	Jan	Feb	March	April	May	June	July	Aug	Sep	Oct	Nov	Dec	Year
1996							0.262	0.295	0.28	0.26		0.196	
1997	0.244	0.29	0.306	0.25	0.218	0.197	0.199	0.233	0.257	0.262	0.253	0.193	**0.242**
1998	0.206	0.241	0.265	0.172	0.153	0.197	0.22	0.196	0.214	0.198	0.163	0.145	**0.197**
1999	0.136	0.162											
PGE avg	0.195	0.231	0.285	0.211	0.185	0.197	0.227	0.241	0.25	0.24	0.208	0.178	**0.221**
FRMH	0.239	0.258	0.262	0.298	0.216	0.168	0.147	0.189	0.195	0.26	0.201	0.208	**0.22**

(1) Source: Jetten (1994a) made humidity recordings from October 1991 to December 1993 in the Forest Reserve Mabura Hill, approximately 15 km South of Mabura Hill.

Table 2.11 Monthly rain (mm) from 1996-2000 in the PGE research area and the average of previous years in the FRMH area[(1)] and the Great Falls Hydromet meteorological station (GF).

	Jan	Feb	March	April	May	June	July	Aug	Sep	Oct	Nov	Dec	Year
1996					598	575	380	240	71	24	271	317	**(2477)**
1997	271	317	112	153	345	*279*	*285*	*152*	*81*	*48*	*116*	*202*	**2362**
1998	*147*	*43*	*20*	543	410	377	281	172	107	85	121	136	**2441**
1999	336	135	220	181	257	425	336	601	135	90	40	23	**2779**
2000	415	110	160	346									**(1032)**
PGE avg	292	151	128	306	403	414	321	291	99	62	137	170	**2527[(2)]**
FRMH	292	151	128	306	402	414	321	291	98	62	137	169	**2772**
GF	163	213	199	214	312	322	405	249	143	105	181	181	**2687**

Note: the ENSO event is shown in italic. (1) Source: Jetten (1994a) made rainfall recordings from October 1991 to December 1993 in the Forest Reserve Mabura Hill, approximately 15 km South of Mabura Hill. Great Falls is an Amerindian village approximately 5 km North of Mabura Hill, where daily meteorological recordings are made by HYDROMET, Ministry of Agriculture. The station has been down for a few years, but is operating again since June 1998. (2) The average yearly rainfall including May-Dec ’96 and Jan-April ’00 was 2772 mm.

3 GAP SIZE EFFECTS ON MICROCLIMATE AND SOIL MOISTURE

with Raymond Sluiter and Niels Smit

Abstract
Microclimate and soil moisture are important parameters for forest regeneration after logging and gap size has a strong influence on these parameters but little in known to what extend. Microclimate and soil moisture was measured in the Pibiri Gap Experiment (PGE) gaps, ranging in size from 40 to 3200m^2, over a period of 3 years.

Microclimate conditions were strongly influenced by gap size and the effect of the gap on the microclimate was noticeable beyond the perpendicular projection of the canopy opening. Gap size had the strongest influence on solar radiation and air temperature, which increased with increasing gap size up to a gap size of approximately 600m^2 after which no increase was found. Soil temperature was more influenced by soil moisture content and soil cover than gap size. Microclimatic gradient from gap centre to forest were less distinct, since abrupt changed were found at the gap edge, especially in the larger gaps.

Soil moisture was affected by a complex interaction of soil evaporation, soil disturbance, soil cover, soil hydrological properties, water consumption by the regeneration vegetation in the gaps, water consumption by the vegetation of the gap edge, rainfall history and macro pores due to dead roots. Differences between soil moisture content in gap centres, gap edges and forest plots were small and not significant. The largest differences were found in the dry season, when soil moisture conditions in gaps smaller than 210m^2 were wetter than the forest, but soil moisture conditions had a tendency to be drier in gaps of 1280m^2 and larger. Gap edges had comparable soil moisture conditions as the forest.

INTRODUCTION

Microclimate and soil moisture in gaps

Any plant, animal or researcher notices the immediate changes in microclimate conditions when a gap is formed in a tropical rain forest. In a gap, the higher amount of direct solar radiation increases air temperature and decreases air humidity, while wind is more noticeable than in the dense forest understory. The changes in microclimate conditions due to the presence of a gap also affect the available moisture in the soil. The topsoil will become drier due to soil evaporation, but the soil moisture conditions of the subsoil will become wetter than the forest due to a reduced transpiration of the vegetation in the gaps (Becker *et al*. 1988, Jetten 1994a, Parker 1985). These changes in soil conditions, which are less discernible to large animals and researchers, are of crucial importance to the plants in the gaps, since the regeneration of the forest is strongly associated with the presence and size of gaps (Brokaw 1992b & 1985b, Hartshorn 1978).

Research in the past decades on tropical forest dynamics and tropical forest diversity has been mostly on competition for light and partitioning of tree species in gaps of different sizes (Denslow 1980, Rose 2000). A number of studies have looked at microclimate changes in gaps (Bazzaz and Wayne 1994, Bongers *et al.* 1988, Brown and Whitmore 1992, Mekkink and Nijmeijer 1998) or clearings (Carmargo and Kapos 1995, Schulz 1960), but few have looked

beyond the perimeter of the gap, into the gap edge area (Popma *et al.* 1988). The microclimate-influenced area (MIA) as defined by Popma and *et al.* (1988) under a canopy opening is usually larger than the perpendicular projection of the gap edge as defined by Brokaw (1982a). Near the edges of large gaps, the microclimatic conditions, both inside the gap and in the gap edge area, can be similar to microclimatic conditions of small gaps (Brown 1993). The extent of the MIA was studied by Popma *et al.* (1988), who noted the increased growth of seedlings in the gap edge area, a few years after gap formation. Within the gap size range of 12 to 223 m^2, they found that the MIA was on average 3.4 times larger than the measured gap size *sensu* Brokaw (1982a). Changes of microclimate in forest edges adjacent to large clearings or pastures have been studied more intensively than changes in gaps (Kapos 1989, Young and Mitchell 1994). The effect of a large clearing did not go beyond 50 to 60m into the forest (Camargo and Kapos 1995). Didham & Lawton (1999) however, suggested that the structure of the edge, either with a closed dense vegetation or more open vegetation, had a large influence on the extent of the influence of the clearing. Gaps are expected to have wetter soil moisture conditions (Becker *et al*. 1988, Vitousek and Denslow 1986) and higher vapour pressure deficit (VPD) than undisturbed forest. Jetten (1994a) estimated that in a 1-year-old logging gap, direct soil evaporation had increased 15 fold, but since transpiration was reduced, total evapotranspiration decreased to 65% of the undisturbed forest. In forest fragments in Brazil, the topsoil in the forest edge was 25% drier than in the more undisturbed forest, but these drier soil moisture conditions were no longer present at 20m from the edge in the forest (Kapos 1989). The denser vegetation at the edge, which had a higher transpiration demand than the forest further away from the edge, most likely caused these drier conditions.

Tree falls or crown snaps create canopy gaps, which are a common feature in a tropical rain forest and which play an important role in the regeneration of the forest (Brokaw 1985b, Denslow 1980, Hartshorn 1978). The regrowth of the vegetation is primarily caused by the increased light intensity. In addition, in gaps, soil moisture conditions can be wetter (Vitousek and Denslow 1986) due to a decrease in water uptake by the vegetation, which in turn alters the amount of percolating water. The change in soil moisture and for example soil temperature affect decomnposition and mineralisation rates, which in turn influence nutrient availability and thereby affect plant growth. The size of a gap is a significant variable that determines which species can regenerate (Rose 2000). In Guyana, selective logging is common practice, which induces more gaps per ha than in undisturbed forest dynamics. But more importantly, the sizes of individual gaps are usually larger, since usually more trees close to each other are felled. A range of microclimatic and soil moisture conditions occur in these gaps of different sizes. However, little in known about the effects of gap size, shape and orientation on microclimate and soil water dynamics, both inside the gap and in the gap edge area. This information is needed to evaluate the effects of logging of the forest. Although the interactions between plant behaviour and changes in microclimate are poorly understood, a first step is to quantify the abiotic conditions in different sized and shaped gaps, before the effects of biological processes can be explained.

Microclimate and water use in and around gaps: a hypothesis

The results of the studies mentioned above suggest that:
1) the influence of a large logging gap (≈ 3500m^2) on microclimate and soil moisture does not extend further into the forest than approximately 50m,
2) soil moisture conditions in the gap are wetter than in the forest,
3) complex edge effects of soil moisture conditions are found and
4) the influence of a gap on the microclimatic and soil moisture conditions in and around the gap the surrounding forest will change in time due to the regrowth of vegetation in the gap and gap edge.

In this study we tested the following hypotheses that are graphically displayed in Figure 3.1:
– Microclimatic conditions like radiation or air temperature decrease with decreasing distance from the gap centre and continue to decrease in the gap edge area into the deep forest understory. A sharp decline can be found at the gap edge (dashed line Figure 3.1). More in general, will microclimatic conditions like air temperature increase with increasing gap size, due to an increase in solar radiation?
– Soil water content in forest is lower than in gaps, because of the higher water consumption of the mature forest trees (solid line Figure 3.1).
– Soil water content at the gap edge is lower than in the forest, because of a larger water use by the vegetation at the gap edge. At the gap edge, a larger surface of the canopy of the tree bordering the gap receives direct radiation (gray area Figure 3.1), which increases the transpiration of that tree. Moreover, understory vegetation at the gap edge also receives direct radiation and their transpiration is also larger than understory plants further away from the gap (solid line Figure 3.1).
– In time, the vegetation in the gap regenerates and the soil water extraction will increase (small plants in gap centre Figure 3.1). Due to regrowth, microclimatic conditions near the soil, like air temperature, will decrease.

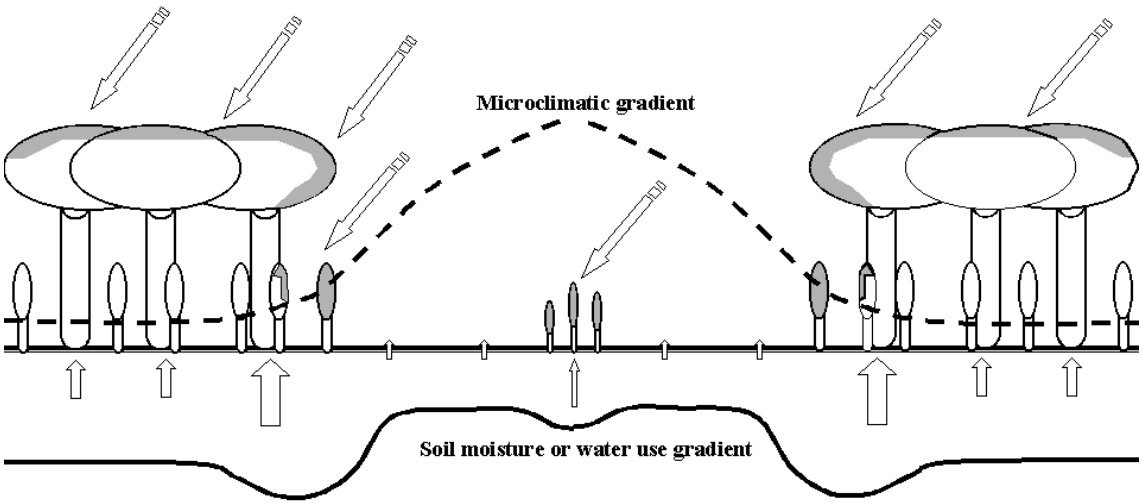


Figure 3.1 Gradients of microclimatic conditions (dashed line) and soil moisture or soil water consumption (solid line and solid arrows) in gaps. The gray areas on the vegetation are parts of the crowns that receive direct solar radiation (dashed arrows) and the small arrows in the gap represent direct soil evaporation. (see text for further explanation)

In this study, we tested the above hypotheses on the spatial and temporal patterns of microclimate and soil moisture conditions in gaps of different sizes. Besides these hypotheses, other questions needed to be answered:
1) Is there a gap size below which microclimatic conditions like soil and air temperature and air humidity are not damaging to regrowth?

It can be assumed that the amount of solar radiation continuously increases with increasing gap size until the logged area can no longer be considered selective logging, but the area resembles clear felling. However, other microclimatic conditions in selective logging gaps might not exhibit continuously increase, but reach a certain maximum, or minimum in the case of air humidity, at a certain gap size. Since the interaction between, for example, air temperature and humidity and regeneration of the indigious species of Guyana are not known, the question translates itself to quantifying the microclimatic conditions in different sized gaps. In a later study, these data can than be used in a biological assessment.

2) At which distance from the gap edge into the forest can the presence of the gap no longer be measured? And in line with this question: What is the extent of the microclimate-influenced area (MIA) and is there a relation between the MIA and gap size?

3) Are there other factors regulating the microclimatic conditions in gaps and which are they?
Although air temperature and humidity most likely have a strong relation with gap size, soil temperature might also be affected by soil conditions like soil moisture or litter cover.

4) Are the gradients in soil moisture conditions consisted throughout the soil profile?
The hypotheses on soil moisture conditions as given above are related to the overall soil moisture content throughout the soil profile. However, increased soil evaporation from the bare soil in a gap can result in drier topsoil conditions than in forest, where less direct radiation reaches the soil and the soil has a thicker litter layer.

The hypotheses and research questions were addressed with two methodologies. Microclimatic and soil moisture conditions were studied by field measurements (this chapter) in undisturbed forest and in 13 experimental gaps of the Pibiri Gap Experiment (PGE) (van Dam *et al.* 1999) and by modelling (Chapter 4 and 5).

The Pibiri Gap Experiment
In July 1996, 24 experimental gaps were created for the Pibiri Gap Experiment (Chapter 2), which ranged in size from 40 to 3200m^2. Trees were felled by directional felling techniques to ensure circular shaped gaps as much as possible. All vegetation left standing in the centre area of the gaps was removed to introduce experimental plants (Rose 2000). All logging debris was removed by hand in gaps smaller than 1000m^2 and in the larger gaps, cleaning of the centre area of the gaps was done by a winch of a skidder. In a 'normal' logging operation, a gap can be divided into 1) a crown zone, where the crowns of the trees that were felled are located and where large piles of deead leaves and branches are found, 2) a skidder zone where a skidder has disturbed the top soil and usually this area can be characterised by larger stretches of bare soil and 3) an'undisturbed' zone, where some vegetation that survived the logging operation can still be found (Brouwer 1996). In the smaller PGE gaps, these zones were not present and in the larger PGE gaps, skidder zones were only found near the gap edge. With a few exceptions which will be explained below, the main data collection was limited to a more or less undisturbed area from gap centre to the western gap edge, where no skidtrails or crowns were present.

Microclimate and soil moisture during the '97/'98 El Niño event

Microclimate and soil moisture data were collected from April 1996 to October 1999. From July 1997 to April 1998, Guyana and surrounding countries experienced extreme dry weather conditions due to an El Niño event (see Chapter 2). This provided a unique opportunity to study the effects of prolonged drought on microclimatic conditions and soil water status, both in undisturbed forest as in gaps. In addition to the research questions postulated above, we wanted to know how the '97/'98 El Niño event affected microclimatic and soil moisture conditions in undisturbed forest and in gaps of different size.

METHODOLOGY

Microclimate measurements

Continuous microclimate measurements were made with the help of two moveable climate stations. From 10 September 1996 to 24 October 1996, soil temperature was measured along a

transect from the gap centre into the forest in a 2950m^2 gap (moveable climate station 1: MCS1). Every hour, soil temperature was measured with 10 soil temperature sensors (thermistors), which were placed along a transect from gap centre to forest understory at 5 cm depth, and connected to a Campbell CR10 data logger. From 14 May 1998 to 19 June 1998, a 2 m tall climate station was installed in the undisturbed forest and in the centres of a 570 and 3200m^2 gap for 2 consecutive periods of 10 days (MCS2). Every hour, measurements were made of air temperature and humidity with a ventilated Vaisala Temperature/Humidity probe, wind speed with a Campbell cup anemometer, rainfall with a Campbell AR100 tipping bucket and temperature with 6 soil temperature sensors (thermistors), that were placed at 1 cm depth, directly under the litter layers.

Weekly recordings were made with twenty-five minimum/maximum thermometers that were installed 1m above the soil in temperature stations along transects from the gap centre into the forest understory. Temperature was measured with 0.5°C precision. Air temperature was measured in a 40, 60, 210, 370, 570, 1280 and 3200m^2 gap. The largest gap had 5 air temperature stations and the smallest gap had 1 station.

At all locations where microclimatic measurements were made, hemispherical photographs were taken with a Nikon/Fujix digital camera fitted with a Sigma 8 mm fish-eye lens. The blue channel of the images was analysed with the computer program WINPHOT (ter Steege 1997) for canopy openness and direct and diffuse light intensity.

Soil moisture measurements

Soil moisture was measured at various locations in all gaps with 4 different methods:
1) Topsoil moisture contents were measured in a 2950 (7/11/96) and 3200m^2 gap (20/11/96) with a *Trime* Time Domain Reflectometer (TDR) 2-wire probe long that was read-out manually with a *Trime* FM2 read-out device. The 2-wire TDR probe consisted of 2 metal pins of 16 cm long that were inserted vertically into the soil. At each soil moisture measurement location, the gap zone cover was noted: crown debris, logs, skidder and undisturbed zone.
2) Top- and subsoil measurements were made with a *Trime* TDR tube probe that was read-out manually with a *Trime* FM2. The TDR tube probe consisted of a 20 cm long plastic casing on which 2 metal strips are attached that are pushed outwards by small springs to ensure good contact with the inside wall of the TDR tubes. The TDR tube probe can be lowered into a TDR tube at any desired depth. In total 60 tubes were placed along transects from the gap centre to forest understorey (GCFU) in a 40, 60, 210, 370, 570, 1280 and 3200m^2 gap. TDR tubes were installed pairwise, with approximately 0.5m between tubes. The number of tubes in the smallest gap was 6 and in the largest gap 12. From July 1997 to June 1999, weekly TDR readings were made at depth intervals of 0-20, 20-40, 40-60, 60-80 and 80-100 cm.
The tube TDR soil moisture measurements were grouped according to:
– location: gap centre, gap edge (depending on gap size from 5.5 m into the forest to 2 m into the gap) or forest (depending on the gap size, but at least 10m from the gap edge) and
– season: wet season (9/12/97 until 18/2/98) and dry season (19/8/98 until 25/11/98). No other season was analysed, because the soil moisture measurements in these other seasons were either too few or the differences in rainfall were insufficient.
3) A 4-wire Frequency Domain Reflectometer (FDR) *ThetaProbe* was attached to the CR10 data logger of the MCS2. The TDR probe consisted of 4 metal wires of 15 cm long that were inserted under an angle of 60° into the soil. Hourly measurements were made with the FDR probe at the same time and locations as the 2 m tall moveable climate station MCS2.
4) At the end of the '97/'98 El Niño event in March 1998, soil samples were collected by auger at 20 cm intervals up to 120 cm depth in a 210, 570, 2180 and 3200m^2 gap. Samples were taken from the gap centres, gap edges and forest understorey plots. The wet soil samples were

weighed, oven dried at 105 °C for 24 hours and reweighed and gravimetric soil moisture content (%) was calculated.
The TDR and FDR soil moisture devices were calibrated to the soil conditions of the research area and the calibration method and results are discussed in Appendix 3.1.

RESULTS

Microclimate in gaps

Radiation
As was expected, canopy openness and radiation in the gap centres and gap edges increased with increasing gap size. However, the canopy openness of the forest – i.e. the small holes in between the leaves of the canopy trees –, the 40 and 60m^2 gap centres and the gap edge locations were nearly identical, although the total radiation in the small gaps and in the gap edges was twice the amount of the forest (Figure 3.2). This can be explained by the large amount of small openings in the forest, which gave a canopy openness similar to a larger opening or a gap, but the total amount of direct radiation through these very small openings is limited and the radiation in a forest understory was almost only diffuse radiation. Moreover, unlike a gap, these openings are not positioned directly overhead, which resulted in lower radiation levels. In the 1280m^2 gap, not all trees were felled, which resulted in a smaller canopy openness and likewise a lower amount of radiation in the edge. On the other hand, in the 3200m^2, no vegetation was left standing, and consequently, the radiation conditions at the edge of the 3200m^2 gap were comparable to the centre of a 570m^2 gap. There were no differences between the radiation levels of the 40 and 60m^2 gaps and the 370 and 570m^2 gaps.

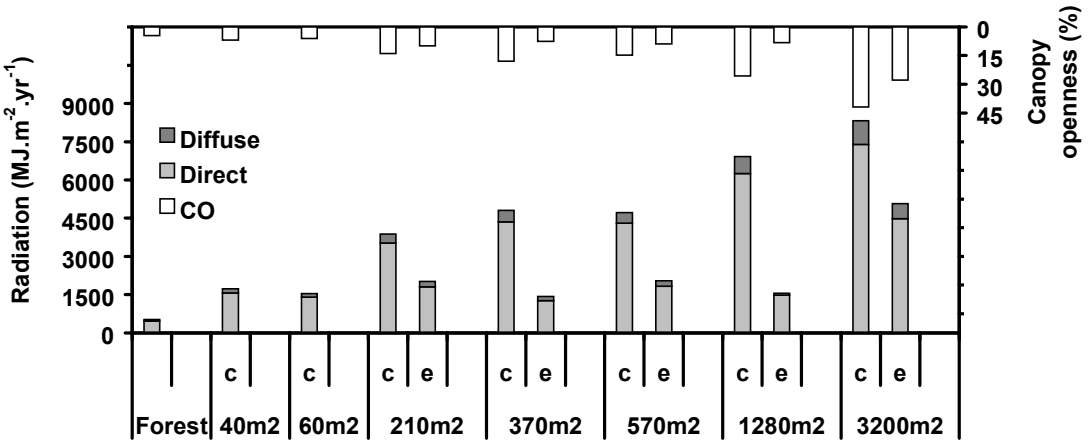


Figure 3.2 Canopy openness, potential direct and diffuse radiation as calculated with WINPHOT from hemispherical photographs that were taken in gap centres and gap edges of gaps of different size. (Note: total radiation is direct plus diffuse radiation, c: gap centre, e: gap edge)

Air temperature, humidity and wind speed
Gap size notably influenced air temperature. The average weekly maximum air temperature in the gap centres increased with increasing gap size from 28.5 °C in the 40m^2 gap to 36.6 °C in the 3200m^2 gap. The average weekly minimum air temperature in the gap centres was 23.0 °C, which was 1 °C lower than in the forest understory (Figure 3.3), but no pattern was found between gap size and nighttime cooling down. A larger amount of outgoning radiation during the night was expected in large gaps with large areas of bare soil, but apparently, this effect did not occur. Maximum air temperature decreased along the GCFU transect, except in the 1280 and 3200m^2 gaps, where high maximum air temperatures were also recorded at the gap edge.

Even so, the maximum air temperature at the 3200m^2 gap edge was equal to the maximum air temperature in the centre of that gap. At 14 m into the forest surrounding the 3200m^2 gap, the influence of the gap on the air temperature could not be measured anymore.

The maximum air temperature at the centres of gaps larger than 370m^2 ranged from 34.7 to 37.0 °C, which was significantly higher (Scheffé test, $p<0.001$) than the maximum air temperature in the smaller gaps (28.5 – 33.4 °C) or the forest (29.5 °C). However, no significant differences (Scheffé-test, $p<0.05$) were found between these large gaps. The maximum air temperature in the gap centres decreased over time. From July to September 1997, the average maximum temperature in the 3200m^2 gap was 39.7 °C, which had decreased to 37.0 °C in the same period in 1998 and to 34.3 °C in 1999. This decrease in temperature in the gaps, which is caused by the growth of the vegetation that shadowed the air temperature plots after 2-3 years, was also observed in the 570 and 1280m^2 gaps, but could not be detected in the smaller gaps.

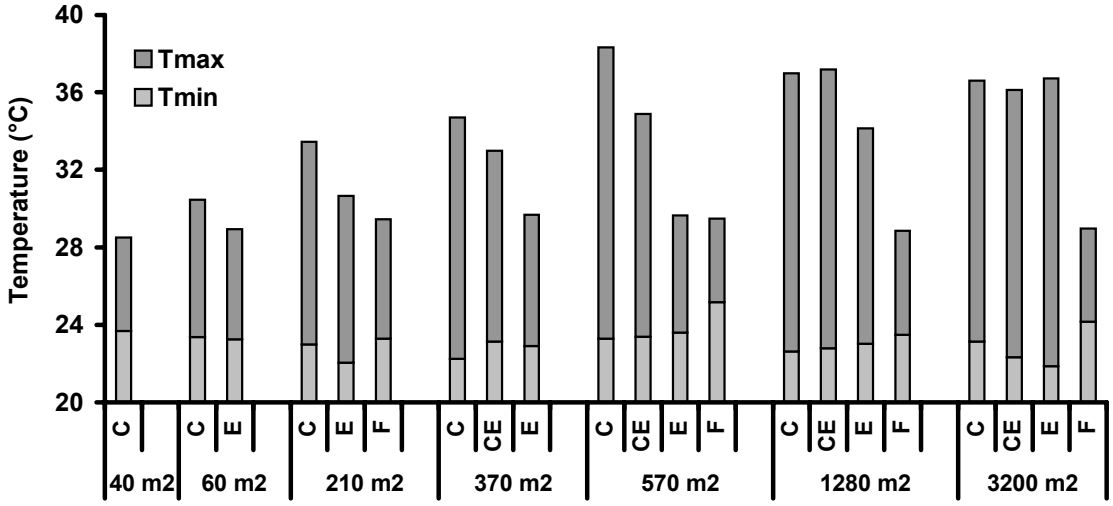


Figure 3.3 Average weekly minimum (Tmin) and maximum (Tmax) air temperature in gap centre (GC), gap centre-edge (CE), gap edge (GE) or forest (F) climate plot in gaps of different size in 1998.

The relative air humidity at 1 m from the forest floor was near saturation during the nighttime and around 90% during mid-day. In the 3200m^2 gap, humidity at night was also near saturation, but could be as low as 60% at mid-day. The lowest humidity was found between 13h and 14h (Figure 3.4). From May to July 1998, there was only wind between 9h and 21h (Figure 3.3). While the average wind in the forest was only 0.021 m.s^{-1}, the average wind in the 3200m^2 gap was 0.167 m.s^{-1}. This suggests that wind is directly related to very local low and high pressure areas following daily radiation.

Soil temperature

The highest soil temperatures in a gap were found in areas with bare soil, like skid trails and the lowest soil temperatures were found in areas with a large litter cover, like the log zone (Figure 3.5). Although the skidder zone at the east side of the gap was not positioned inside the gap, the open edge of the gap enabled the solar radiation to heat-up the bare soil from 12h to 16h, when the sun was setting at the west side of the gap. These large temperature variations were not found in the dense undergrowth of the forest, where the vegetation overhead created a more moderate microclimate. The soil temperature in the forest was between 23.6 and 25.5 °C. Night-time cooling in the gaps was only 1 °C less than the 22.5 °C night time soil temperature of the forest (Figure 3.4).

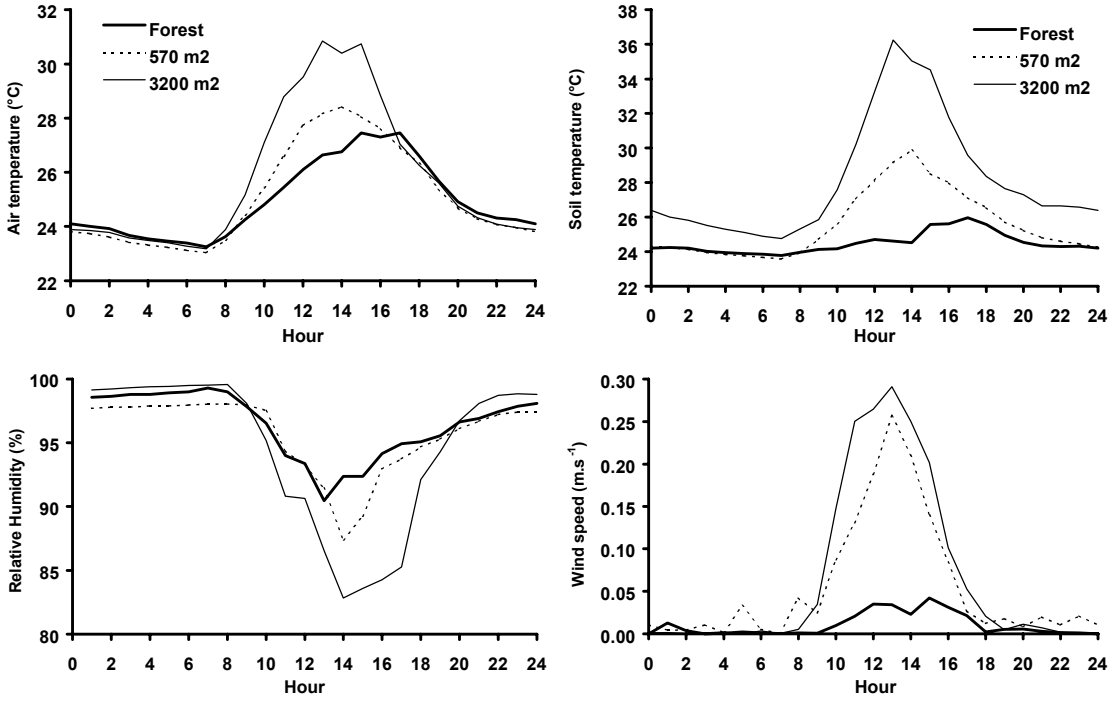


Figure 3.4 Average daily fluctuations of air and soil temperature, relative humidity and wind speed in the forest and in a 570 and 3200m2 gap from May to June 1998.
(Note: due to malfunctioning, the humidity in the forest was measured with a hygrograph and not with the moveable climate station).

Soil temperature measurements at only one location gave an erroneous impression. For example in July 1998 at mid-day, the average soil temperature of 6 sensors placed within 1 m^2 at the centre of a 3200m^2 gap was 38.6 °C (σ 7.84 °C), while the lowest temperature was 33.0 °C and the highest 53.7 °C. Soil attributes like litter cover, moisture content or bulk density probably caused these local differences.

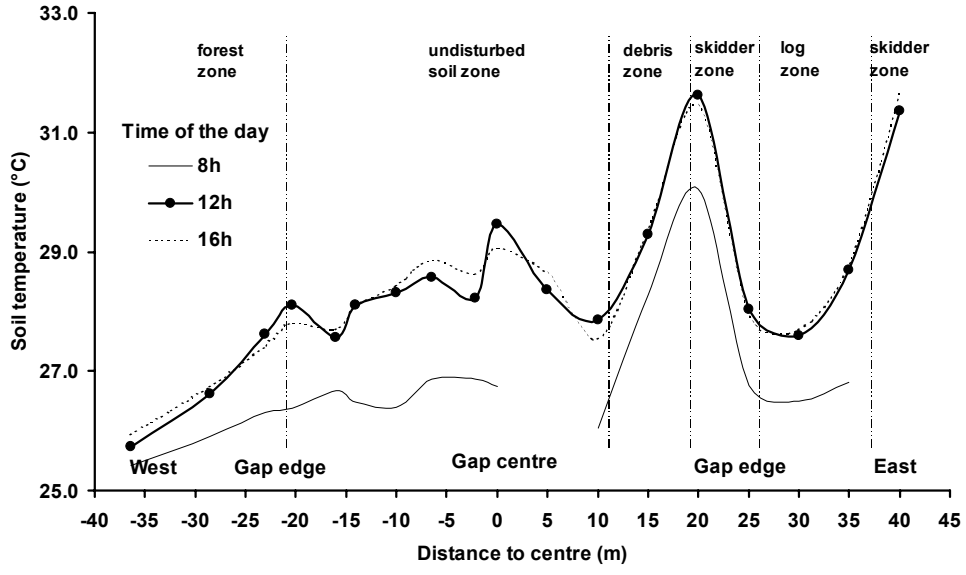


Figure 3.5 Soil temperature fluctuation during a day (7 November 1996) in a 2950m^2 gap along a Western Edge – Gap Centre – Eastern Edge transect through different zones in the gap.

Soil moisture in gaps

Topsoil moisture in different gap zones

Topsoil moisture content (0-16 cm) in the 2680 and 3200m^2 gaps was largely influenced by the different zones in the gaps (Table 3.1). Four zones were distinguished: 1) The skidder zone had a heavily disturbed topsoil where all vegetation had been removed by a skidder. This zone was near the gap edge, because no skidding activities were allowed in the centres of the experimental gaps. The absence of vegetation that extracted soil water and the location near the gap edge which received less solar radiation made the skidder zone the wettest zone in the gaps. 2) The log zone was positioned at the gap edge and was characterized by the presence of the logs of the trees that were felled to create the gap. Although these logs almost completely covered the soil and thus limited soil evaporation, the roots of the trees at the gap edge extracted a large amount of soil moisture, which dried out the topsoil. The water consumption of large trees was also clearly reflected by the lowest soil moisture conditions in the forest itself. 3) The crown debris zone contained large piles of organic debris that were left behind after the logging and most of the vegetation in this zone was killed. The large soil cover reduced direct soil evaporation and the uptake by the vegetation was limited, thereby creating an area of wetter topsoil conditions in the centre of the gap. 4) The remaining zone in the gaps were the more or less undisturbed zones, where few logging activities had taken place and where some small trees and shrubs had survived the felling and cleaning of the experimental gaps. Topsoil moisture conditions in the undisturbed zone were lower compared to the other gap zones.

Table 3.1 Topsoil moisture content in gap zones of two large gaps and surrounding forest (measured with a 2-wire TDR probe).

	3200m^2, 20/11/96				2680m^2, 18/19-11-96				
Gap zone[2]	**N**	**θ (%)**	**std. err.**	**Indexed θ[1]**	**N**	**θ (%)**	**std. err.**	**Indexed θ[1]**	**Avg. index**
Skidder zone	13	12.1	1.1	115	12	31.0	0.6	117	116
Log zone	11	9.8	1.1	93	9	25.4	1.5	96	95
Crown debris zone	15	11.7	0.9	112	20	25.1	0.8	95	103
Undisturbed zone	41	9.8	0.4	93	34	26.1	0.5	98	96
Gap average	80	10.5	0.4	100	75	26.5	0.4	100	100
Forest	20	6.5	0.3	62	33	20.6	0.8	78	70

Note (1): Indexed θ: to compare the two gaps, the average θ of the gap was taken as 100 and the corresponding index of each zone was calculated. Note (2): Gap zones are explained in the text above.

The amount of rainfall in the day prior to the soil moisture measurements in these two gaps was different. On the days prior to the sampling of the 2680m^2 gap, 17/11/96 and 18/11/96, rainfall was 17.1 and 19.6 mm respectively, while on 19/11/96, the day prior to the sampling of the 3200m^2 gap, only 0.2 mm of rain fell. This difference in rainfall was reflected by a difference in topsoil moisture content (Table 3.1), since the topsoil of the 2680m^2 gap was wetter than the 3200m^2 gap. Moreover, topsoil moisture was clearly only influenced by the amount of rainfall in the previous day, since the amount of rainfall in the previous 2 or 3 days did not increase the topsoil moisture conditions in the 3200m^2 gap. To compare the moisture conditions of the two gaps, the soil moisture contents (θ) were indexed, where the average soil moisture content per gap was taken as 100 (Table 3.1). The skidder zone was the wettest zone and the undisturbed and log zone were the driest zones. The forest was drier than any gap zone.

The rapid drainage of the topsoil was found both in forest and in gap environments (Figure 3.6). After rainstorm of 5 mm or more, soil moisture content increased to 35%, near saturation, but rapidly decreased within the following 12 hours to field conditions around 20%. Unfortunately, the rainfall patterns between the measuring periods were too different to distinguish differences between forest and gap.

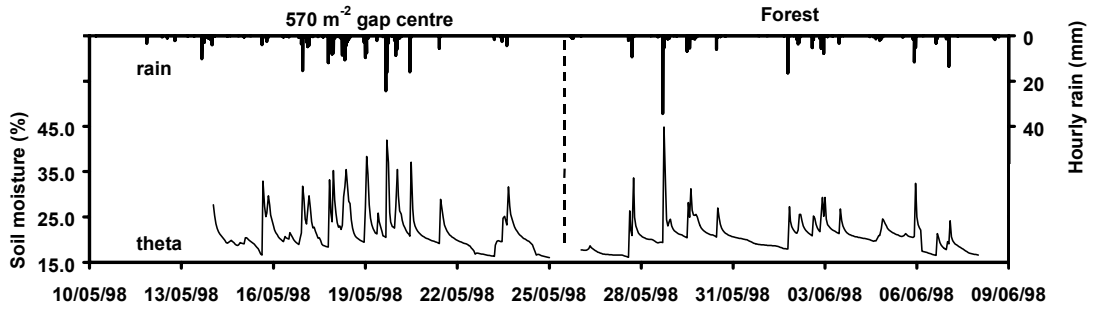


Figure 3.6 Hourly changing topsoil (0-15cm) moisture content in a 570m^2 gap centre and the forest (measured with a 4-wire FDR attached to a data logger).

Soil moisture conditions in gaps of different size

Soil moisture conditions were not significantly different (two-way ANOVA per layer per gap) at any depth, neither between gaps of different size nor between gap centre, gap edge or forest locations (Figure 3.7). In every plot, topsoil moisture conditions (0-20cm) in the dry season were about 5% significantly drier than in the wet season (Scheffé test, $p<0.001$) and in the 210 and 370m^2 gap, subsoil moisture conditions (20-40, 40-60, 60-80 & 80-100cm) were also significantly drier in the dry season than in the wet season (Scheffé test, $p<0.001$). The average topsoil moisture content in the wet season was 13.85 % (σ 0.98) and in the dry season 8.72 % (σ 0.70), while the average subsoil moisture content in the wet season was 14.23 % (σ 2.72) and in the dry season 12.60 (σ 1.86). In conclusion, the difference in topsoil and subsoil moisture content was much larger in the dry season than in the wet season. Typical soil moisture profiles per season per location in a gap are given in Table 3.2 and in greater detail in Figure 3.7.

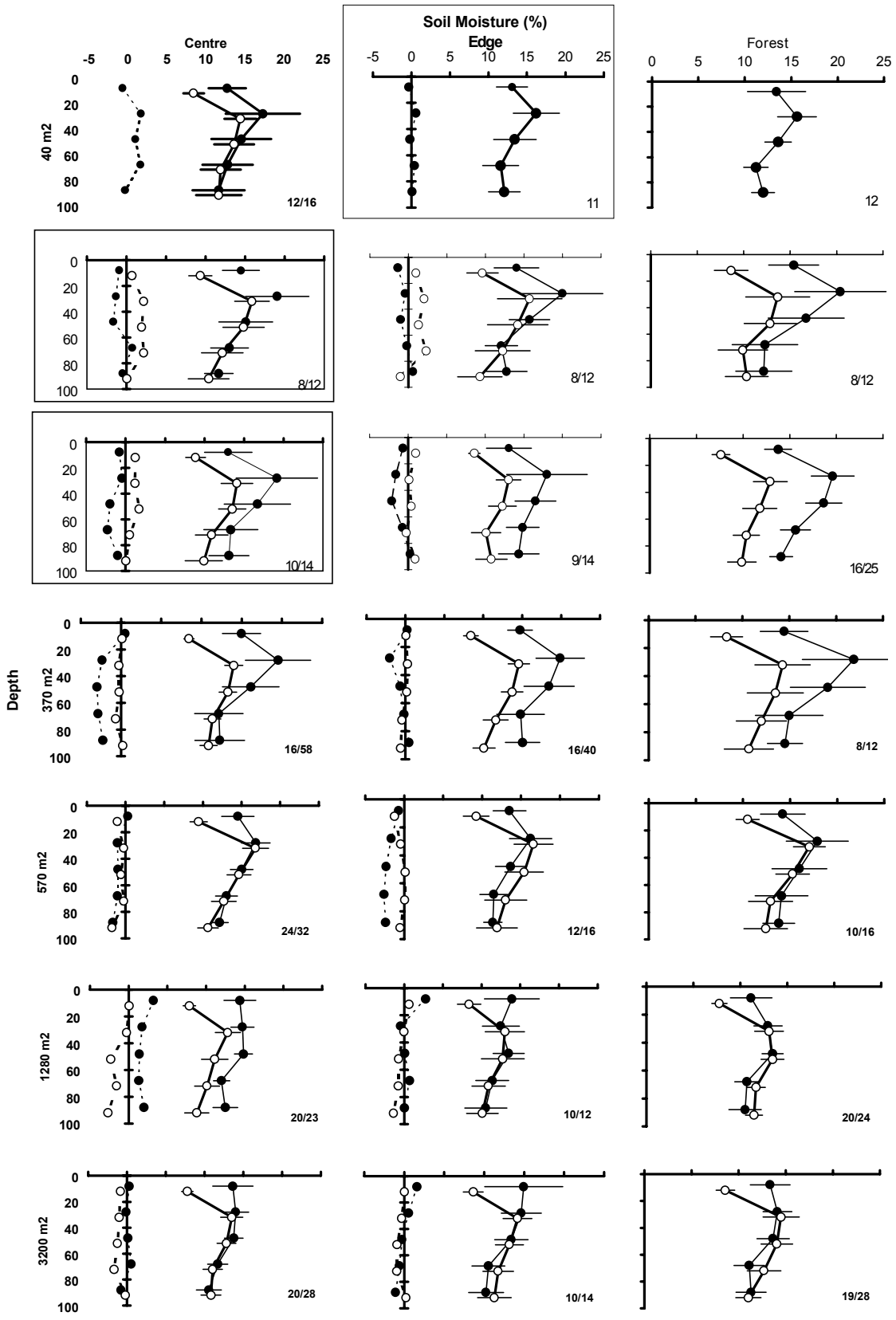
Table 3.2 Average soil moisture content (%) per depth and season of gap centre, gap edge or forest (measured with the tube TDR probe). The value between brackets is the 2·standard error.

		0-20	20-40	40-60	60-80	80-100
DRY	**Centre**	8.54 (0.37)	14.45 (0.63)	13.34 (0.62)	11.46 (0.61)	10.54 (0.61)
	Edge	8.72 (0.54)	14.58 (0.89)	13.64 (0.89)	11.64 (0.92)	10.54 (0.84)
	Forest	8.45 (0.49)	14.11 (0.87)	13.43 (0.79)	11.69 (0.76)	10.98 (0.71)
WET	**Centre**	14.06 (0.91)	16.76 (1.15)	15.03 (0.90)	12.48 (0.78)	11.94 (0.76)
	Edge	13.95 (1.03)	16.90 (1.33)	15.14 (1.06)	12.52 (0.94)	12.45 (0.83)
	Forest	13.32 (0.91)	16.59 (1.13)	15.45 (0.92)	12.57 (0.83)	12.51 (0.71)

Soil moisture content was markedly influenced by local soil hydrological properties, which was best shown by the absolute differences between the wet and dry season (Figure 3.7). Soil physical properties like texture and bulk density varied between the gaps and consequently, the soil water retention characteristics varied between gaps. To compare gaps with each other, these differences in soil moisture retention were eliminated by subtracting the soil moisture content of the forest plot near a gap from the soil moisture content of the gap centre or edge plot (see Figure 3.7, the left side of the charts, displayed by the dashed lines around 0% θ).

Figure 3.7 – Next page – Volumetric soil moisture content per depth in the wet (closed circles) season (9/12/97-18/2/98) and dry (open circles) season (19/8/98-25/11/98) in centre, edge and forest plots of the 40, 60, 210, 370, 570, 1280 and 3200m^2 gap. The error bars are two times the standard error. The dashed lines around 0% represents the soil moisture content of that plot at that depth subtracted from the corresponding soil moisture content of the forest with closed circles for the wet season and open circles for the dry season. Consequently, a value larger than zero indicates a soil moisture content wetter than the forest plot and vice versa. The numbers represent the number of observations per period, e.g. 20/23 equals #20 wet

season and #23 dry season. Note that for comparison of the error bars, the position of the markers in a layer are placed at different depths, although they are in fact representing a layer of 20 cm.



Differences in soil physical properties were most evident for the soil moisture profiles of the 210 and 370m^2 gaps compared with the other gaps. These two gaps are positioned only 150m away from each other and the subsoil of in these two gaps had a higher clay content (pers. obs., see soil map Appendix 2.2). These soil properties reduced the percolation rate of rainfall to deeper soil layers thereby increasing the soil moisture content in the wet season in these gaps compared to the other gaps with sandier subsoils. The tube TDR probe recorded volumetric soil moisture but unfortunately, there are no data to examine each gap for differences in matrix potential instead of moisture content, which would have overcome the differences in soil hydrological properties.

Although differences between gaps and between locations in a gap were small, certain patterns were found. In the dry season, soil moisture conditions at centres of gaps up to 210m^2 were wetter than the forest, but gradually changed to drier conditions than the forest in the largest two gaps. The opposite trend was found in the wet season, which had drier conditions than the forest in the smallest gaps and wetter conditions than the forest in the largest gaps. With a few exceptions, soil moisture conditions in the gap edges were almost equal to the conditions of the forest (see the left side of the charts of Figure 3.7). Although differences between forest and gaps were small and not significant, gaps did influence the soil moisture content. Since the soil moisture content in the gap edges was almost similar to the forest, the deviation in soil moisture content in the gaps compared to the corresponding forest sites could not be explained by differences in soil hydrological properties alone. Apparently, the effects of the gaps and gap size were not as straightforward as was assumed.

Microclimate and soil moisture during the '97/'98 El Niño event

In March 1998, at the end of the '97/'98 El Niño event, there was no rain for 3 consecutive weeks. In March 1998, only 20mm of rain was recorded, which was only 12% of the average rainfall in the same month in 1997, 1999 and 2000. In March 1998, humidity at mid-day (11-13h) was 62.3%, which was 8.7% lower than in the same month in 1997 (Figure 3.8). Temperature at mid-day in March 1998 was 28.5°C, which was 1.5°C higher than in March 1997.

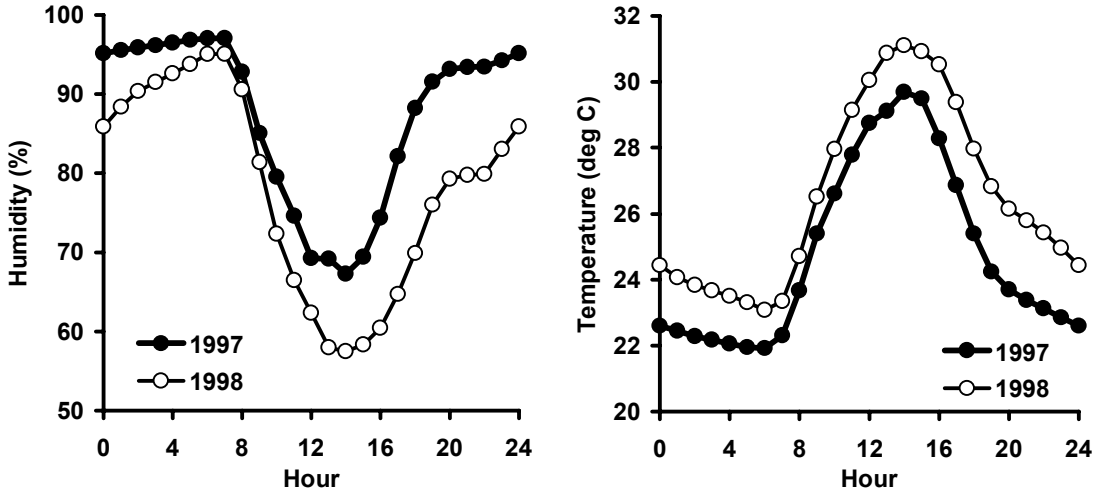


Figure 3.8 Average daytime fluctuation of humidity and air temperature during in March 1998, at the end of the '97/'98 El Niño event, compared March 1997.

At the end of the El Niño event, the smaller transpiration loss in the gaps resulted in gap centres being moister than forest plots or gap edge plots (Figure 3.9). None of the soil moisture profiles were significantly different between the gap centres, gape edges or forest locations (ANOVA per gap, $p<0.05$), except for the soil moisture conditions in the 210m^2 gap at 40-60 cm depth, which was wetter during El Niño. In March 1998, the volumetric soil moisture content was on average 0.23% drier than during the dry season (Figure 3.7 & 3.9), but the gaps were on average 2.59% wetter during the El Niño month than the average during a normal dry season. This is most likely caused by a difference in soil moisture measurement methodology. The El Niño soil moisture content was measured gravimetrically and corrected with bulk density to give volumetric soil moisture content, while soil moisture during the dry season was measured with the TDR tube probe.

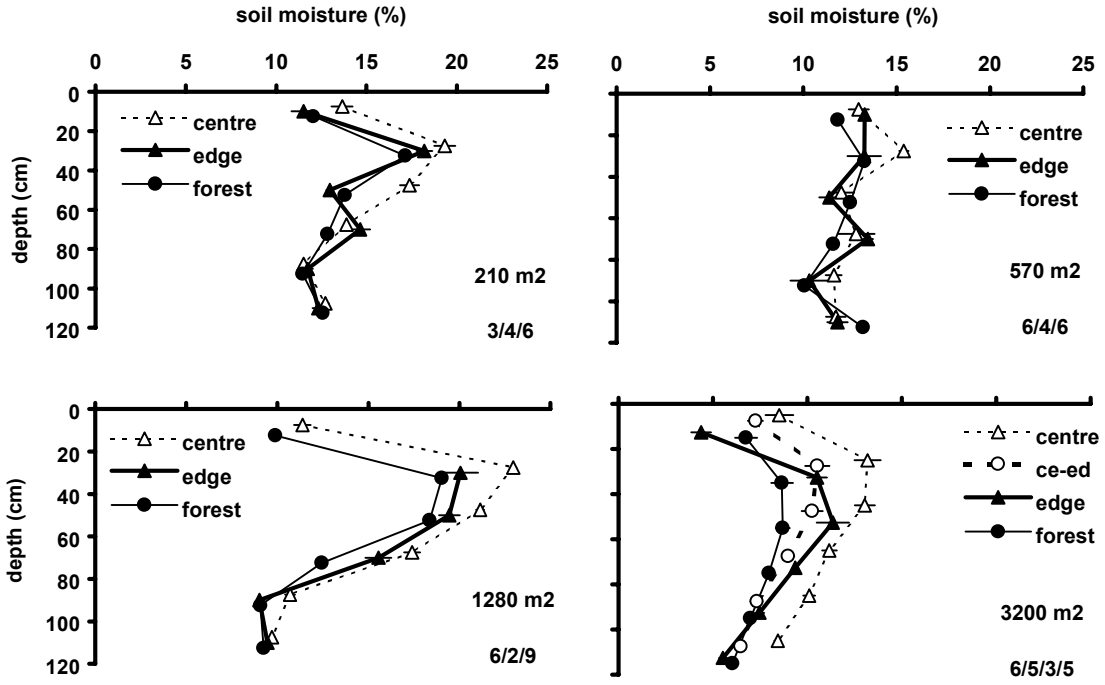


Figure 3.9 Volumetric soil moisture profiles in a 210, 570, 1280 and 3200m^2 gap centre, gap edge and forest at the end of the dry period of the '97/'98 El Niño event (March 1998). The numbers below the gap size represent the number of observations per location, e.g. 3/4/6 equals #3 centre plot, #4 edge plot and #6 forest plot. Note that for comparison of the 1 standard error bars, the position of the markers in a layer are placed at different depths, although they are in fact representing a layer of 20 cm. Volumetric data is based upon measured gravimetric soil moisture content multiplied by the corresponding bulk density per depth.

DISCUSSION

Gap size and gap shape affecting microclimate

Microclimate conditions were strongly influenced by gap size and the effect of the gap on the microclimate was noticeable beyond the perpendicular projection of the canopy opening. Gap size had the strongest influence on solar radiation and air temperature, which increased with increasing gap size up to a gap size of approximately 600m^2 after which no increase was found. The effect of a gap on the air temperature decreased over time, as the vegetation in the gap was regenerating. The influence of a very large gap did not extend further into the forest than 12 m.

The microclimate-influenced area (MIA) of the smallest gaps was 2.0 times larger than the actual gap size and MIA decreased to 1.5 times the actual gap size for the largest gap. Microclimatic conditions did not change gradually from gap centre to forest, since abrupt changes were found at the gap edge, especially in the larger gaps.

These conclusions confirm the hypotheses on microclimate and gap size, although gap size was not the only parameter that influenced the microclimate. Solar radiation was only measured at one location in the 3200m^2 gap centre. However, the analysis of the hemispherical photographs gave an indication of the amount of potential radiation on different locations in the gaps. Gap size was not a good parameter to describe the radiation potential of the 570m^2 gap, since the canopy openness and potential solar radiation was smaller than that of the 370m^2 gap. Moreover, gap size measurements in general are highly subjective to interpretations of the vegetation that forms the gap perimeter and errors of a few to several m^2 in the estimation of the gap size are likely to occur.

The maximum air temperature in gaps was directly related to the total amount and duration of direct solar radiation. However, in very small gaps (< 100m^2), direct radiation could not reach inside the gap during certain periods of the year when the sun is near one of the two tropics. In effect, during those periods of the year, there was no hole in the canopy. This shading effect at low solar altitudes was also important in large gaps with irregular shaped gap edges. Although the gap size *sensu* Brokaw (1982a) might determine a large gap, the gap itself might actually be a group of small connecting gaps with diurnal fluctuations in light, temperature and humidity that were more associated with a smaller sized gap or even forest (Chazdon & Fetcher 1984). These low light levels during certain periods of the year can be of importance to the timing of the gap creation in combination with the germination and early survival of the regenerating vegetation in these small gaps.

Air temperature did not increase above a gap size of approximately 600m^2. The average maximum temperature in these gaps confirms well with the temperature recordings in a 1 ha clearing by Schulz (1960). Air temperature at 1 m above the soil in the largest gaps was influenced by the regrowth of the vegetation. When the vegetation in the gap started to overgrow the temperature stations, the air temperature decreased. In 1998, the high temperature in the 570m^2 gap compared to the air temperature of the 1280 and 3200m^2 gaps was caused by the shading effects of the regenerated vegetation in the larger gaps, while in the 570m^2 and smaller gaps, the vegetation in the gaps did not have any significant effect on the air temperature (Figure 3.2). A relation exists between canopy openness and maximum air temperature (Figure 3.10), which was also found by other researchers working at the same latitude in tropical rain forest gaps in Sabah, Malaysian Borneo (Brown 1993, Whitmore *et al.* 1993). Moreover, Whitmore *et al.* (1993) found that solar radiation significantly correlated with soil and air temperature and humidity in tropical rain forest gaps.

Gap size hardly affected soil temperature, which was more influenced by soil cover. Besides the amount of plant litter on the soil, we expect that soil temperature was also affected by soil moisture content and the vegetation cover. Schulz (1960) showed that soil texture had little effect on soil temperature. Clearly, soil temperature measurements at only one location can give erroneous results. More detailed research is needed to test these assumptions and to determine the precise influence of these parameters on soil temperature.

The influence of the 3200m^2 gap did not extend further into the forest than 12 m from the gap edge. Although the sun did reach further into the forest at low solar altitudes during the early morning or late afternoon, these few hours with low radiation intensity had little influence. Williams-Linera (1990) reported a distance of 20m into the forest edge of a clearing, after which no changes in vapour pressure deficit (VPD) could be measured, while in the edge of a forest fragment, Kapos (1989) reported that at 60m into the forest, the clearing no longer influenced

the VPD. In a later study Camargo and Kapos (1989) found no effect on VPD into the edge of the same forest fragment. The regenerating plants in the edge of a clearing or a gap, can create large local differences that change over time, as was also found in this study.

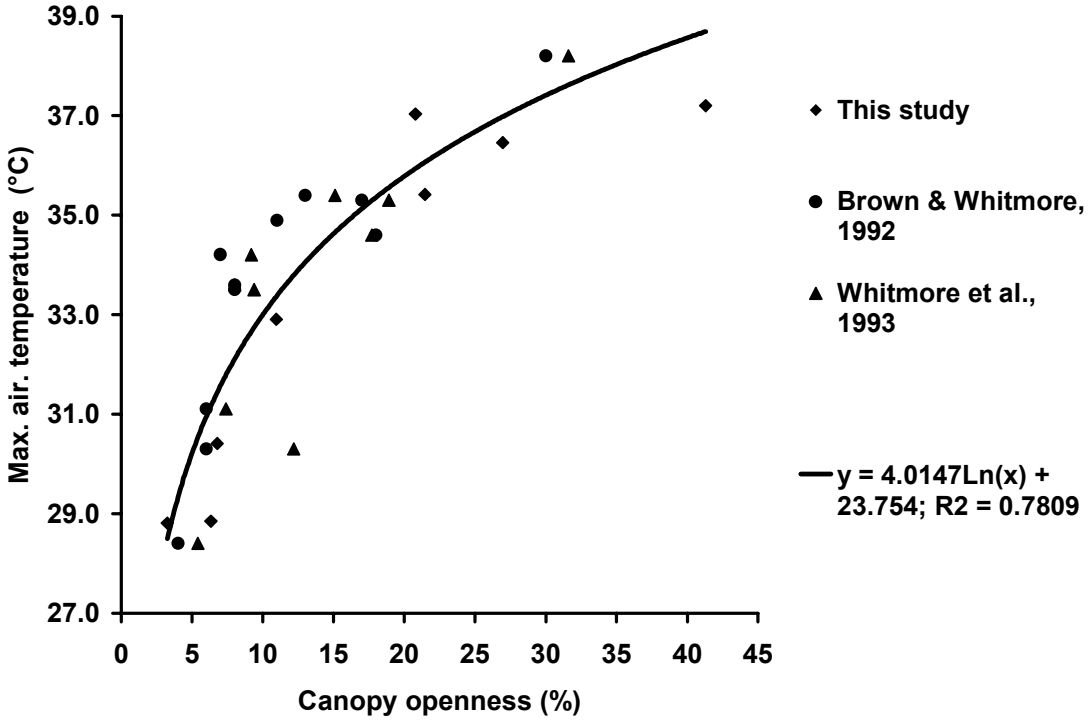


Figure 3.10 Relation between canopy openness and maximum air temperature in tropical rain forest gaps at 5° N.

Complex interaction in gaps on soil moisture

The obvious effects of gap size on microclimate were not found for soil moisture conditions. Instead, the amount of soil moisture was affected by a complex array of soil evaporation, soil disturbance, soil cover, soil hydrological properties, water consumption by the regeneration vegetation in the gaps, water consumption by the vegetation of the gap edge, rainfall history and macro pores due to dead roots. Differences between soil moisture content in gap centres, gap edges and forest plots were small and not significant. In general, in the dry season, soil moisture conditions in gaps smaller than 210m^2 tended to be wetter than the forest, but soil moisture conditions had a tendency to be drier in gaps of 1280m^2 and larger. In contrast, in the wet season, the soil in small gaps was drier than the forest and wetter conditions prevailed in the very large gaps. Gap edges had soil moisture conditions nearly identical to the forest. The hypotheses on soil moisture conditions in gaps, gap edges and forest could be confirmed.

These conclusions are in contrast to the findings in literature, where gaps were found to be wetter than forest (Becker *et al*. 1988, Fetcher *et al*. 1985, Jetten 1994a, Parker 1985, Veenendaal *et al.* 1995, Vitousek and Denslow 1986). On Barro Colorado Island, Panama, Becker *et al.* (1988) measured soil water dynamics in a small gap with canopy openness of 3.8-10.4 % and in a large gap of approximately 160m^2 with canopy openness of 12.0-16.5 %. These gaps can be compared with the smallest gaps of this study, which also had a tendency to have of wetter soils in the dry season. The differences between the published studies and our study can be explained by:

1) The timing of the soil moisture measurements with the TDR tube probe were not in line with the rate of change of the soil moisture content. As shown in Figure 3.6, soil moisture conditions in the topsoil returns to soil moisture content near field capacity within half a day, after which the decrease in soil moisture conditions slowed down markedly until the next rainfall event. For example, a rainstorm of 9.4 mm increased the soil moisture content from 20.9 to 33.6% within one hour, and after 6 hours was the soil moisture content decreased to 20.8%. On the other hand, a period of 36 hours without rain only resulted in a decrease in soil moisture content from 17.7 to 16.1%. Logistical constraints and a limited life time of the battery of the *Trime*FM2 readout device prohibited an adequate sampling procedure with the TDR tube probe. The effect of the amount of rainfall in the preceding day or days on the soil moisture content at any depth was assessed, but no patterns were found. Again, the short reaction time of rainwater drainage to deeper soil layers and high evapotranspiration rates made the analysis not possible.

2) The majority of the soil moisture measurements were taken between 1.5 and 2.5 years after gap creation. Especially in the larger gaps, regeneration of the vegetation had taken place and fast growing pioneer species had attained heights of between 3 to 5 m. Although these relatively young and still small plants are likely to have smaller water consumption than a mature climax tree, their rapid growth rate and high density most certainly was accompanied by a large water use. Consequently, the water demand in the large gaps was larger than in the smaller gaps. Lower soil moisture contents in the large gaps compared to the small gaps will be the result of transpiration loss. As was shown in Table 3.1, in December 1996, half a year after gap creation, the topsoil in gaps was wetter than the forest, which suggested that the water extraction was still small. Mature canopy trees on the gap edge also had a part of their root network situated in the gap. This root network can be well developed 1.5 to 2.5 years after gap creation and these roots can extract vast amounts of water from the gap. The effect of root ingrowth from the gap edge will be larger in small gaps, since the distance to the gap centre is smaller. In conclusion, the difference between gaps of different size will be small, since water consumption in small gaps is dominated by the vegetation at the gap edge and water use in large gaps is subjected to the fast growing pioneer species. Vitousek and Denslow (1986) measured in young (< 7 months) natural tree fall gaps in Costa Rica, which ranged in size between 197 and 600m^2. They found that the crown zone of these gaps was always wetter than the forest. As explained above, this was most likely caused by a limited transpiration in the gap, since the vegetation in the gap is still very young, if present at all.

3) Logging gaps are likely to have more dead roots than natural tree fall gaps. In our study, 54% of the belowground biomass is located in the top 20 cm (see Chapter 2). The sudden death of a mature and healthy tree creates a large amount of dead roots. This is in contrast to a natural tree fall gap, where the tree was slowly dying before it created the gap and a large amount of the roots of the tree had already been decomposed or replaced by other roots from other living trees. Most likely, some of the dead roots in logging gaps had decomposed after 1.5 to 2.5 years after gap creation, leaving behind a network of macro pores. Although the majority of these macro pores run laterally through the soil, the few that do run down vertically might enhance the drainage of rainfall through the soil column.

4) Differences between gaps or within gaps can be caused by differences in soil hydrological properties, like texture and bulk density, which determine the water retention characteristics and the hydraulic conductivity of the soil. These attributes can have much short range spatial variability (Jetten 1994a), which makes the comparison between gaps a difficult one. Even within gaps there can be large differences, as was shown by the effects of gap zones (Table 3.1). These differences are a result of differences in soil cover, like litter layer thickness and type (leaves, branches) or felling debris (logs). The importance of the soil cover was also pointed out by Vitousek and Denslow (1986), who also found large differences in soil water content between different zones in a gap. The crown zone of a gap, in which a large amount of dead leaves and branches were piled up restricting soil evaporation, was almost twice as moist as the root-throw zone of a gap, which consisted mainly of bare soil.

5) Differences between gaps can also be related to the shape of the gap edge. An irregularly shaped edge usually created more shaded areas in a gap during certain periods of the day, which reduced the amount of soil evaporation. Gap heterogeneity is influenced by: size, orientation, shape, underlying topography and height of the surrounding vegetation. Gap shape can be the main factor controlling light penetration into gaps which in turn influences the soil evaporation rate in the gaps (Salvador-van Eysenrode *et al.* 1998).

El Niño

The '97/'98 El Niño event was the most severe drought of the past hundred years (Chapter 2). During the last month of this event, in March 1998, air temperature was higher and air humidity was lower compared to the same month in 1997. This resulted in a larger vapour pressure deficit and consequently, more soil evaporation in the gaps and more transpiration by the vegetation. During this month, the wilting vegetation in gaps and forest had been scouting for soil water and the soil moisture distribution reflected the effects of evapotranspiration only, since the differences in net rainfall – the amount of water, after interception by the vegetation and the litter on the soil, that is actually entering the soil – had vanished. The hypothesis on wetter soils in gaps than in forest was only confirmed in the 1280 and 3200m^2 gaps, but no conclusive evidence was found for an even drier soil in the gap edge. Unfortunately, it was not possible to compare the soil moisture content during the El Niño period and the dry or wet season, because of the differences in soil moisture measurements.

The effects of the dry periods of El Niño were not as severe as one would expect. Small saplings and seedlings in gaps died, although many survived (pers. obs). Litter fall in the forest increased (see Chapter 6) and a thick litter layer developed. Small areas of less than 1 ha near the PGE research area burned, which were almost all human induced, but some trees also survived. The presence of a charcoal layer at approximately 40-45 cm depth (van Dam 1998) suggested that these forest fires have occurred in the past more frequently (Hammond and ter Steege 1998). El Niño and forest fires are normal, though extreme, phenomena of tropical rain forest dynamics.

CONCLUSIONS

Microclimatic conditions are not neccessarily gap size dependend. Air temperature did not increase continuously with gap size, but remained at a hight level in gaps larger than 600m^2. Soil temperature was probably lilewise, or even more, affected by soil cover and soil moisture. The extent of the gap on microclimatic variables was noticeable up to 10m from the gap edge.

Soil moisture was highly variable, both in time – not only between seasons, but also between days, depending on the rainfall history – and in space. No distinct soil moisture patterns were found although topsoil moisture in gaps was generally drier than forest, due to more soil evaporation and soil moisture conditions of the whole soil column was in generally drier in the forest than in the gap, but differences were not significant. No edge effects were found.

Acknowledgements
This study could not have been made without the help of many: Martijn Mekkink, Raymond Niemeijer and Norland Bovell made an almost infinite amount of soil moisture measurements, Bas van Dam and Marcel van Maarseveen provided technical assistance with the constantly failing electronically devices and the powering-up of semi-dead batteries, the ODA (currently DFID) project of David Hammond funded a large part of the TDR tubes, Edzer Pebesma helped with the (statistical) analysis of the soil moisture data and Victor Jetten, Hans ter Steege and Peter Burrough made many useful comments on earlier versions of this paper.

Appendix 3.1 Calibration of the TDR tube probe

The TRIME FM2 read-out device had a build-in calibration curve, which calculated the output of the TDR tube sensor in Volts to volumetric soil moisture content θ ($dm^3.dm^{-3}$). For each tube type, the TDR output (θ in %) was calibrated with gravimetric volumetric soil moisture measurements (θ in %). Two types of TDR tubes were used. Tube 1 was a 1m long TRIME glass-fibre tube with a 1 mm thick wall and Tube 2 was a 1m long glass-fibre tube with a wall thickness of 0.6mm. TDR tube 1 and 2 were calibrated separately by taking soil samples in $100cm^3$ metal rings at 10-15cm and 25-30cm within a 30cm radius of the tubes and comparing the volumetric soil moisture content of these samples with the TDR output. These calibration measurements were made in the dry and wet season of 1999 to obtain a wide range of soil moisture values. The calibration methodology disturbed the soil surrounding the TDR tubes, which meant that no other TDR measurements could be made after a TDR tube was calibrated. No soil samples in $100cm^3$ metal rings were made at depths over 40cm, because this would cause a too much disturbance, since a soil pit of more than $1m^3$ would be required. The assumption was made that the soil physical characteristics of the 20-25 cm sample was representative for the whole subsoil, since the average bulk density (BD) of the topsoil (0-20 cm) was 1.32 $kg.m^{-3}$ (range 1.21-1.43) and of the subsoil was 1.43 $kg.m^{-3}$ (range 1.34-1.54) and the average sand content of the topsoil and subsoil was 92% (range 88-97%) and 81% (range 77-84%), respectively. The results of the TDR tube probe calibration per tube type per depth are given in Table 3.3. On average, the measured TDR value was 26% higher (4.4% θ) than the actual θ and the TRIME tube (tube 1) overestimated the actual θ more than tube 2.

Table 3.3 Calibration results of 2 types of TDR tubes at 2 depths (BD: bulk density $kg.m^{-3}$, VSM: volumetric soil moisture $dm^3.dm^{-3}$, A & B linear regression parameters).

		BD	TDR			VSM			TDRcal = A · TDRread + B		
		avg	avg	range	n	avg	range	n	A	B	R^2
Tube 1	**5-10 cm**	1.27	19.9	12.8-24.7	8	13.5	9.2-19.2	8	1.959	-6.503	0.975
Tube 1	**20-25 cm**	1.41	23.4	16.2-28.0	8	19.1	12.9-25.7	6	0.911	5.228	0.978
Tube 2	**5-10 cm**	1.30	20.5	10.9-35.2	25	16.4	5.9-25.7	23	1.528	-1.110	0.921
Tube 2	**20-25 cm**	1.35	21.2	12.4-27.0	21	18.5	9.6-27.4	17	0.968	1.578	0.904

(Note: TDRread is the output of the TRIME FM2 device. TDRcal is the calibrated TDR soil moisture content and equals the measured VSM.)

The 4-wire FDR probe had been calibrated by Sluiter and Smit (1999) and their calibration data was used. Due to premature malfunction, the TDR 2-wire probe could not be calibrated for the PGE soil, but the manufacturers mineral soil calibration was used.

Trime TDR tube probe

4 FORGAP: A MODEL FOR SOLAR RADIATION, EVAPOTRANSPIRATION AND SOIL WATER DYNAMICS IN TROPICAL RAIN FOREST GAPS

with Theo van Asch

Abstract
A PCRaster model called FORGAP, *FORest GAP*, is presented that calculates radiation, evapotranspiration and soil water dynamics in and around forest gaps. Model structure, equations, input and output are discussed. After optimalisation with the program PEST, the calibrated model calculated soil water content of the topsoil well.

INTRODUCTION

Modelling a forest-gap system

Microclimate and soil hydrology in tropical rain forest gaps involves form spatial and temporal patterns, some of which are gap independend, some have an obvious relation with gap size and some are also dependend on for example vegetation attributes (see Chapter 3). Factors that contribute to these complex patterns are the variability of soil hydrological parameters, the degree of disturbance in the gap, the soil cover, the differences in the amount of vegetation that survived the logging, the gap shape and the orientation of the gap to the sun. Modelling the microclimate and water balance of forest is a useful method to study these complex interactions, and such a model can identify the parameters that have the largest impact on the microclimate and soil water balance.

Many forest hydrological models have been made and are used in a wide variety of forest related problems (Bouten 92, Dekker 2000, Dolman 1987, Draaiers 1993, Jetten 1994a, Noij *et al.* 1993, Robberts *et al.* 1993, Schellekens 2000, Schuttleworth *et al*. 1984a). Unfortunately, none of these models were designed to adress the specific problems associated with forest gaps. Most of these models are one-dimensional and would simulate gap environments by simply running the model with very small plants representing seedlings and saplings or with no vegetation at all (e.g. Jetten 1994a). Modelling spatial patterns in a gap and its surroundings would require a large number of input data and subsequent model runs. Also, it would be impossible to study the effects of multiple gaps in a small area (e.g. 1 ha). Therefore, a new modelling approach was necessary.

The *FORest GAP* model FORGAP was written in the PCRaster dynamic modelling language (PCRaster 1996, Wesseling *et al.* 1996). PCRatsre consist of a set of tools for storing, manipulating, analysing and retrieving geographic data. PCRaster is a raster Geographical Information System (GIS) augmented with a programming language that enables the construction of dynamic spatial models. PCRaster is DOS based, using a simple ASCII editor to write a model script. FORGAP was developed for the Pibiri Gap Experiment (PGE) and although the major components are one dimensional, FORGAP has 3D features. A one-dimensional water balance is calculated for each grid cell. The height of vegetation that is present in that cell determines whether the cell is forest or gap. The amount of cells assigned as gap that lie next to each other determine the gap size. Besides rainfall, the driving force of all

hydrological fluxes in terrestrial ecosystems is solar radiation. Solar radiation regulates soil evaporation and transpiration by plants. Therefore, one of the important components of FORGAP is the modelling of the amount of solar radiation. This radiation component of the model has 3D features, since the shading effects of the trees at the gap edge are an essential part of the calculation of radiation.

Calibrating FORGAP with PEST

FORGAP consists of many model parameters and variables, which are either based upon field data, literature information or which have to be estimated. A model parameter is a fixed value of a property that does not change in time or space, while a variable is a changing property either in time or in space or both. There are two types of variables: input variables like microclimatic data and model variables. The output of the model must be verified with observations: model output property for which there is a corresponding 'real-world' measurement. These observations are used to fine-tune the model parameters or variables. In the case of FORGAP, soil moisture measurements were the only observations that could be used to calibrate the model. Soil hydrological parameters were selected in the calibration process.

Calibrating a model is done by running the model various times thereby constantly changing a model parameter in the search for the best estimate of the model output with the observations. This process becomes complex if there are many model parameters that have to be calibrated, since each combination between two or more parameters have to be tested. This iterative procedure was facilitated by the software program PEST (Watermark Computing 1994), which is discussed in the last section of this chapter.

Model structure of FORGAP

FORGAP is based upon the one-dimensional finite-element model SOAP (Jetten 1994a & 1994b) and consists of three sub-modules that are executed in subsequent order (Figure 4.1). The time step of the model is one hour and although every microclimatic variable or water flux can be exported per time step, daily, monthly or yearly sums are also reported. Changes in time for selected cells can be reported as separate ASCII files.

The radiation sub-module calculates the potential radiation on the vegetation – either mature forest or saplings in the gap – and on the soil. The calculation of the solar radiation is mainly based upon WINPHOT (ter Steege 1997) and Oke (1987). Latitude and altitude of the study area and information on the height of the vegetation is used. The height difference between the undisturbed forest and the seedlings and saplings in the gap creates shaded parts in the gap in early morning and late afternoon. During those hours of low solar altitude, solar radiation can penetrate into parts of the forest at the gap edge. Thus, these differences in the amount of radiation in certain parts of a gap create spatial patterns of radiation.

Potential evapotranspiration, interception evaporation and through fall are calculated in the evaporation sub-module. Vegetation parameters like leaf area index, canopy openness and litter mass are needed in this module as well as microclimatic data. A sapling growth model is incorporated into this sub-module, which is based upon height growth data during the first three years after logging in the PGE (Rose 2000). Rainfall interception is based upon Rutter *et al.* (1971) and evapotranspiration is calculated with Penman and Penman-Monteith as used in SOAP (Jetten 1994b) and SWATRE (Feddes *et al.* 1978).

The soil water sub-module consists of soil physics based on the Richards equation for unsaturated flow and the pedo-transfer functions of Mualem (1976) and van Genuchten (1978, 1980). A finite-difference method is used in solving the partial differential non-linear flow equations, based upon SWATRE (Feddes *et al.* 1978). Actual transpiration is calculated with a reduction function related to the amount of soil moisture.

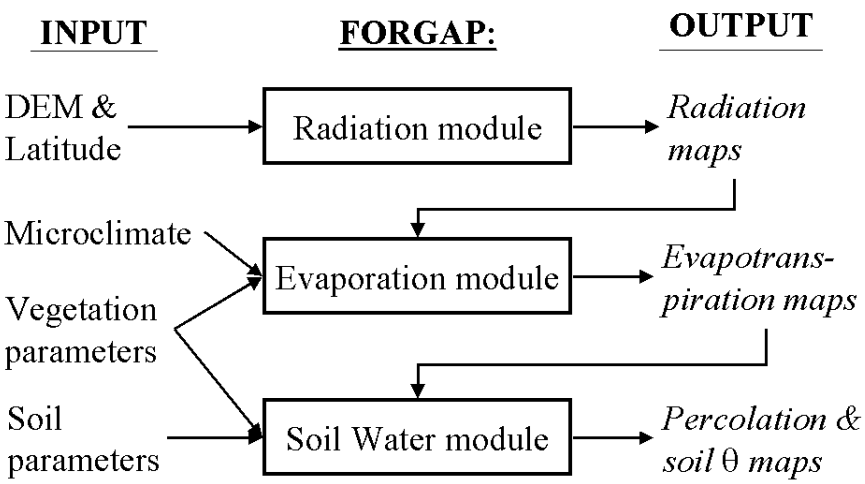


Figure 4.1 Model structure of FORGAP with user input, sub-modules and output maps. (DEM: Digital Elevation Model, θ: soil moisture content)

The following sections describe subsequent sub-modules of FORGAP based upon literature equations. Model equations that are based upon research observations are described in the appendices of this chapter. Appendix 4.9 contains a list of all model parameters used in this chapter.

SOLAR RADIATION

Solar radiation on terrestrial ecosystems

Life on earth is predominantly influenced by the amount of solar radiation, water and nutrients. Solar radiation is the most important source of energy for any vegetated land surface. Moreover, a major component of the hydrological cycle – whether on a catchment scale or globally – is the evaporation of water due to solar energy. Shading effects of objects like mountains, buildings or tree stands can create spatial patterns in the distribution of solar radiation. Solar radiation in these different geographical settings can relatively easily be modelled. Several GIS based radiation models exist that calculates solar radiation on a land surface. Kumar *et al.* (1997) calculated the annual solar radiation distribution for a mountainous terrain with the integration of shaded areas. McKenney *et al.* (1999) applied the model solar radiation model SRAD to forested areas. Both models calculate solar radiation on the top of a land surface only, which are the treetops for a forested area, and do not provide information on solar radiation inside the forest stand. This information is essential for the light competition between regenerating trees species in forest gaps and gap edges (Poulson and Platt 1989). Unobstructed direct solar radiation can only reach the forest floor through an opening in the canopy. The size of a forest canopy gap has a direct influence on the amount of irradiance in the gap, where seedlings are germinating and small saplings are establishing. It is not difficult to imagine that in small gaps ($< 100m^2$), light only reaches the soil with the sun directly overhead, while on the other hand, large gaps ($> 500m^2$) receive direct radiation during several hours of the day. Besides the large variation in light intensity between gaps of different sizes, there is also a large spatial variation of radiation within gaps. The within-gap variation is caused by gaps of different shapes and orientations to the sun. In addition, the gap edge area – the area under the closed forest but on the edge of the gap – also receives direct radiation during certain hours of the day and the amount of radiation increases with increasing gap size. As a consequence, the actual or effective gap area (Popma *et al.* 1988) is usually larger than the perpendicular projection of the gap perimeter (Chapter 3) and can be of major importance for forest regeneration.

Layout of the radiation sub-module

The radiation sub-module calculates the flux of incoming potential radiation on 1) the top of the vegetation; average height of the trees of the forest and the seedlings in the gap, 2) the seedlings or saplings in the gap edge and 3) the soil surface, either in the gap or in the forest. The main input for this module is a digital elevation model DEM that describes the height of the vegetation (Figure 4.2). Additional information is required on the latitude and the altitude of the research area. The radiation sub-module consists of three sections. The first section deals with the position of the sun. The second section calculates the amount of solar radiation on a surface. The third section calculates the effect of shading and the radiation extinction through the vegetation. The model time step is one hour, so daily and annual variability can be calculated.

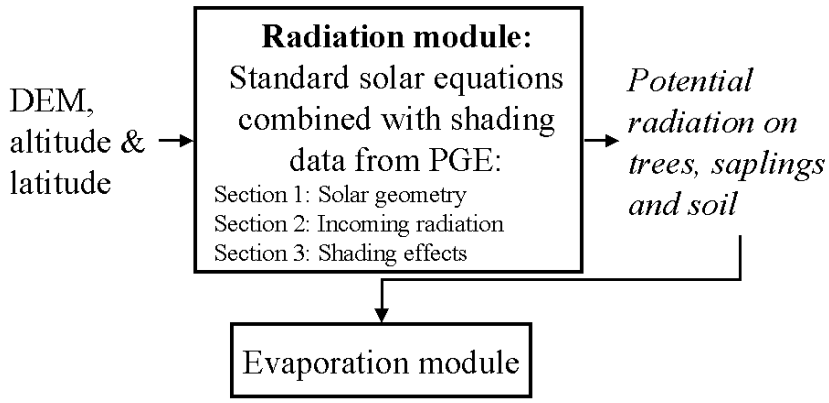


Figure 4.2 The radiation sub-module of FORGAP.
(DEM: Digital Elevation Model of the vegetation height)

Solar geometry and incoming solar radiation

Solar geometry
Potential solar radiation is the radiation of an unobstructed or cloudless sky. The magnitude of the potential solar radiation depends on the position of the sun – the solar altitude or solar angle – during the day, the inclination of the solar rays with the earth's surface, the amount of radiation at the outer layer of the earth's atmosphere, the transmissivity of the sky and the altitude of the earth's surface. The position of the sun and inclination of the solar rays is calculated with standard solar geometry functions, as given below.

Movement of the sun Solar declination is the annual fluctuation of the sun between the two tropics and varies between –23 and +23 degrees latitude. Solar declination δ (deg) is calculated per *Day* (Julian day number) (Supitt et al. 1994):

$$\delta = -23.4 \cdot \cos(360 \cdot (Day + 10) / 365) . \quad (1)$$

The hour angle describes the movement of the sun around the earth in 24 hours, which equals 15 degrees longitude per hour (360°/24h). The hour angle η (deg) is calculated for each *Hour* (whole hour of the day):

$$\eta = 15 \cdot (Hour-12) . \quad (2)$$

The position or height of the sun above the horizon is called the solar altitude or solar angle. Solar altitude α (deg) is calculated for each location, determined by the location's latitude φ (deg), declination and hour angle (Gates 1980):

$$\sin \alpha = \sin \varphi \cdot \sin \delta + \cos \varphi \cdot \cos \delta \cdot \cos \eta \ . \quad (3)$$

Solar azimuth Solar azimuth is the angle between the solar rays and the North-South axis of the earth. Solar azimuth β_s (deg) is calculated by (Oke 1987):

$$\cos \beta_s = (\sin \delta \cdot \cos \varphi - \cos \delta \cdot \sin \varphi \cdot \cos \eta) / \cos \alpha \ , \quad (4)$$
for *Hour* ≤ 12: $\beta_s = \beta_s$,
for *Hour* > 12: $\beta_s = 360 - \beta_s$.

Surface azimuth or aspect and slope Surface azimuth or aspect β_l (deg) is the orientation of the land surface or slope to the North-South axis of the sun. Slope χ (deg) is the maximum rate of change in elevation. Both aspect and slope are predefined functions in PCRaster. However, the models of the experimental gaps that were used in the FORGAP were flat, with zero slopes and zero aspect.

Incidence of the solar rays on the surface The angle of incidence is the angle between the perpendicular plane of the incoming solar rays and the surface on which they are projected, defined by the aspect and slope of that surface. The angle of incidence ι (deg) is calculated with the solar angle α (deg), the slope of the land surface χ (deg), the azimuth of the sun β_s (deg) and azimuth of the land surface β_l (deg) (Campbell 1981):

$$\cos \iota = \cos \alpha \cdot \sin \chi \cdot \cos(\beta_s - \beta_l) + \sin \alpha \cdot \cos \chi \ . \quad (5)$$

Solar radiation
The second section of the radiation sub-module of FORGAP calculates the potential solar energy. The amount of solar radiation that reaches the outer atmosphere is decreased by the travelling distance of the solar rays through the sky to the surface, the transmissivity of the sky and the cloud factor.

Radiation in the outer atmosphere Solar energy at the outer layer of the atmosphere S_{out} (W.m^{-2}) is calculated by (Kreider & Kreith 1975):

$$S_{out} = S_c \cdot (1 + 0.034 \cdot \cos(360 \cdot Day/365)) \ , \quad (6)$$

where S_c (W.m^{-2}) is the solar constant of 1367 W.m^{-2} (Duffie & Beckman 1991). The solar 'constant' is subject to much discussion. Gates (1980) gives a value of 1360 W.m^{-2}. The NASA reports a value of 1353 W.m^{-2} (Jansen 1985), while Duncan *et al.* (1982) give a value of 1367 W.m^{-2}. Monteith and Unsworth (1990) measured the highest value of 1373 W.m^{-2}. The World Radiation Centre uses a value of 1367 W.m^{-2} (Duffie & Beckman 1991) and this value is also used in this study.

The solar radiation energy that reaches the earth's surface is decreased due to the length of the air mass it has to pass through and the transmissivity τ (% or fraction) of the sky. The radiation flux through a hypothetical plane normal to the beam S_{nor} (W.m^{-2}) is given by (Gates 1980):

$$S_{nor} = S_{out} \cdot \tau^{Mh} \ , \quad (7)$$

in which M_h (% or fraction) is the relative path length of the optical air mass at altitude h (m). Transmissivity τ is usually between 0.5 and 0.8, but can be as low as 0.4 in the tropics (Whitmore *et al.* 1993), but mostly – as in this study – the value of 0.6 is used (Gates 1980). To calculate the relative path length of an optical air mass at altitude h (m), the relative path length

of an optical air mass at sea level M_0 (% or fraction) is corrected for the atmospheric pressure at altitude h. M_h (% or fraction) is calculated using (Kreider & Kreith 1975):

$$M_h = M_0 \cdot P_h / P_0 , \tag{8}$$

in which P_h / P_0 (mbar.mbar^{-1}) is an atmospheric pressure correction. The relative path length of the optical air mass at sea level M_0 is obtained by (Kreider & Kreith 1975):

$$M_0 = \sqrt{(1229 + (614 \cdot \sin \alpha)^2)} - 614 \cdot \sin \alpha . \tag{9}$$

The atmospheric pressure correction P_h / P_0 is written as (List 1984):

$$P_h / P_0 = ((288 - 0.0065 \cdot h) / 288)^{5.256} . \tag{10}$$

Radiation at earth surface The incoming radiation normal to the beam S_{nor} must be corrected by the orientation and slope of the surface, defined by the angle of incidence ι, to calculate the incoming radiation S_{dir} (W.m^{-2}) on the earth's surface:

$$S_{dir} = S_{nor} \cdot \cos \iota . \tag{11}$$

Direct light is scattered in the atmosphere. This daylight scattering or diffuse radiation is approximately 15% of direct radiation (Gates 1980). A more accurate empirical estimation for diffuse radiation S_{dif} (W.m^{-2}) in a clear not dust-free sky reads as (Liu and Jordan in Gates 1980):

$$S_{dif} = S_{out} \cdot (0.271 - 0.294 \cdot \tau^{Mh}) \cdot \sin \alpha . \tag{12}$$

During daylight when the sun is above the horizon, it is assumed that all cells receive the same amount of diffuse radiation as calculated with equation 12. Total incoming radiation S_{in} (W.m^{-2}) is the sum of direct and diffuse radiation:

$$S_{in} = S_{dir} + S_{dif} . \tag{13}$$

Total incoming radiation S_{in} as calculated with equation 13 is actually a radiation flux for that moment. In the procedure give above, radiation is calculated per time step, being one hour. If this amount of radiation is used in a water balance model, the amount of radiation and therewith the amount of evapotranspiration will be overestimated or under estimated, depending on the time of the day and the position of the sun. To compensate for that, the average radiation of the present time step and the previous time step is calculated, which is valid for the present time step.

Radiation in forest and gap

A seedling or sapling in a gap does not receive direct solar radiation if the angle to the top of the trees at the gap edge, in the azimuth direction of the sun β_s, is steeper than the angle of the rays of the sun; the solar angle or solar altitude α (Figure 4.3). At high solar altitudes, the shaded part of a gap will be small or absent. Shaded areas only receive diffuse radiation plus a small portion of direct radiation that penetrates through the vegetation that surrounds the gap. In this forest/gap system, radiation is calculated for (Figure 4.3):

– Radiation on the mature forest trees and the seedlings in the gap that are not in the shade; vegetation radiation R_{veg} (W.m^{-2}).
– Radiation on the seedlings in the shaded part of the gap; R_{shad} (W.m^{-2}).

– Radiation on the seedlings in the gap edge area, under closed forest, that receive direct radiation due to the presence of the gap; edge radiation R_{edge} (W.m^{-2}).
– Radiation on the soil; R_{soil} (W.m^{-2}). A vegetated surface has holes in the canopy through which light can reach the soil directly. The amount of radiation on the soil depends on the structure of the vegetation above, which determines the canopy openness, and the proximity of open spaces in the forest, e.g. forest gaps. The openness of the canopy differs per forest type and depends to a large extent on leaf area *LA* (m^2), or expressed as leaf area per ground area, the leaf area index *LAI* (m^2.m^{-2}).

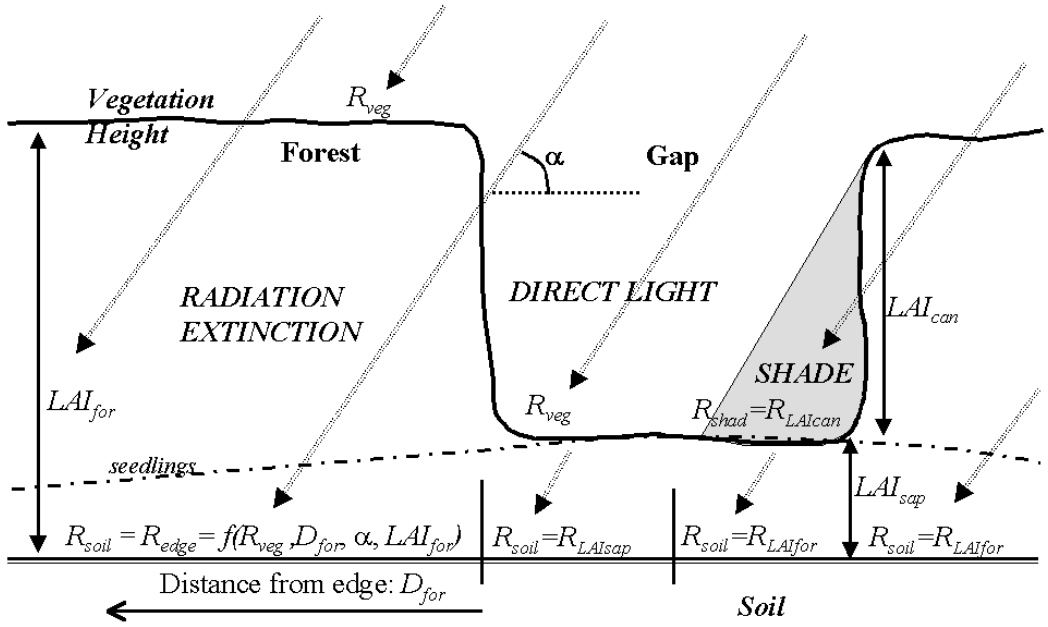


Figure 4.3 Hypothetical forest gap with different effects of shading on soil and sapling radiation. The grey area is in shade. (See text for the explanation of the abbreviations)

A well-known function for the radiation extinction through the vegetation was given by Monsi and Saeki (1953) as $R_{soil} = R_{top\ vegetation} \cdot e^{-k \cdot LAI}$, in which *k* (-) is a radiation extinction factor. The extinction factor is small for vertically inclined leaves (e.g. grasses), but high for horizontally arranged leaves (forests between 0.4 and 0.8) and it also depends on wavelength. A value of 0.6 is normally used (Roberts *et al.* 1993). However, at low solar altitude, the travelling distance of the solar rays through the vegetation is longer and consequently, a larger leaf area is encountered. Therefore, equation 14 is adjusted for solar altitude α and the radiation at the soil R_{soil} (W.m^{-2}) becomes now:

$$R_{soil} = R_{veg} \cdot e^{-k' \cdot LAI / \sin \alpha} . \qquad (14)$$

A new value for the extinction coefficient *k'* was found of 0.29 (Appendix 4.1). Three different values of *LAI* are recognised: 1) LAI_{for}, which is the *LAI* of the undisturbed 28 m height forest of 5.91 m^2.m^{-2}, 2) LAI_{sap}, which is the *LAI* of the saplings as a function of sapling height (Appendix 4.6) and 3) LAI_{can}, the *LAI* of the forest above the saplings for which is valid $LAI_{can} = LAI_{for} - LAI_{sap}$. These three *LAI* values are used in equation 14 to calculate R_{soil}, whereby LAI_{for} is used to calculate R_{soil} in the forest understorey on the shaded side of the gap, LAI_{sap} is used to calculate R_{soil} in the illuminated part of the gap and LAI_{can} is used to calculate R_{soil} in the shaded part of the gap.

The soil radiation in the illuminated gap edge area can be modelled with a double extinction coefficient, since it consists of radiation through the vegetation from above and radiation through the vegetation – mostly tree stems – from the gap edge. The radiation on the soil in the

illuminated part of the gap edge area R_{edge} or R_{soil} (W.m^{-2}) is calculated analogous to equation 14, but with a correction for distance to the gap edge D_{for} (m) and a second extinction factor c:

$$R_{edge} = (R_{veg} - R_{veg} \cdot e^{-k' \cdot LAIfor / \sin\alpha}) \cdot e^{-c \cdot Dfor / \sin\alpha} + R_{veg} \cdot e^{-k' \cdot LAIfor / \sin\alpha} \quad (15)$$

The extinction factor c (-) can be viewed as a measure for the extinction through the stems and small vegetation in the understorey and was determined experimentally at 0.295 (Appendix 4.1). The radiation on the soil in the gap is determined with equation 14 with *LAIsap* and the radiation on the soil in the understorey is calculated with equation 15.

EVAPOTRANSPIRATION

Layout of the evaporation sub-module

The water balance of the aboveground part of the forest is calculated in two flow directions: rainfall and through fall to the soil and evapotranspiration return to the atmosphere. The radiation sub-module produced maps of potential radiation that are needed as input in the evaporation sub-module and additional input is required on microclimate and vegetation parameters. The evaporation sub-module produces maps with potential evapotranspiration and net-rainfall, which are used in the soil water sub-module. The aboveground water balance of a forest / gap system consists of three sections that calculate: 1) the net radiation, 2) the potential evapotranspiration fluxes and 3) the rainfall and throughfall fluxes.

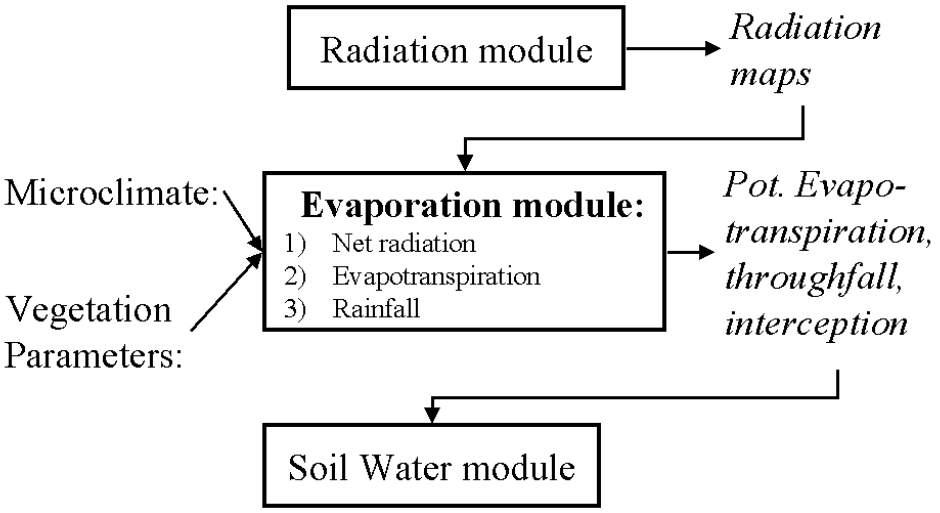


Figure 4.4 The evaporation sub-module with the required input and resulting output within the FORGAP model structure.

Net radiation

The energy that is available for evapotranspiration is net radiation, which is also used to calculate the sapling growth rate in the gaps. Sapling growth is not an integral part of the model, but a correlative relation between sapling growth and the net radiation sum has been used (Appendix 4.2). Net radiation Rn (W.m^{-2}) is the sum of short wave and long wave radiation:

$$Rn = S_{in} - S_{out} + L_{in} - L_{out} . \quad (16)$$

The incoming short-wave radiation S_{in} (300-3000 μm wavelength) is equal to the global radiation, which is R_{veg}, R_{edge} or R_{soil} as calculated in the radiation submodule. The outgoing

short-wave radiation S_{out} is the reflected part of S_{in} on the earth's surface. The short-wave radiation balance (W.m^{-2}) can be rewritten as:

$$S_{in} - S_{out} = (1\text{-}r) \cdot cl \cdot S_{in} , \quad (17)$$

with r (-) the reflection coefficient or albedo and cl the cloud factor (fraction; 1 clear sky, 0 completely obstructed sky, see Appendix 4.3). The albedo determines the amount of S_{in} that is being reflected by the earth's surface. Shuttleworth *et al.* (1984b) found a relation between the albedo of an Amazonian tropical rain forest and the solar angle α (deg):

$$r = 0.1509 - 0.00136 \cdot \alpha + 1.23 \cdot 10^{-5} \cdot \alpha^2 . \quad (18)$$

Equation 18 results in an average daytime albedo of the research area of 0.125. The long-wave radiation balance $L_{in} - L_{out}$ (W.m^{-2}) depends on the air temperature T (°C) and the actual vapour pressure e_a (mbar) and is corrected by the cloud factor cl and the leaf area of the vegetation, expressed as leaf area index LAI (m^2.m^{-2}) (Goudriaan 1977). The incoming long wave radiation L_{in} and outgoing long wave radiation L_{out} depend on the bulk air temperature and emissivity of the surface. The long-wave radiation balance can be approximated by:

$$L_{in} - L_{out} \cong L_{out} = - \sigma (T+273.15)^4 \cdot (0.56 - 0.079 \sqrt{e_a}) \cdot (0.1 + 0.9\ cl) , \quad (19)$$

where σ is the Stefan Boltzman constant ($5.67 \cdot 10^{-8}$ W.m^{-2}.K^{-1}). L_{out} fluctuates markedly throughout the day and its magnitude is much greater than L_{in} (Oke 1987). The actual vapour pressure is a measure for the amount of water that can evaporate into the moist air until the air is saturated:

$$e_a = RH \cdot e_s , \quad (20)$$

with RH the relative humidity (% or fraction) and e_s the saturated vapour pressure (mbar). The saturated vapour pressure depends has an empirical relationship with temperature T (°C) (Tetens 1930):

$$e_s = 6.107\ e^{(17.27 \cdot T) / (T + 237.3)} . \quad (21)$$

Analogous to the potential radiation, the average value of the long-wave radiation balance of the current and the previous time step is used to calculate Rn for the current time step. In the forest understory, the net radiation cannot be based upon a long wave radiation that is valid for an exposed surface like a gap. The microclimate of the understory has a lower temperature and a higher relative humidity (see also Chapter 3). A correction is needed for the microclimate as measured in a gap, which is valid in the forest understory. The calculation of these corrected temperature and humidity are based upon field data (Appendix 4.3).

Evapotranspiration

Evapotranspiration is the combined term for evaporation of intercepted water – either on the leaves of the vegetation or on the soil litter –, soil evaporation and transpiration of the vegetation. Three types of evapo(transpi)ration are calculated:
1. Evaporation of a wet vegetated surface; evaporation of rain that was intercepted by the vegetation and that remained on the vegetation after a rainstorm: interception evaporation,
2. Evaporation of a dry vegetated surface; potential transpiration of the vegetation and

3. Evaporation of open water or Penman evaporation; this evaporation flux is used to calculate the potential soil evaporation and the evaporation of rain that remained on the litter layer after a rainstorm: litter evaporation.

Evaporation of a wet vegetated surface
Evaporation of a wet vegetated surface E_{wet} determines the potential amount of interception evaporation E_i (mm). The actual amount of E_i depends on the amount of water on the vegetation that is available for E_{wet}, which is the amount of water that is stored of the leaves and stems of the vegetation (see also rainfall section). E_{wet} (mm) is calculated by (Monteith 1965, 1981):

$$E_{wet} = \frac{s \cdot Rn_{veg} + \rho \cdot Cp \cdot (e_s - e_a) / r_a}{\lambda \cdot (s + \gamma)} \quad , \tag{22}$$

s : slope of the vapour pressure curve (-),
Rn_{veg} : net radiation on the vegetation (W.m^{-2}),
λ : latent heat of evaporation (J.kg^{-1}),
ρ : air density (1.2047 kg.m^{-3}),
Cp : specific heat of air at constant pressure (1013 J.kg^{-1}.°C^{-1}),
r_a : aerodynamic resistance (s.m^{-1}),
γ : psychrometric constant (mbar.°C^{-1}).

The slope of the vapour pressure curve s (-) is calculated with the empirical relation (Tetens 1930):

$$s = 4098\, e_a / (T + 237.3)^2 \, . \tag{23}$$

The latent heat of evaporation λ (J.kg^{-1}) (Harrison 1963) and the psychrometric constant γ (mbar.°C^{-1}) (Brunt 1952) are calculated by:

$$\lambda = 2.051 \cdot 10^6 - 2370 \cdot T \quad \text{and} \tag{24}$$

$$\gamma = (Cp \cdot P_a \cdot 100) / (\varepsilon \cdot \lambda) \, , \tag{25}$$

where P_a is the air pressure (mbar) and ε is the ratio of the molecular weight of water vapour and dry air (0.622). The aerodynamic resistance r_a (s.m^{-1}) depends on the prevailing wind according to:

$$r_a = u_c / (u_f)^2 \, , \tag{26}$$

where u_c (m.s^{-1}) is the wind speed above an object and u_f (m.s^{-1}) is the friction velocity of the object: the vegetation. In the model, the aerodynamic resistance is restricted to 85 s.m^{-1}, as was found in an Amazonian rain forest (Shuttleworth *et al.* 1984a). The evapotranspiration flux is strongly influenced by the vapour pressure of the air directly above the evaporating surface: the boundary layer. Evapotranspiration becomes limited in air with a vapour pressure near saturation. Wind is constantly mixing the moist air of the boundary layer with dryer air above the boundary layer. The aerodynamic resistance of the object determines the total mixing area. The aerodynamic resistance of an object depends on the height of the object and the roughness of the object. The friction velocity u_f is a measure for the drag force of an object to the prevailing wind above that object u_c. Under neutral conditions, the following relation is valid (Thom 1975):

$$u_f / u_c = \kappa / \ln((H - d) / z_0) , \quad (27)$$

κ : von Karman constant (0.41),
H : height vegetation,
d : zero-plane displacement (m): $d = 0.7 \cdot H$, (28)
z_0 : roughness length (m): $z_0 = 0.1 \cdot H$. (29)

If wind speed is not measured above the vegetation that is being studied, but in a nearby meteorological station, the measured wind speed in that meteo station u_{met} (m.s^{-1}) has to be transformed to the actual wind speed above the forest u_c. Wind speed increases logarithmically with height and at certain height above the ground; the 'meso' wind speed is equal for surfaces with a different roughness below (Wieringa and Rijkoort 1983). The wind speed at any height above a surface with roughness length z_0 (m) can be calculated from wind speed measurements at a nearby meteo station with a different measuring height and roughness length. For tall objects like a forest, the extrapolation height H (m) also has to be corrected for the zero-plane displacement d of the forest. Wind speed above a forest u_c (m.s^{-1}) can be found with:

$$u_c = u_{met} \frac{\ln((H-d)/z_0) \cdot \ln(z_{meso} / z_{0met})}{\ln(z_{meso} / z_0) \cdot \ln(H_{met} / z_{0met})} , \quad (30)$$

with z_{0met} ($z_{0met} = 0.1 \cdot H_{met}$) the roughness length of the meteorological station (m) with wind speed measurements at height H_{met} (m). The height of the meso wind z_{meso} is taken at 60m. Specific details of wind speed measurements and the wind profile of the study area can be found in Appendix 4.4.

Evaporation of a dry vegetated surface
Dry vegetation evaporation or potential transpiration E_{tp} (mm) is calculated according to Penman-Monteith (Monteith 1965, 1981):

$$E_{tp} = \frac{s \cdot Rn + \rho \cdot Cp \cdot (e_s - e_a) / r_a}{\lambda \cdot (s + \gamma \cdot (1 + r_c / r_a))} , \quad (31)$$

where Rn (W.m^{-2}) is the net radiation and r_c is the canopy resistance, which is a measure of bulk stomatal resistance. In a 35-40m tall Amazonian forest, Shuttleworth *et al.* (1984a) reported a value of 130 s.m^{-1}, while in a mountainous forest of 20-25 m in Puerto Rico, Schellekens *et al.* (2000) found an R_c of 58 s.m^{-1}. The PGE forest has a height of 28-32 m and therefore the average value of 94 s.m^{-1} is used in the model. The net radiation on the vegetation Rn_{veg} is used for the potential transpiration of the forest and the seedlings in the gap and the net radiation on the seedlings in the understorey Rn_{edge} is used for the transpiration of the saplings in the gap edge area. The actual transpiration depends on the soil moisture condition and is explained in the section describing the soil water sub-module.

Evaporation of open water or Penman evaporation
Potential soil evaporation E_{sp} and litter evaporation E_l (mm) are calculated with Penman's (1948) open water evaporation E_{pen}. The net radiation on the soil Rn_{soil} (W.m^{-2}) is used in the equation as well as the climatic data corrected for forest understorey conditions, as explained above (see also Appendix 4.3). E_{pen} (mm) reads as:

$$E_{pen} = (s_s \cdot Rn_{soil}) / (\lambda_s \cdot (s_s + \gamma_s)) . \quad (32)$$

Note that, at the soil surface, wind is assumed nil and the aerodynamic resistance can therefore be neglected. The potential soil evaporation E_{sp} (mm) equals E_{pen}, which is a measure for the moisture demand of the air above the soil. The actual soil evaporation depends on the soil moisture conditions and is calculated in the water balance module. Evaporation from the litter mass E_l (mm) depends on the amount of water stored on the litter mass and the amount of water that can evaporate, given by E_{pen}. This is explained further in the rainfall section.

Potential evapotranspiration
Potential evapotranspiration E_p (mm) is the sum of interception evaporation, potential transpiration, potential soil evaporation and litter evaporation:

$$E_p = E_i + E_{tp} + E_l + E_{sp} \; . \tag{33}$$

E_i consists of evaporation from the wet leaves E_{can} and the tree stems E_{st}. It is assumed that during a rainstorm there is no evapotranspiration. This is not entirely true, since leaves also have stomata at their bottom side, from which transpiration is possible. However, it is assumed that during a rainstorm the air surrounding the leaves becomes saturated, so e_a equals e_s and no more moisture can be supplied to the air. All evapotranspiration fluxes (e.g. E_i, E_l, E_{tp} and E_{sp}) are corrected for the fraction of the hour in which evapotranspiration is possible (Appendix 4.5).

Rainfall and interception

Figure 4.5 shows the pathway of water through the vegetation and the litter on the soil as modelled in FORGAP. The leaves of the vegetation and the litter layer on the soil are modelled as reservoirs of water storage. Their capacity is limited and water in access of this capacity is drained to the following reservoir or the soil. Water that remains behind in the reservoir is available for evaporation.

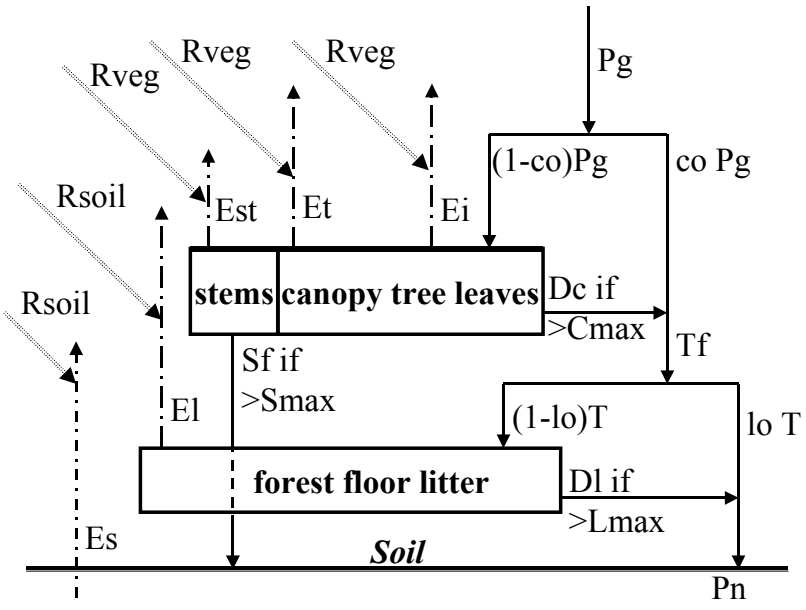


Figure 4.5 Pathways of rainfall through the vegetation and soil litter and evapotranspiration. (See text for the explanation of the abbreviations).

Gross rainfall P_g (mm) enters the forest system at the top of the vegetation. The part of the rainfall that is intercepted by the vegetation P_i (mm) is given by:

$$P_i = (1 - co) \cdot P_g \,, \tag{34}$$

in which co ($m^2.m^{-2}$) is the cell openness, which is the canopy openness of one grid cell (Appendix 4.6). Jetten (1996) measured stem flow as proportion of a rainfall event: *Stem flow* = 0.0086 · *Rainfall* − 0.0373. This indicates a storage on the tree stems of 0.0373 mm per rainfall event. However, this regression does not compensate for canopy openness. The formula of Jetten was applied to the 1997 rainfall in the research area and the new stem flow relation was found:

$$S_f = 0.0043 \cdot P_i - 0.0373. \tag{35}$$

with S_f (mm) the stem flow. The storage capacity of the stems S_{max} (mm) remains 0.0373 mm. Stemflow only occurs if the stem storage capacity is filled. After rainfall, the water in the stem storage capacity will evaporate (E_{st}), which is added to the interception evaporation. The amount of rain that can be stored on the leaves of the vegetation depends on the storage capacity of the vegetation C_{max} (mm) and the amount of water left over from the previous rainfall event. During a rainstorm, the storage capacity of the vegetation is filled. Since the model time step is one hour, a drainage function such as defined by Rutter *et al.* (1971) is not necessary. All rain in excess of C_{max} drains to the litter layer or soil:

$$\begin{aligned} D_c &= P_i - S_f - C_{max} && \text{for } P_i - S_f > C_{max} \,, \\ D_c &= 0 && \text{for } P_i - S_f \le C_{max} \,. \end{aligned} \tag{36}$$

The value of C_{max} depends on the amount of leaf area of the vegetation (Appendix 4.6 and 4.7). After the rainstorm, the intercepted water that remained on the leaves will evaporate, provided that the evaporative demand E_{wet} is large enough. The actual interception evaporation E_i is the minimum of the amount of water stored on the vegetation or the maximum amount that can evaporate. Water that does not evaporate during a time step, is available for evaporation in the next time step. The amount of through fall T_f is modelled as:

$$T_f = co \cdot P_g + D_c \,, \tag{37}$$

where D_c (mm) the amount of rain water draining from the canopy after saturation of the leaves (C_{max}). The amount of through fall that is intercepted by the litter mass L_i (mm) is calculated analogous to the canopy interception P_i:

$$L_i = (1 - lo) \cdot T_f \,, \tag{38}$$

in which lo ($m^2.m^{-2}$) is the litter openness. Litter openness is the fraction of soil area covered by litter and the total area (Appendix 4.7). The amount of through fall that can be stored on the litter depends on the storage capacity of the litter leaves L_{max} (mm) and the amount of water left over from the previous rainfall event. Through fall in excess of L_{max} drains to the soil. The intercepted water that remains on the litter will evaporate, provided that E_{wet} is large enough. Litter evaporation E_l is the minimum amount of water stored on the litter or E_{wet}. Not evaporated water during one time step is available for evaporation in the nest time step. Finally, the amount of rain that enters the soil, the net precipitation P_n (mm), reads:

$$P_n = lo \cdot L_i + D_l \,, \tag{39}$$

with D_l the litter mass drainage (mm), which is determined analogous to D_c:

$$D_l = T_f - L_{max} \quad \text{for } T_f > L_{max}\,, \qquad D_l = 0 \quad \text{for } T_f \le L_{max}\,. \tag{40}$$

The total amount of water entering the soil P_{soil} (mm) is the net precipitation P_n plus the stem flow S_f. The storage capacity of the litter mass L_{max} depends on the amount of litter mass on the soil, which in term is a function of litter fall and decomposition. The results of the research of litter fall (Chapter 6) and decomposition (Chapter 7) have been incorporated in FORGAP and their implementation is explained in Appendix 4.8.

SOIL WATER DYNAMICS

The soil water sub-module in a nutshell

The soil water sub-module calculates soil moisture fluxes with a one-dimensional finite water transport model. The model is based on Darcy's law for stationary flow and water fluxes are in the vertical direction only. There is no capillary rise from a ground-water table, since the groundwater in the research area is very deep, usually deeper than 10m. There is no lateral water flow. The amount of water that can infiltrate is regulated by the maximum possible flux through the topsoil. All rainfall in excess of this flux is stored on the soil as ponded water and can infiltrate later. However, in sloping terrain, this ponded water is removed as run-off. Water percolating below the lowest layer is lost from the root system of the forest and water is also removed from the soil through direct soil evaporation and transpiration. The main input from the evaporation sub-module is the net precipitation and the potential soil evaporation and transpiration (Figure 4.6). The soil is subdivided into four layers, which are characterized by their thickness, soil hydrological parameters and root content.

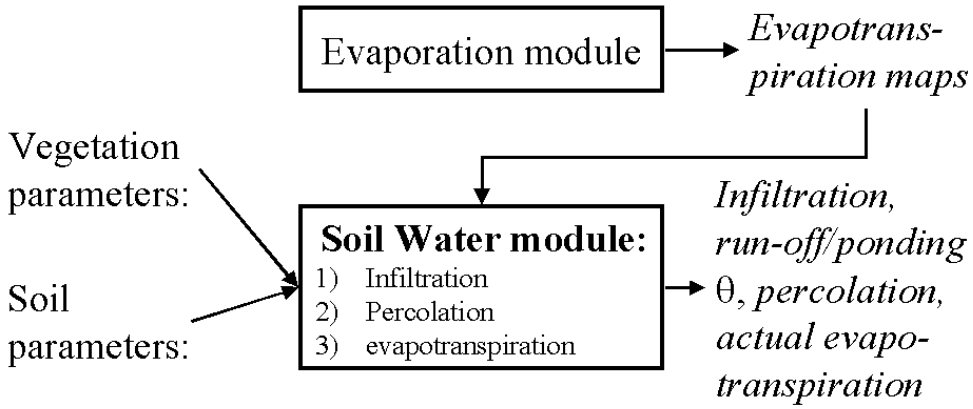


Figure 4.6 The soil water sub-module with the required input and resulting output within the FORGAP model structure. (θ volumetric soil moisture content)

Concepts of unsaturated flow

Water flow in unsaturated soil is generated by differences in water potential ψ between different layers of the soil column. The two main potentials in the soil are the matrix potential ψ_m and the gravitational potential ψ_g, provided that the overburden pressure on the soil, the external gas pressure and the osmotic pressure are negligible. The matrix potential arises from interactions between water and the soil particles, the capillary forces. The gravitational potential is caused by a difference in height between the two observation points. For a one-dimensional solution, the mass conservation law for a point in the soil states that the change in soil moisture content Δ θ is determined by the amount of water entering at that point minus the amount of drainage water and loss through evapotranspiration. For any soil layer this means:

$$\Delta\,\theta = q_{in} - q_{perc} - E\,, \tag{41}$$

q_{in} : percolation from a soil layer above or net precipitation for the topsoil layer (cm),
q_{perc} : percolation to a deeper soil layer (cm).
E : evapotranspiration loss (cm).

Water flow between two layers is caused by a difference in water potential between these two layers and is expressed as flux density q. This flux density q (cm.h^{-1}) is calculated with Darcy's law for stationary flow according to:

$q = -k(\psi)\frac{\delta(\psi)}{\delta(z)} = -k(\psi_m)\frac{\delta(\psi_m + \psi_g)}{\delta(z)}$, which in terms of pressure head rewrites to

$$Q = -k(h)\frac{\delta(h+z)}{\delta(z)} = -k(h)\left(\frac{\delta(h)}{\delta(z)} + 1\right), \tag{42}$$

ψ, ψ_m, ψ_g : water potential (matrix or gravitational) (J.kg^{-1}),
$k(\psi)$, $k(h)$: hydraulic conductivity (cm.h^{-1}) as function of potential ψ or head h,
h : pressure head (cm),
z : gravitational head (cm).

The pressure head h and hydraulic conductivity k change with the volumetric soil moisture content θ (cm^3 H_2O.cm^{-3} dry soil) of the soil. The non-linear relation between pressure head and soil moisture is calculated with the effective soil moisture θ_e (cm^3.cm^{-3}), which is the fraction of the pore space filled with soil moisture (van Genuchten 1980):

$$\theta_e = (\theta - \theta_r) / (\theta_s - \theta_r)\,, \tag{43}$$

where θ_s is the saturated volumetrci soil moisture content (cm^3.cm^{-3}) and θ_r the residual soil moisture content (0.01 cm^3.cm^{-3}). The residual soil moisture content is the amount of soil moisture which is bounded at molecular level to the soil and which will always remain in the soil. The $h(\theta_e)$ and $k(h)$ functions can be calculated according to (Mualem 1976; van Genuchten 1978, 1980):

$$h(\theta_e) = [(\theta_e{}^{(-1/m)} - 1)^{(1/n)}] / \alpha\,, \tag{44}$$

$$k(h) = k_s\,[1 - (\alpha h)^{n-1}\,(1 + (\alpha h)^n)^{-m}]^2 / [1 + (\alpha h)^n]^{(m/2)}\,, \tag{45}$$

n : Mualem's n (-),
m : Mualem's $m = 1 - 1/n$ (-),
α : Mualem's α (-),
k_s : saturated hydraulic conductivity (cm.h^{-1}).

Solution of the water balance

The water balance for the soil profile is solved within one time step, resulting in new soil moisture contents for the next time step. It is not possible in PCRaster to solve the $h(\theta)$ and $k(h)$ relations in an iterative procedure, so θ, $h(\theta)$ and $k(h)$ are cosiddered stationary within one time

step. Water potentials between layers are calculated between a point that represents the layer and another point that represents a lower layer. These points or nodes are positioned in the middle of the layer. The top boundary is positioned at the soil surface. Bottom boundary conditions are calculated with a hypothetical fifth layer that has the soil moisture status of the fourth layer of the previous time step. A schematic representation of the soil water module is given in Figure 4.7. The water balance sub-module consists of three section: 1) infiltration, 2) percolation and 3) actual soil evaporation and transpiration.

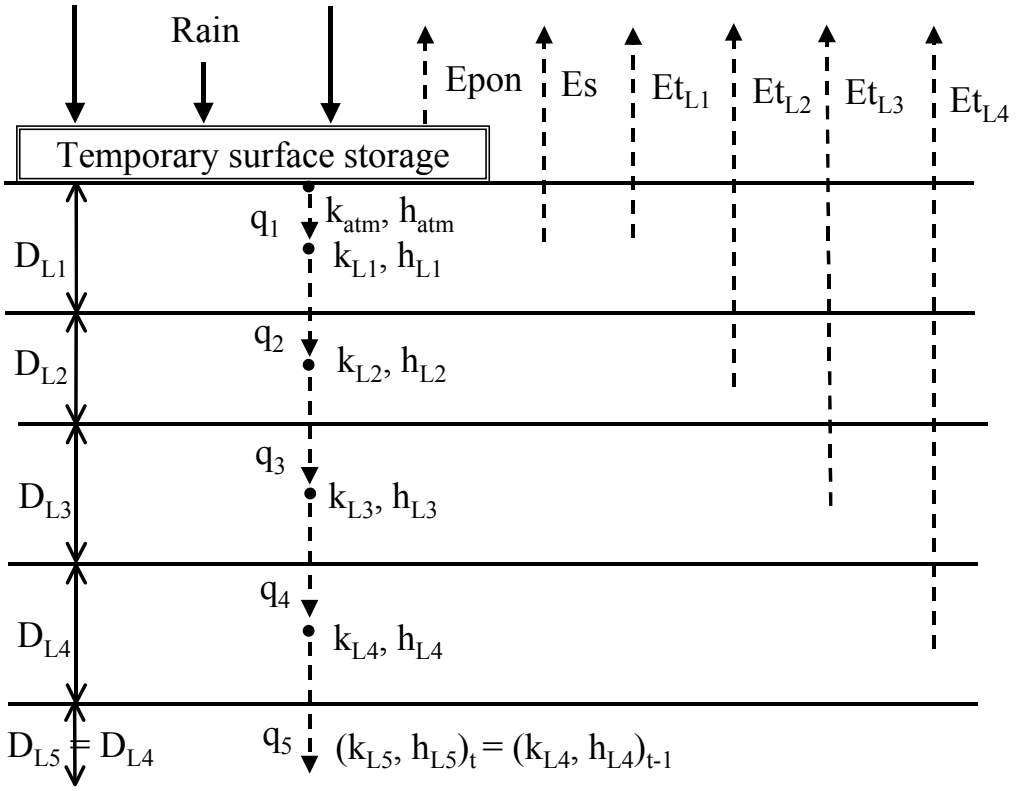


Figure 4.7 Schematic representation of the soil water sub-module. The hydraulic conductivity and pressure head are calculated on the node of a layer, positioned in the middle of the layer and represented by a •. (Epon: evaporation of ponded water, Es: soil evaporation, Et_{L1}: transpiration from layer 1, D_{L1}: thickness layer 1, k: hydraulic conductivity, h: pressure head, q: flux density)

Infiltration

The first step in calculating infiltration of rainfall is the calculation of the effective soil moisture content, the resulting pressure head and hydraulic conductivity with the soil moisture conditions at time step *t-1*. For the first time step, initial soil moisture contents are provided. Potential infiltration at the top layer I_{pot} (cm.h^{-1}) is calculated by:

$$I_{pot} = -\sqrt{(k_{atm} \cdot k_{L1})} \cdot [h_{atm} - h_{L1} / (D_{L1} / 2) + 1] , \qquad (46)$$

whereby h_{atm} (cm) is the pressure head of the soil surface at the atmosphere and k_{atm} (cm.h^{-1}) the corresponding hydraulic conductivity and h_{L1} (cm) the pressure head of the first layer with thickness D_{L1} (cm). The potential infiltration is the flux from the surface node to the top node, so z equals $D_{L1}/2$. At the soil surface, the pressure head of the soil, h_{atm}, is in equilibrium with the atmosphere. The atmospheric head h_{atm} (cm) is a function of temperature T (°C) and relative humidity RHs (fraction) (Feddes *et al.* 1978):

$$h_{atm} = \frac{R \cdot (T + 273.15)}{g \cdot M} \cdot \ln(RH) , \qquad (47)$$

R : universal gas constant 8.3144 ($J.mol^{-1}.K^{-1}$),
g : gravitation acceleration 9.8 ($m.s^{-2}$),
M : molecular weight water 0.018 ($kg.mol^{-1}$).

A distinction is made between forest and gap in relation to the temperature and humidity that is used in equation 45. In a gap, T and RH as measured in the meteo station are used and in the forest, the corrected Ts and RHs are used (Appendix 4.3).

At the beginning of a time step, net rainfall is temporarily stored at the soil surface for infiltration or, if the infiltration capacity is exceeded, as ponded water (*Pond* in cm). If the slope of the area is steeper than 0.5° than the amount of ponding water is discharged as run-off. The temporal storage generates a k_{atm} that equals k_s and h_{atm} of 0. The actual infiltration is the minimum of I_{pot}, the amount of water available for infiltration in the temporarily surface storage: P_{in} + *Pond* or the maximum amount of water that can enter in the top layer: $(\theta_s - \theta_r - \theta) \cdot D$ (cm). The amount of soil moisture in a layer can be expressed in units of water height (cm) by multiplying the volumetric soil moisture content θ ($cm^3.cm^{-3}$) with the thickness of the layer D_L (cm). The new amount of ponded water is calculated by subtracting the evaporation of ponding water E_{pon} ($mm.h^{-1}$) from the surface storage.

Percolation
The percolation to deeper soil layers, e.g. q_{perc12}; percolation between layer 1 and 2 ($cm.h^{-1}$), is found by calculating:

$$q_{perc12} = -\sqrt{(k_{L1} \cdot k_{L2})} \cdot [(h_{L2} - h_{L1}) / (D_{L1} + D_{L2})/2 + 1] . \qquad (48)$$

The percolation can never be more than the amount of water present in the layer; $(\theta - \theta_r)/D$ (cm) and the amount of available storage in the layer below; $(\theta_s - \theta - \theta_r)/D$ (cm). The hydraulic conditions of the deepest or fifth layer; n, m, α, k_s and D are equal to the conditions of the forth layer and the soil hydrological conditions of this layer constitute the lower boundary conditions of the model. The soil moisture conditions in the lowest layer are not calculated, but are set equal to the soil moisture conditions of the fourth layer at t-1.

Actual soil evaporation and transpiration
The actual soil evaporation E_{sa} ($mm.h^{-1}$) is the minimum of the flux through the top layer or the water demand of the air: the potential evaporation (equation 32). The maximum flux is regulated by the water potential between the atmosphere, determined by h_{atm} and k_{atm} (equation 46 and 44), and the first node. There is no actual soil evaporation if the temporarily surface storage is filled. The soil evaporation E_{soil} ($mm.h^{-1}$) is calculated with analogous to I_{pot}:

$$E_{soil} = -\sqrt{(k_{atm} \cdot k_{L1})} \, [(h_{L1} - h_{atm})/(D_{L1}/2) + 1] , \qquad (49)$$

and likewise, the soil evaporation flux is calculated from the surface to the first node, so z equals $D_{L1}/2$. The actual soil evaporation E_{sa} is the minimum of the potential soil evaporation E_{sp}, as calculated in the evaporation sub-module and E_{soil}.

The actual transpiration E_{ta} (mm.h^{-1}) depends on the amount of water in the soil available for transpiration and the potential transpiration E_{tp}. At high matrix potentials, plants will find it more difficult to extract water from the soil and consequently, plants need to reduce their transpiration flux. The transpiration reduction function ETr (-) (Figure 4.8) is related to the pressure head and is affecting E_{tp} (van Genuchten 1978):

$$\begin{aligned} ETr &= 0 && \text{for } 0 < h < 0.1, \\ ETr &= 1.111 \cdot h - 0.111 && \text{for } 0.1 < h < 1, \\ ETr &= 1 / (1 + h/H_{50})^{\zeta} && \text{for } 1 < h < 10^6, \\ ETr &= 0 && \text{for } h > 10^6 . \end{aligned} \qquad (50)$$

in which H_{50} (cm) is the pressure head where E_{ta} is only 50% of E_{tp} and ζ (-) is a constant that determines the steepness of the curve. Van Genuchten (1978) proposed a value of 3500 cm for H_{50} and ζ is set to 1.5 (-).

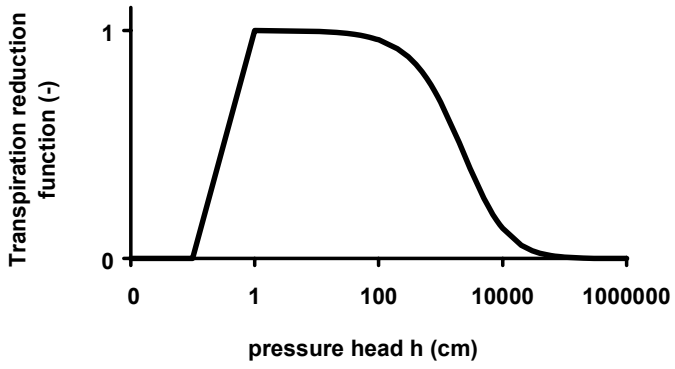


Figure 4.8 ranspiration reduction function *Etr*.

The actual transpiration is now calculated with:

$$E_{ta} = \beta_{Ln} \cdot Etr \cdot E_{tp} . \qquad (51)$$

in which β_{Ln} (fraction) equals the fraction of the root content of nth layer Ln. β_{Ln} is the root content as a fraction of the total amount of roots in the whole profile. For the entire profile this means that $\beta_{L1} + \beta_{L2} + \beta_{L3} + \beta_{L4} = 1$.

The new soil moisture content of, for example the top layer, for the next time step $\theta_{1,t+1}$, is calculated with:

$$\theta_{L1,t+1} = (\theta_{L1,t} \cdot D_{L1} + I_{ac\text{-}t} - q_{perc12\text{-}t} - E_{sa\text{-}t} - E_{taL1\text{-}t}) / D_{L1} . \qquad (52)$$

The new soil moisture content for the next time step for the second through fourth layer is calculated likewise, without soil evaporation loss and a percolation from a layer above instead of net precipitation. The soil moisture output of FORGAP was used to calibrate some of the model's hydraulically parameters, as discussed in the following section.

CALIBRATION WITH PEST

The calibration of FORGAP was carried out with the software programme PEST (Watermark Computing, 1994). PEST is a model-independent computer program for Parameter ESTimation. For linear models (i.e. models for which observations are calculated from parameters through a matrix equation with constant parameter coefficients), optimisation can be achieved in one step. However for non-linear problems like FORGAP, parameter estimation is an iterative process. PEST uses the Gauss-Marquardt-Levenberg algorithm (Levenberg, 1944; Marquardt, 1963) to solve the non-linear weighted least squares parameter estimation. At the beginning of each iteration, the relationship between model parameters and model-generated observations is linearised by formulating it as a Taylor expansion about the currently best parameter set (Taylor, 1982); hence the derivatives of all observations with respect to all parameters must be calculated. This linearised problem is then solved for a better parameter set, and the new parameters are tested by running the model again. By comparing parameter changes and objective function improvement achieved through the current iteration with those achieved in previous iterations, PEST can tell whether it is worth undertaking another optimisation iteration; and if so the whole process is repeated (Watermark Computing, 1994).

Calibration: parameters, observations and input data

FORGAP is based on many model parameters that were measured in the PGE gaps and forest. Most of these parameters are related to vegetation characteristics or information on soil cover. Measurements of hydrological fluxes were limited to soil moisture only, since no observations were made of evapotranspiration fluxes. Therefore, soil moisture measurements were used to calibrate FORGAP. There were many model parameters that could be optimised. However, the parameters were limited to those parameters that: 1) had a large influence on soil moisture content, 2) were parameters of which accurate field measurements were lacking or 3) were parameters with a large natural variability. Model runs prior to the actual calibration showed that the soil hydrological parameters and root content met all the above requirements. Therefore, saturated soil moisture content θ_s, saturated hydraulic conductivity k_s, soil moisture retention parameters n and α and root content of the top layer were selected (Table 4.1).

Table 4.1 Calibration parameters per soil layer: initial value and possible range (θ_i: initial soil moisture content, θ_s: saturated soil moisture content, k_s: saturated hydraulic conductivity, n & α: parameters in the van Genuchten-Mualem equations 44 and 45, g: gap, f: forest)

Layer	Depth	Roots (%)		θ_i (%)		θ_s (%)		k_s (cm.h^{-1})		n (-)		α (-)	
	(cm)	initial	range	initial	range	initial	range	initial	range	initial	range	initial	range
L1 g	15	0.7	0.6-0.9	21.6	17-27	52	45-55	12	1-15	1.385	1.2-1.5	0.098	0.07-0.11
L1 f	15	0.7	0.6-0.9	16.6	12-22	52	45-55	12	1-15	1.385	1.2-1.5	0.098	0.07-0.11
L2 g	25	0.2	0.1-0.4	26.0	15-35	48	38-50	9	1-10	1.262	1.2-1.3	0.026	0.02-0.50
L2 f	25	0.2	0.1-0.4	20.0	10-30	48	38-55	9	1-13	1.262	1.2-1.3	0.026	0.02-0.50
L3 g	40	0.05	0.05-0.10	24.0	10-40	47	38-50	8	1-10	1.221	1.2-1.3	0.073	0.07-0.11
L3 f	40	0.05	0.05-0.10	18.0	5- 40	47	38-55	8	1-13	1.221	1.2-1.3	0.073	0.07-0.11
L4 g,f	60	0.05		= L3		= L3		= L3		= L3		= L3	

Note: The depth of the layers was not adjusted during calibration and the hydrological conditions of layer 4 were set equal to layer 3.

To reduce the number of parameters during optimalisation, the parameters of the forth layer was set equal to the third layer. The user of PEST must supply some prior information on the parameters that are used in the optimisation process: initial values, lower and upper limits and whether a parameter is correlated to another, i.e. that parameter will only change at the same rate as the parameter to which it is fixed. This information was based upon data that were collected in the PGE research area, i.e. soil profile descriptions or pore volume (Chapter 2), and data collected by Jetten (1994a and unpublished data).

In 1998, a 16 cm long *Trime* 4-pins Frequency Domain Refraction (FDR) soil moisture probe was attached to a data logger, which recorded hourly soil moisture in the topsoil in a 570m^2 gap and in the forest (Chapter 3). The forest and the gap were calibrated separatly with each three days of soil moisture measurements that were used as observation data. It would have been possible to calibrate gap and forest together, but this method considerably speeded the optimalisation, since less time steps had to be calculated. Another set of FDR soil moisture measurements in the forest and the gap were used to validate the model. Although other soil moisture measurements had been made throughout the research period and in other gaps, the hourly recordings of the FDR were the best data to calibrate the model. Accurate meteorological data was available from January 1997 until October 1998 and FORGAP was run with these data to initialise some of the model parameters like litter mass, sapling height and soil moisture content of the lower layers. The initial soil moisture content of the upper layer was set equal to the first FDR observation.

Calibration results and validation

The optimised model gave a good estimated of the topsoil moisture content (0-15cm). The correlation coefficient of the optimisation of the gap data was R^2 = 0.728 and the topsoil moisture content as calculated with FORGAP had a sums of square of SS = 989 (nr. of observations N = 96) (Figure 4.9: Gap). On average, FORGAP overestimated the soil moisture content by 0.13 %, with the highest overestimation of 8.72% and the highest underestimation was 11.28%. The correlation coefficient of the optimisation of the forest data was R^2 = 0.767 and the topsoil moisture content as calculated with FORGAP had a sums of square of SS = 607 (nr. of observations N = 96) (Figure 4.9: Forest). On average, FORGAP overestimated the soil moisture content by 0.01 %, with the highest overestimation of 4.90% and the highest underestimation was 11.69%.

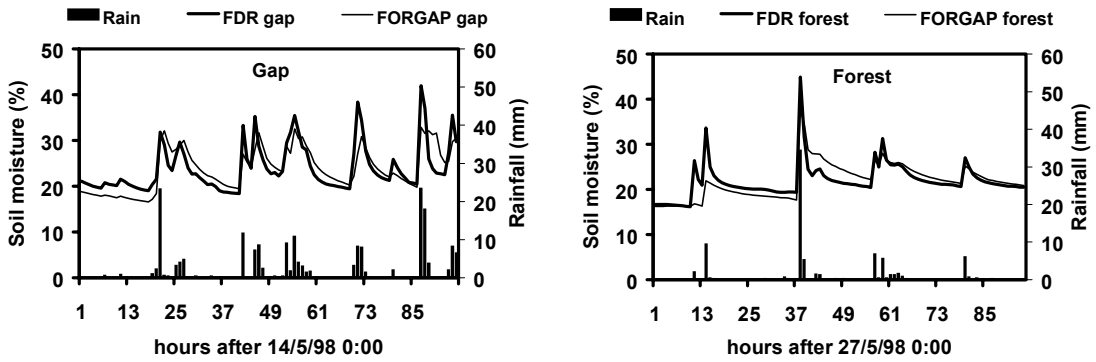


Figure 4.9 Calibration results: calculated and observed topsoil moisture content and rainfall.

Overestimation by the model occurred after a heavy rainstorm (> 10 $mm.h^{-1}$), when soil moisture content was near saturation and soil drainage was delayed compared to the measured soil moisture. It was apparently not possible to model the maximum peak in soil moisture conditions near saturated conditions during a heavy rainstorm. The optimised values of the soil

hydrological parameters, as generated by PEST, are given in Table 4.2. The van Genuchten-Mualem parameter n was always at the upper limit and α usually at the lower limit. Apparently, a better mathematical solution would have been possible the boundaries of the calibration parameters could be set beyond the current range. This range was based upon field data and covered a large natural variability. This does not mean that parameter values outside these ranges are not possible, but they were simply not found and are most likely associated with much moere clayey soils. Because the model calibration was satisfactory with the optimised parameters, no other solution was sought after.

Table 4.2 Calibrated parameters per soil layer: results. (θ_i: initial soil moisture content, θ_s: saturated soil moisture content, k_s: saturated hydraulic conductivity, n & α: parameters in the van Genuchten-Mualem equations 44 and 45, g: gap, f: forest)

Layer	roots (%)	θ_i (%)	θ_s (%)	k_s (cm.h^{-1})	n (-)	α (-)
L1 g	0.79	23.7	36.1	8.34	1.50	0.100
L1 f	0.78	17.7	45.0	15.00	1.50	0.070
L2 g	0.11	22.6	50.1	9.39	1.30	0.051
L2 f	0.10	30.0	51.2	13.00	1.30	0.020
L3 g	0.05	39.7	46.0	7.83	1.30	0.070
L3 f	0.07	31.9	43.7	10.99	1.30	0.070

The validation of FORGAP with the parameter values of Table 4.2 and other observations that were made in the gap and forest performed somewhat less well than the calibration in the gap, but somewhat better in the forest. The correlation coefficient in the gap was $R^2 = 0.492$ (SS = 1034, N = 118) (Figure 4.10, Gap) and in the forest $R^2 = 0.861$(SS = 165, N = 118) (Figure 4.10, Forest). Again, during heavy rainstorm, soil moisture content was underestimated and after that heavy rainstorm, soil moisture was overestimated. Moreover, the soil moisture conditions, as calculated by the model, were lower when rainfall was absent for a longer period, which indicate a larger water use by the vegetation than that was actually occurring.

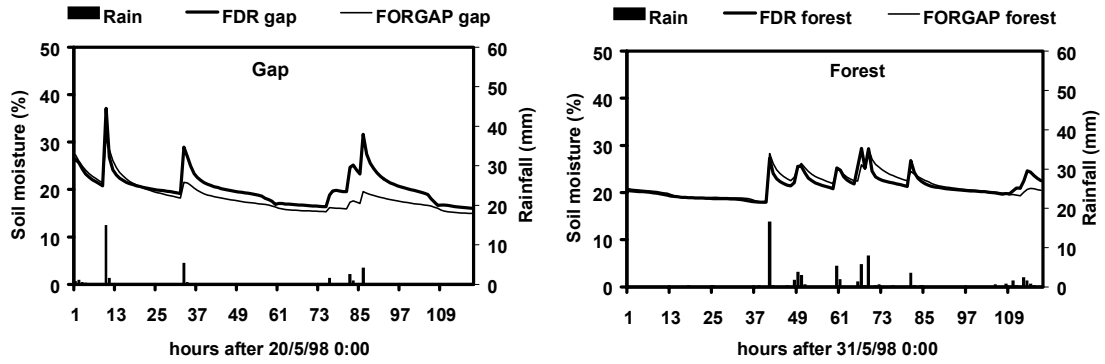


Figure 4.10 Validation of FORGAP:observations and model output in forest of soil moisture.

Acknowledgements
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Appendix 4.1 Determining the *k'* and *c* radiation extinction coefficients

The vertical and lateral radiation extinction constants *k'* and *c* were determined by analysing hemispherical photographs that were taken along transects from the gap edge into the dense forest understorey. Four transects in N, S, E and W direction in a 570m^2 and a 410m^2 gap were chosen. The first photo was taken on the gap edge, the following photo at 2.5 to 3 m distance, the next at 6 m, 9 m, 12 m and the longest transect at 15 m from the gap edge (Figure 4.11). Total incoming radiation per hour for 6 days in a year (15 January, 15 March, 15 May, 15 July, 15 September and 15 November) were calculated with WINPHOT (ter Steege 1997).

Figure 4.11 Example of radiation extinction in gap edge area: photo A was taken on the edge of a 400m^2 gap, photo B at 3 m from the edge, photo C at 6 m from the edge and photo D in the deeper understory, 15 m from the edge.

Radiation extinction coefficient k'

The understorey photographs furthest away from the gaps were used to calculate the radiation below the vegetation. This below canopy radiation was used to determine *k*' with equation 14 ($R_{soil} = R_{veg} \cdot \exp(-k' \cdot LAI/\sin\alpha)$). The radiation above the vegetation, as calculated by WINPHOT, was used for R_{veg} and an *LAI* of 5.91 m^2.m^{-2} was used. Solar altitude was calculated per hour for the same 6 days in a year as used above. The extinction coefficient *k'* of 0.290 gave the lowest sum of squares between the below canopy radiation of WINPHOT and the soil radiation of equation 14.

Radiation extinction coefficient c

Per gap, the average radiation per hour in relation to the distance to the gap edge was calculated to determine the coefficient *c* using equation 15 ($R_{edge} = (R_{veg} - R_{soil}) \cdot \exp(-c \cdot D_{for}/\sin\alpha) + R_{soil}$). Initially, *c* was determined per gap, which resulted in the lowest sum of squares between the below canopy radiation of WINPHOT and the radiation according to equation 15 with a *c* of 0.40 of the 410m^2 gap and a *c* of 0.19 for the 570m^2 gap. The difference between the two gaps can be related to 1) the difference in gap size and thus light intensity, and 2) the difference in gap age, since the photos in the 410m^2 gap were taken 1.5 year after gap creation and the 570m^2 gap already existed for 3.5 year. The vegetation in the 570m^2 gap had grown to 3.5 m and was partly blocking the camera's view. Especially the vegetation in the gap edge was much higher in the older gap than in the younger one. Due to this regrowth in the gap edge area, hemispherical photographs along gap-edge/-forest transects were only available for these two gaps. Analysis of more hemispherical photographs can result in a better estimate of *c* or a better gap edge radiation extinction formula than equation 15. In FORGAP the average value for *c* of 0.295 (-) is used (Figure 4.12).

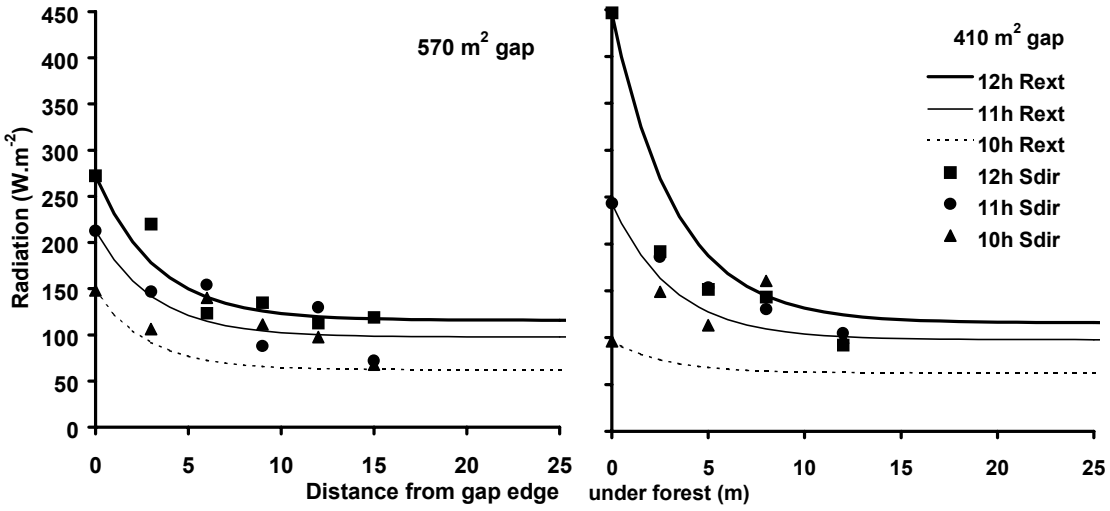


Figure 4.12 Soil radiation in two gap edges with a combined gap edge radiation extinction and leaf area extinction function (equation 15). The fit through the data points is made with a edge extinction coefficient *c* of 0.295.

Appendix 4.2 Seedling and sapling growth

Seedling and sapling growth in a gap is calculated in the evaporation sub-module. Plant growth is related to the amount of transpiration. A sigmoidally growth relation was found between sapling transpiration as modelled by FORGAP and the growth rate of the experimental sapling in the gaps. The demography of the experimental sapling and seedling was monitored from October 1996 to March 1999 for ten replicates of eight different tree species. The tree species were *Chlorocardium rodiei* (Greenheart), *Catostemma fragrans* (Sand Baromalli), *Pentaclethra macroloba* (Trysil), *Ormosia coccinea* (Barakaro), *Sclerolobium guianense* (Kaditiri), *Laetia procera* (Warakairo), *Goupia glabra* (Kabukalli) and *Cecropia obtusa* (Congo pump). These tree species were chosen on a gradient from light favouring or pioneer species to shade tolerant or climax species. Height growth was recorded 8 times (Rose 2000). In the growth-transpiration analysis, only the tree species with the tallest seedlings that formed the top layer of leaves that intercepted radiations were used and consequently, *Ormosia coccinea* and *Laetia procera* were not used in the analysis. At the planting date in November 1996, the initial height of all seedlings of all species was almost equal of on average 19.6 cm (range 17.7 — 22.8 cm). The growth curve of all species in all gap sizes showed a sigmoidally relation in time (Figure 4.13).

Model runs of FORGAP were performed with gaps with corresponding gap size as the PGE gaps: 54, 108, 208, 404, 804, 1608 and 3180m^2. The vegetation height in the gaps was taken constant: 50 cm in 1997, 150 cm in 1998 and 225 cm in 1999. The total amount of actual transpiration on the vegetation in the centre of each gap was calculated. A sigmoidally relationship was found between seedling growth and net radiation in the gaps (Figure 4.14) using CurveExpert (vs 1.34 D. Hyams 1997):

$$H_{sap} = (a \cdot b + c \cdot \Sigma \mathrm{ETsap}^d) / (b + \Sigma \mathrm{ETsap}^d) , \qquad (53)$$

H_{sap} : sapling height (m),
a, b, c, d : coefficients: a=0.264, b=1521946, c=29.104 and d=1.529,
$\Sigma ETsap$: sum of transpiration by the saplings (mm) since gap creation.

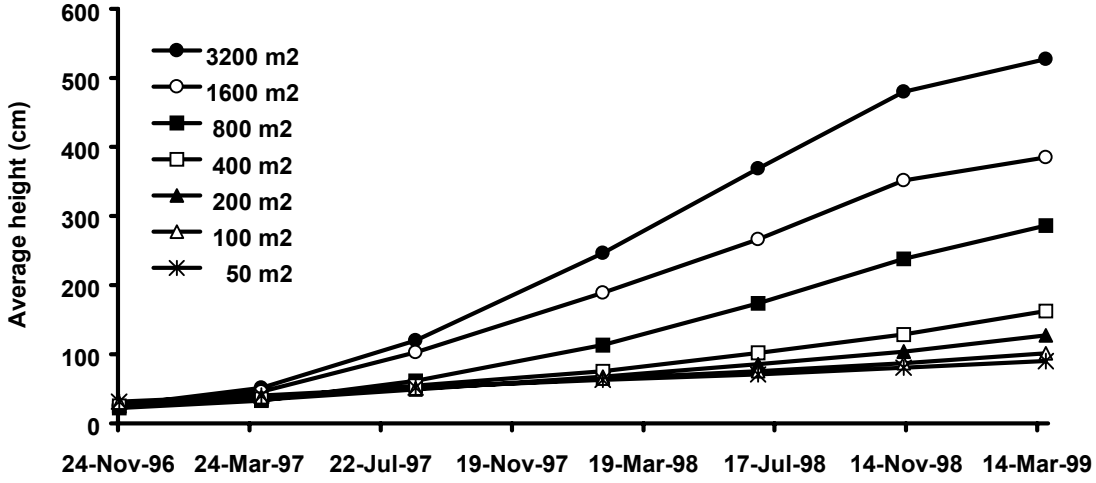


Figure 4.13 Average seedling height per gap size during the research period (884 days). Data courtesy S. Rose (2000).

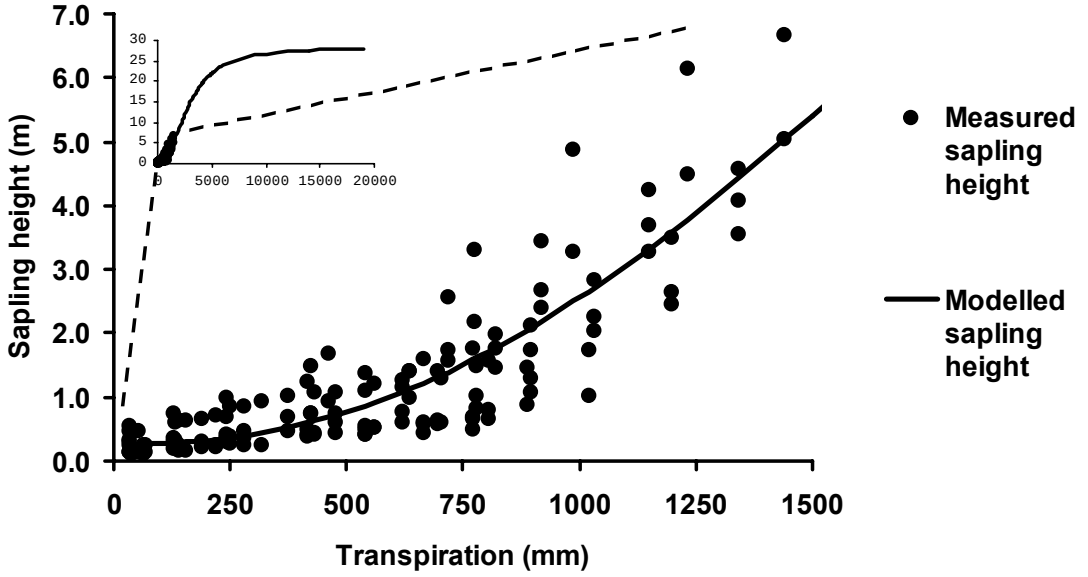


Figure 4.14 Sigmoidally function fitted through the sum of transpiration and sapling height in the PGE gaps (sapling height data by Rose, 2000).

Appendix 4.3 Cloud factor and understorey microclimate

Cloud factor The cloud factor *cl* (-) is defined as:

$$cl = S_{in,a} / S_{in,p} \tag{54}$$

in which $S_{in,a}$ is the actual incoming short-wave radiation (W.m^{-2}) and $S_{in,p}$ the potential incoming short-wave radiation (W.m^{-2}). Actual global radiation $S_{in,a}$ or S_{in} (W.m^{-2}) was measured with a KIPP pyranometer in the Pibiri weather station (van Dam 1999, but see

Chapter 2). Potential global radiation $S_{in,p}$ (W.m^{-2}) was calculated per hour with the radiation equations of the radiation module.

Understorey microclimate The potential transpiration of the saplings in the forest understorey, $E_{tp\text{-}sap}$, cannot be calculated with equation 31 directly, because different microclimatological conditions prevail in the forest undergrowth as those measured in the meteorological station. The temperature at 1m above the soil under a closed forest fluctuates less during the day than in a gap. Air humidity at 1m above the ground under closed forest is on average more saturated than in a gap. Simultaneous measurements in microclimate stations in a gap and under closed forest were made to find correlations between the gap and the undergrowth microclimate. These empirical relations were used to calculate undergrowth temperature, humidity and vapour pressure. The following microclimatic relationships were found:

$$RHs = 0.0965\ RH + 89.892\ , \quad (55)$$

$$Ts = 0.5243\ T + 11.206\ , \quad (56)$$

$$us = 0.1889\ u_{met}^{2} + 0.0523\ u_{met} + 0.0013\ , \quad (57)$$

RHs : relative humidity under closed forest (%),
Ts : temperature under closed forest (°C); note T also in °C,
us : wind speed under closed forest (m.s^{-1}),
u_{met} : wind speed in climate station (m.s^{-1}).

The forest humidity RHs and forest temperature Ts were used to calculate the forest latent heat of vaporisation λ_s (J.kg^{-1}), the forest slope of the pressure curve s_s (-), the forest psychrometric parameter γ_s (Pa.K^{-1}) and the forest saturated $e_{s\text{-}s}$ and $e_{a\text{-}s}$ actual vapour pressure (mbar). Th wind above the seedlings in the gap was calculated with H_{sap} (m) instead of H (note that in the gap $H = H_{sap}$) and us. This wind above the seedlings u_{sap} (m.s^{-1}) is used to calculate the seedling aerodynamic resistance $r_{a\text{-}sap}$ (s.m^{-1}). These corrected microclimate parameters were used to calculate ET_{sap} in the forest understorey.

Appendix 4.4 Wind profiles

Wind speed measurements in a meteorological station u_s (m.s^{-1}) at a measuring height z_s (m) must meet with the requirement that $z_s \geq x / H$, where x (m) is the distance to the nearest tall object up wind with height H (m) (Wieringa & Rijkoort 1983). In case of the PGE meteorological station in the large 3200m^2 gap, z_s was 10m, x was approximately 27m and H was on average 28m, so the requirement was met, 10m ≥ 27/28 m.

Wind speed measurements with anemometers at different heights above a vegetated surface can be used to determine d and z_0. A minimum of three anemometers is needed to estimate the logarithmic wind profile with some accuracy. In this research, only 2 anemometers were installed at 6 and 10m height. The average wind speed at 6m was 0.232 m.s^{-1} and 0.266 m.s^{-}1 at 10m height. In Figure 4.15, the wind profiles above the meteo tower and extrapolated above the forest are displayed, which were valid for the wind speeds at 10m between 0.2 and 0.3 m.s^{-1}. For each wind speed, a different wind profile can be drawn. The 6m measurement point coincided well with the measured wind profile as calculated for the 10m point. This suggests that for this wind speed, the roughness length z_0 and zero-plane displacement d are set correct. Wind speeds between 0.2 and 0.3 m.s^{-1} accounts for 11.4% of the measured wind speeds. Another wind profile analysis revealed that 20.3% of the wind speed measurements are also valid with $z_0 = 0.1 \cdot H$ and $d = 0.7 \cdot H$. Especially between 0 and 0.1 m.s^{-1} the logarithmic wind profile did not

exist, when frequently, higher wind speeds were measured at 6 m than at 10m height. These wind speeds accounts for 35.9% of the measured wind speeds.

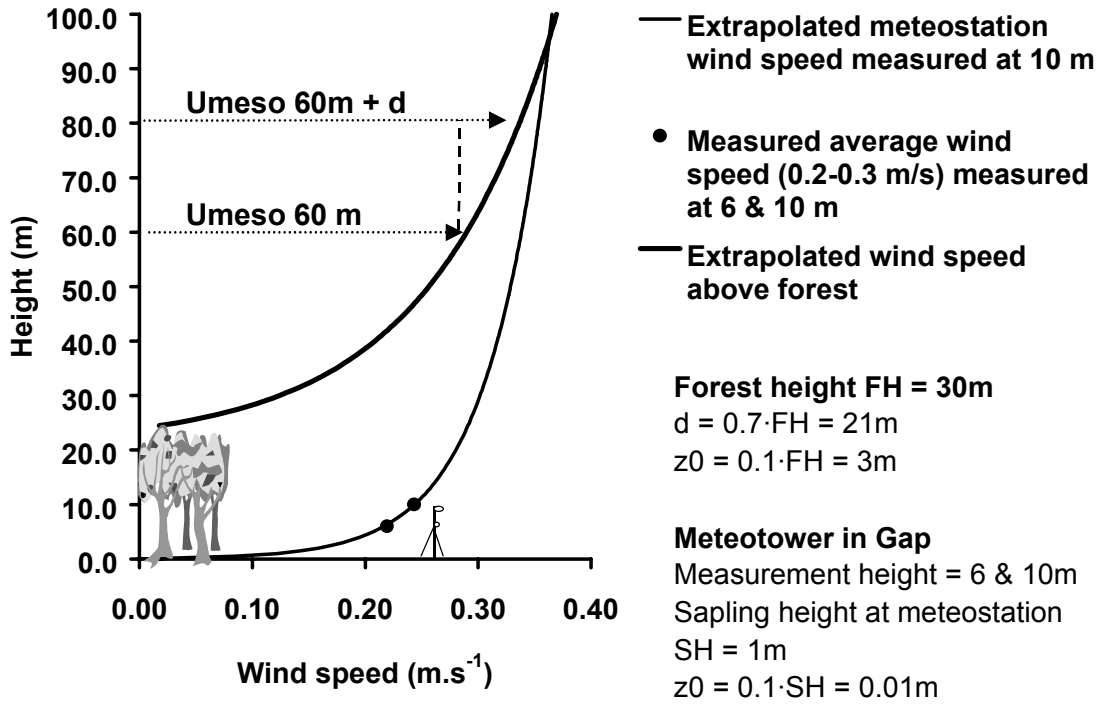


Figure 4.15 Wind profiles at the climate station in a large gap and extrapolated above the forest. Note that the measured values are the average values of wind speeds between 0.2 and 0.3 $m.s^{-1}$. For each wind speed different wind profiles are valid.

Appendix 4.5 Reduction of evapotranspiration fluxes during rain

In FORGAP, it is assumed that there is no evapotranspiration during rainstorms. This implies that the evapotranspiration fluxes as calculated in the evaporation sub-module are limited to the period during which there is no rainfall. An evapotranspiration correction factor is needed that reduces the evapotranspiration fluxes during the time span of the time step (hour), when there is no rainfall. The rainfall data of the PGE climate station was analysed for the amount and the duration of single rainstorms (Figure 4.16). An evapotranspiration reduction function was determined, based upon this data, which is applied to all evapotranspiration calculations. The rain-evapotranspiration reduction $\Re_{rain}$ (-) function depends on the gross rainfall P_g (mm):

$$\Re_{rain} = 1 - (3.6542 \cdot P_g / 60) \; . \qquad (58)$$

This reduction function indicated that there was no evapotranspiration when rainfall P_g was equal to or larger than 16.42 mm, since this amount of rain was equal to a rainstorm of one hour.

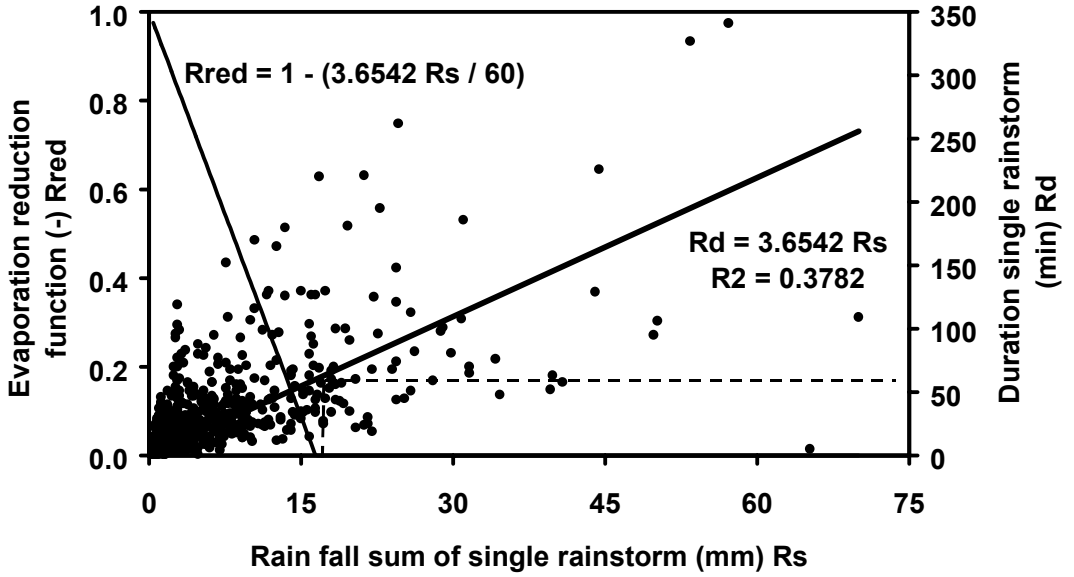


Figure 4.16 Relation between sum of rain and duration of one rainstorm and the evapotranspiration reduction function.

Appendix 4.6 Leaf area index, grid cell canopy openness and throughfall

Leaf area index

In undisturbed Amazonian forests, leaf area index *LAI* increased linearly with vegetation height (Figure 4.17A, adapted from Robberts *et al.* 1993). The data of Saldarriaga (1994) showed a linear increase of *LAI* in time (Figure 4.17B), although Parker (1985) showed that the *LAI* of the regenerating vegetation in gaps had a sigmoid relation with the height of the saplings (see Figure 2.10B). Unfortunately, no information is available about the *LAI* in the PGE forest or of the regenerating vegetation in the gaps, so a simple linear relationship has been used. The *LAI* in the model was calculated with a linear regression based on the data of Robberts *et al.* (1993), and a minimum *LAI* of 0.1 $m^2.m^{-2}$:

$$LAI = 0.2076 \cdot H + 0.1 \; . \qquad (59)$$

Equation 59 resulted in an *LAI* of 5.913 $m^2.m^{-2}$ at 28 m tree height.

Grid cell canopy openness and throughfall

In 1998, 19 hemispherical photographs were taken in the understorey of the undisturbed forest of the PGE research area. The photographs were analysed with the computer programme WINPHOT (ter Steege 1997) for canopy openness *co*. The average *co* of a closed forest was 3.30 % (σ 0.816; range 1.65-4.58). The canopy openness *co* (%) in forest or gaps depends on the amount of leaves in a 180° hemisphere. Canopy openness has been used as a good measure for the amount of solar radiation at a point (ter Steege 1997, Whitmore *et al.* 1993). Canopy openness has not been used in throughfall studies, since rainfall and throughfall follow a vertical pathway through the canopy. However, the canopy openness of a smaller area directly above the point of interest might give an indication into the amount of throughfall at that point. In a model

that uses grid cells like FORGAP, the term canopy openness should than be replaced by cell openness.

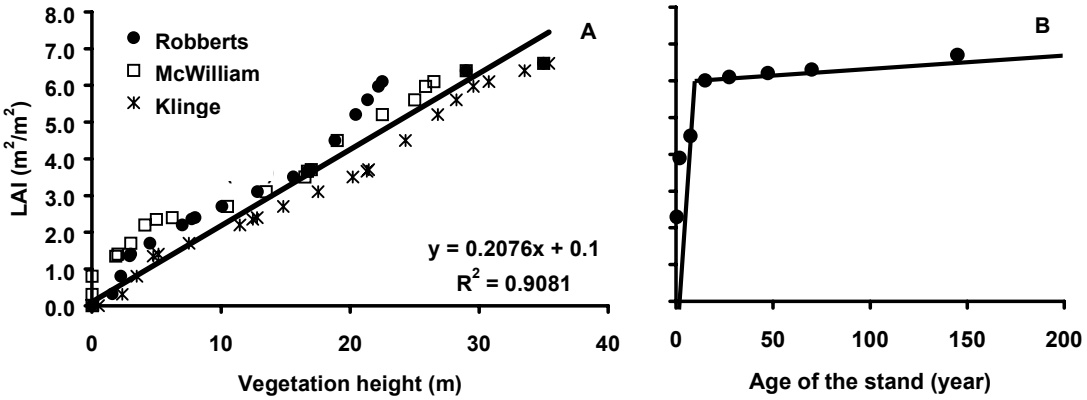


Figure 4.17 Relationships between A) vegetation height and Leaf Area Index *LAI* (adapted from Jetten 1994a) and B) increase in *LAI* in time (adapted from Saldarriaga 1994).

In 1998, another study was carried out to assess the relationship between cell openness and throughfall. Within a closed undisturbed forest, a new series of 44 hemispherical photographs were taken. At the same locations as the hemispherical photos, twenty through fall measurements were made, which were compared with gross rainfall data from the PGE meteo station. The hemispherical photographs were analysed for canopy openness with WINPHOT (ter Steege 1997) and the sub-circle option was used to analyse canopy openness in a smaller part in the centre of the photo. Normally, in the analysis of hemispherical photographs, a circle openness of 90° is used, which is equal to 180° of the hemisphere. A sub-circle of 7° equals a ground projection of a circle with a radius of 3.4m – assuming a tree height of 28m – that is almost equal to the 2×2 m area of the grid cells of the model. The 7° sub-circle was used to analyse the relation between throughfall and cell openness. The average cell openness was 27.4 % (σ 17.21, range 13.82-84.64 %). The average throughfall was 84.6 % (σ 28.13, N 727, median 84.3, range 7.29-295.81 %). There was no good relation between cell openness and throughfall: $T_f = 0.2567 \cdot co + 5.694$ ($R^2 = 0.0178$, N = 37). Therefore, the average throughfall percentage was used in FORGAP.No information is known about the relation between canopy openness or cell openness and vegetation height, either in undisturbed forest or in gaps. Since *LAI* increases linear with vegetation height and *LAI* and *co* are closely related, a linear relation was assumed between *co* (as fraction) and vegetation height *H* (m), based upon a *co* of 27.4 % when *H* is 28 m and a *co* of 100 % when H is 0m :

$$co = 1 - 0.0259 \cdot H \,. \qquad (60)$$

Appendix 4.7 Canopy and litter storage capacity

Canopy storage

The amount of water that can be stored in the canopy depends on the area on which it can be stored, mainly the leaf area, expressed as leaf area index. In previous studies, the interception reservoir of the undisturbed forest, s_{can}, was determined as 0.89 mm (Jetten 1994a) and the leaf area index *LAI* of the undisturbed forest was determined at 5.913 $m^2.m^{-2}$ (Appendix 4.6). In FORGAP, a direct relation is used between the *LAI* and the storage capacity C_{max} :

$$C_{max} = s_{can} / LAI_{for} \cdot LAI = 0.89 / 5.913 = 0.1505 \cdot LAI \,. \quad (61)$$

Litter storage

Analogous to the water storage in the canopy, the storage of water on the litter layer depends on the amount of litter on the soil, which are mainly leaves. The average leaf mass in the forest LM_{for} was 228.1 g.m^{-2} and a good relationship was found between leaf mass in a gap LM_{gap} (g.m^{-2}) and the distance to the gap edge D_{edge} (m) (see Chapter 7):

$$LM_{gap} = 183.83 \cdot e^{-0.1002 \cdot Dedge} \,. \quad (62)$$

The storage capacity of the leaf litter mass was determined experimentally. A rainfall simulator (area 154 cm^2) produced rain with an average intensity of 0.37 mm.min^{-1}. Total rain P_{sim} (mm), splash S_p (mm) and through fall T_{sim} (mm) during a rain fall experiment and drain from the leaves D_{sim} (mm) after a rain experiment as well as leaf openness and dry leaf weight (70°C, 48h) of the experimental leaves were recorded. The storage capacity L_{max} (mm) can be calculated with:

$$L_{max} = P_{sum} - S_p - T_{sim} - D_{sim} \,. \quad (63)$$

A relation was found between the leaf storage capacity and leaf weight (Figure 4.18). The large variability in storage capacity was caused by the large variability of the leaves. The variability of L_{max} can be explained by the leaves that came from different tree species, the leaf size, the state of decomposition, the presence of mosses, the moisture content, a hollow or convex position and the number of overlying leaves. Consequently, a large number of experiments had a negative water balance and the results of these experiments could not be used.

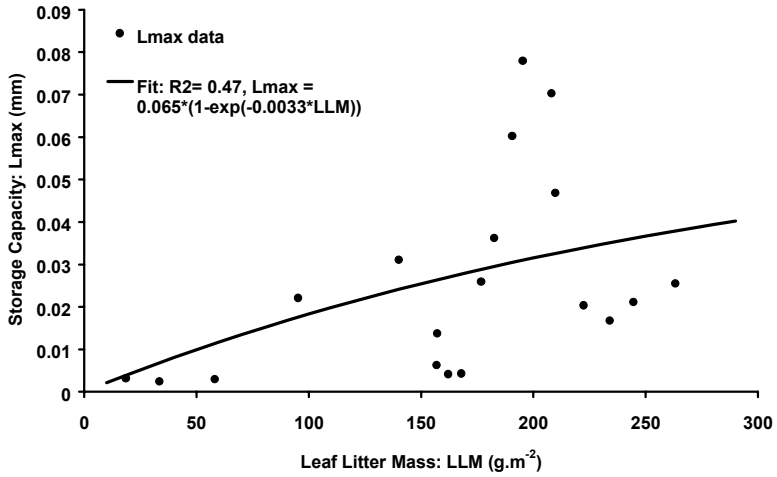


Figure 4.18 Storage capacity of leaf litter versus leaf weight.

It was assumed that the water storage on other litter parts than leaves, e.g. branches, was negligible small compared to the storage capacity of leaves. Consequently, L_{max} (mm) is a function of leaf mass LM (g.m^{-2}) according to:

$$L_{max} = 0.065 \cdot (1 - e^{-0.0033 \cdot LM}) \,. \quad (64)$$

The litter openness lo (m^2.m^{-2}) is the ratio between that part of the soil that is not covered by leaves or other litter and that part that is covered. This ratio was determined experimentally. A wooden frame with 24 · 24 = 576 nails was inserted into the litter layer in the forest understorey

and in the PGE gaps. The number of nails that were not in contact with any part of the litter was divided by the total number of nails. All litter within the frame was dried (70°C, 48h) and weighed *lw* (g.m^{-2}). Litter openness *lo* (m^2.m^{-2}) was related to litter mass according to (Figure 4.19):

$$lo = \mathrm{e}^{-0.0143 \cdot LM} \tag{65}$$

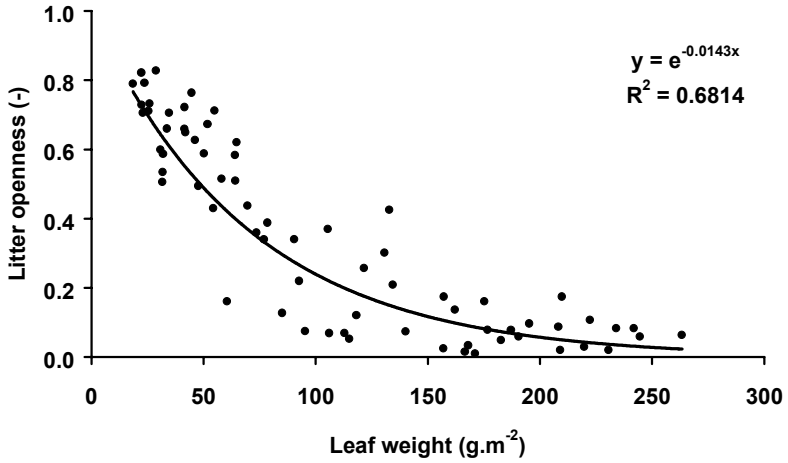


Figure 4.19 Litter openness versus leaf litter weight.

Appendix 4.8 Litter fall and decomposition

The amount of leaf litter mass on the soil, *LM*, is a function of leaf litter fall and leaf litter decomposition. These topics are discussed in detail in Chapter 6 (litter fall) and Chapter 7 (decomposition) and only the implementation in FORGAP is discussed here.

Litter fall

Litter fall in gaps and forest were determined empirically and were calculated as the sum of 1) litter fall from the vegetation that is surrounding the gap, the edge litter fall and 2) litter fall from the vegetation in the gap itself, the gap litter fall. Edge litter fall LF_{edge} (g.m^{-2}.h^{-1}) had a sigmoidally relation with the distance from the gap edge D_{edge} (m):

$$LF_{edge} = \frac{LF_{for}}{1+e^{-0.0439+0.2037 \cdot D_{edge}}} \cdot \frac{100}{8760} , \tag{66}$$

with LF_{for} the leaf litter fall of the undisturbed forest (5.6133 t.ha^{-1}.yr^{-1}) and with a correction factor 100/8760 to convert t.ha^{-1}.yr^{-1} to g.m^{-2}.h^{-1}. Gap litter fall LF_{gap} (g.m^{-2}.h^{-1}) had an empirical relation with the height of the vegetation in the gap H_{sap} (m):

$$LF_{gap} = (0.7616 \cdot H_{sap} + 0.1) \cdot 100/8760 . \tag{67}$$

Litter fall at any point in the gap or in the forest *LF* (g.m^{-2}.h^{-1}) was the sum of LF_{edge} and LF_{gap}, but litter fall was restricted to the maximum amount of litter fall of the undisturbed forest LF_{for} (0.064 g.m^{-2}.h^{-1}).

Decomposition
Decomposition was modelled with the decomposition coefficient or *k*-factor K_{dec}, as introduced by Nye (1961) and adjusted in FORGAP as:

$$K_{dec} = LF_{for} \cdot 100 / LM_{for} . \quad (68)$$

This decomposition coefficient assumes a steady state of litter fall and decomposition. This assumption is valid for the time step of the model, both in gaps and in forest. The amount of leaves that are being decomposed in one time step *DEC* ($g.m^{-2}.h^{-1}$) can now be calculated:

$$DEC = LM \cdot K_{dec} / 8760 , \quad (69)$$

with *LM* ($g.m^{-2}$) the amount of leaf litter mass on the soil. The new litter mass is obtained by:

$$LM_{t+1} = LM_t - DEC + LF . \quad (70)$$

Appendix 4.9 FORGAP model parameter descriptions

Radiation sub-module

Parameter	Description	Units
c	gap edge radiation extinction factor: 0.295	-
Day	Julian day number	day
D_{for}	distance in forest to the gap edge	m
k'	*LAI* radiation extinction factor: 0.290	-
LAI, LAI_{for}, LAI_{can}, LAI_{sap}	leaf area index of forest, canopy above saplings or saplings	$m^2.m^{-2}$
M_0 , M_h	relative path length an optical air mass at sea level and at altitude *h* (m)	-
P_h / P_0	atmospheric correction path length of the optical air mass	-
R_{edge}	radiation penetrating into the gap edge	$W.m^{-2}$
R_{LAI}	radiation through vegetation with , LAI_{for}, LAI_{can} or LAI_{sap}	$W.m^{-2}$
R_{shad}	radiation on the saplings in the shaded part of a gap	$W.m^{-2}$
R_{soil}	radiation on the soil	$W.m^{-2}$
R_{veg}	radiation on the vegetation	$W.m^{-2}$
S_c	solar constant: 1367	$W.m^{-2}$
S_{dif}	diffuse (indirect) radiation	$W.m^{-2}$
S_{dir}	incoming (direct) radiation	$W.m^{-2}$
S_{in}	Total incoming radiation	$W.m^{-2}$
S_{nor}	radiation normal to the beam	$W.m^{-2}$
S_{out}	solar radiation energy at the outer layer of the atmosphere	$W.m^{-2}$
α	solar altitude	deg
β_s	solar azimuth	deg
β_l	surface azimuth or aspect	deg
δ	solar declination	deg
η	solar hour angle	deg
ι	angle of incident of solar beams	deg
τ	transmissivity: 0.6	-
φ	latitude study area	deg
χ	slope	deg

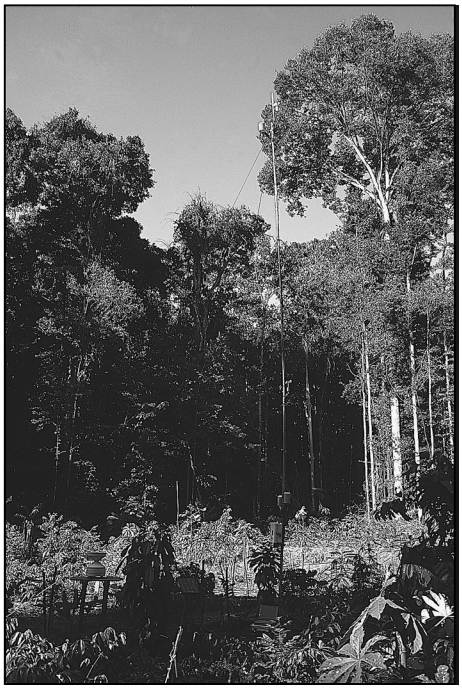
Evaporation sub-module

Parameter	Description	Units
cl	cloud factor (1: clear sky, 0: completely obstructed sky)	-
C_{max}	water storage capacity of the vegetation	mm
co	canopy openness	-
Cp	specific heat of air at constant pressure: 1004	$J.kg^{-1}.°C^{-1}$
d	zero-plane displacement	m
D_c	canopy drainage	mm
DEC	leaf litter decomposition	$g.m^{-2}$
D_{edge}	distance in gap to the gap edge	m
D_l	litter mass drip	mm
D_{sim}	water drip after rainfall experiment	mm
e_a, e_s	actual and saturated vapour pressure	mbar
$e_{a\text{-}s}$, $e_{s\text{-}s}$	actual and saturated forest vapour pressure	mbar
E_i	interception evaporation	mm
E_l	litter evaporation	mm
E_p	potential evapotranspiration	mm
E_{pen}	open water evaporation (Penman)	mm
E_{sp}	potential soil evaporation	mm
E_{st}	evaporation of intercepted water on the tree stems	mm
E_{tp}	potential transpiration	mm
$E_{tp\text{-}sap}$	potential transpiration of the seedlings/saplings	mm
E_{wet}	evaporation of a wet vegetated surface	mm
H_{veg}	height vegetation	m
H_{met}	height wind speed measurements in climate station	m
H_{sap}	height seedlings / saplings	m
Hs_i, Hs_{i-1}	seedling height at time step i or i-1	m
$Hsi_{1997/1998}$	initial seedling height in 1997 or 1998	m
K_{dec}	decomposition coefficient	yr^{-1}
LF, LF_{edge}, LF_{for}, LF_{gap}	litter fall, from the vegetation at the gap edge, in the forest and from the vegetation in the gap	$g.m^{-2}$
L_i	through fall intercepted by litter mass	mm
L_{in}	incoming long wave radiation	$W.m^{-2}$
L_{max}	storage capacity of the litter leaves	mm
LM, LM_{for}, LM_{gap}	leaf litter mass, in the forest and in the gap	$g.m^{-2}$
lo	litter openness	-
L_{out}	outgoing long wave radiation	$W.m^{-2}$
P_a	air pressure	mbar
P_g	gross rainfall	mm
P_i	intercepted rain by the vegetation	mm
P_n	net rainfall	mm
P_{sim}	rainfall of rainfall simulator	mm
P_{soil}	rain water entering the soil	mm
r	albedo or reflection coefficient	-
r_a	aerodynamic resistance	$s.m^{-1}$
$r_{a\text{-}sap}$	aerodynamic resistance seedlings	$s.m^{-1}$
r_c	canopy resistance: 130	$s.m^{-1}$
RH, RHs	relative humidity and relative humidity under forest	-
Rn, Rn_{edge}, Rn_{sap}, Rn_{soil}, Rn_{veg}	net radiation on the illuminated part of the gap edge area, on the saplings, on the soil and on the vegetation	$W.m^{-2}$
s, s_s	slope of the vapour pressure curve and s under forest	-
s_{can}	interception reservoir of closed forest:0.89	mm
S_{in}, $S_{in,a}$, $S_{in,p}$	incoming short-wave radiation, actual and potential	$W.m^{-2}$
S_{max}	Storage capacity of tree stems	mm
S_{out}	outgoing short-wave radiation	$W.m^{-2}$

Parameter	Description	Units
S_p	splash water during rainfall experiment	mm
S_f	stem flow	mm
T, Ts	air temperature, normal and under forest	°C
T_f	through fall	mm
T_{sim}	through fall during rainfall experiment	mm
u_{met}, u_c, $u_{sap,}$ us	wind speed in meteorological station at height H_{met}, corrected for the height of the vegetation like saplings and wind in forest	$m.s^{-1}$
u_f	friction velocity	$m.s^{-1}$
z_0	roughness length of vegetation	m
z_{0met}	roughness length of vegetation at wind measurement	m
z_{meso}	meso wind height: 60	m
ε	ratio molecular weight of water vapour and dry air: 0.622	-
κ	von Karman constant: 0.41	-
λ	latent heat of evaporation	$J.kg^{-1}$
λ_s	forest latent heat of evaporation	$J.kg^{-1}$
ρ	air density: 1.2047	$kg.m^{-3}$
σ	Stefan Boltzman constant: $5.67 \cdot 10^{-8}$	$W.m^{-2}.°C^{-1}$
γ	psychrometric parameter	$mbar.°C^{-1}$
γ_s	forest psychrometric parameter	$mbar.°C^{-1}$
$\Re_{rain}$	rain-evapotranspiration reduction	-

Soil Water sub-module

Parameter	Description	Units
D_{Ln}	thickness of soil profile layer n	cm
E_{sp}, E_{sa}	potential and actual soil evaporation	mm
E_{soil}	soil evaporation flux through topsoil, determined by matrix potential	mm
E_{pon}	evaporation of ponded water	mm
E_{tp}, $E_{ta\text{-}Ln}$	potential and actual transpiration of layer n	mm
ETr	transpiration reduction function	-
g	gravitation acceleration: 9.8	$m.s^{-2}$
h, h_{Ln}	pressure head in n^{th} layer	cm
H_{50}	pressure head where E_{ta} is 50% of E_{tp} : 3500	cm
h_{atm}	pressure head of the atmosphere (for calculation of E_{soil})	cm
I_{act}, I_{pot}	actual and potential infiltration rate	$cm.h^{-1}$
k, k_{atm}, k_s	hydraulic conductivity, at the soil-atmosphere and saturated	$cm.h^{-1}$
m, n	parameters in $h(\theta_e)$ and $k(h)$ relation	-
M	molecular weight water: 0.018	$kg.mol^{-1}$
P_{in}	water entering the profile or layer at the top	cm
q, q_{in}, q_{perc23},	Darcy's water flux or flux density, inflow in a layer and outflow to a layer, e.g. from layer 2 to 3	$cm.h^{-1}$
R	universal gas constant: 8.3144	$J.mol^{-1}.°C^{-1}$
RH	relative humidity	-
T	absolute temperature	°C
z	gravitational head	cm
α	parameter in $h(\theta_e)$ and $k(h)$ relation	-
β_{Ln}	fraction of total profile root content layer n	-
θ, θ_e, θ_{ini}, θ_r, θs, $\Delta\theta$	soil moisture content: effective, initial, residual (0.01) or saturated and change in soil moisture content in a layer	$cm^3.cm^{-3}$
ψ, ψ_m, ψ_g	water potential or hydraulic head (matrix or gravitational)	$J.kg^{-1}$
ζ	parameter in transpiration reduction function: 1.5	-



The Pibiri climate station in a 3200m^2 gap

5 MODELLING RADIATION AND WATER DYNAMICS IN DIFFERENT SIZED GAPS WITH FORGAP

Abstract
The PCRaster model FORGAP was used to calculate radiation, evapotranspiration and soil water dynamics in 6 experimental gaps, ranging in size from 60 to 3200m^2. Using hypothetical gaps, the effects of gap shape, orientation to the sun, multiple gaps and long-term effects on the microclimate, water balance and vegetation growth were analysed.

The annual potential radiation in the centre of a 60m^2 gap was 37% of the radiation on the surrounding forest and increased with gap size to 89% in a 3200m^2 gap. This resulted in a gradient of potential evapotranspiration of 469mm in a 60m^2 and 977mm in a 3200m^2 gaps, compared to 1356mm of the forest. This pattern of potential evapotranspiration was found for the transpiration of the vegetation, interception loss and soil evaporation. Although it was expected that rainfall interception on the litter layer could be substantial, it was only 0.5% in forest and 0.1% in the centre of the 3200m^2 gap, which can be attributed to the small amount of litter in this large gap. In the topsoil, pressure heads lower than –1000cm hardly occurred in gaps smaller than 200m^2, but were more frequent in gaps larger than 1000m^2. The driest soil moisture conditions were found at the gap edge, where additional soil moisture was extracted from the soil by the regenerating vegetation under the trees, which received more radiation than vegetation under the trees in the undisturbed forest.

The model results clearly showed the effect of gap shape and orientation to the sun of elongated gaps. Along an irregular shaped gap edge, microclimatic and soil moisture conditions can occur that are associated with small gaps and these areas can decrease the total gap area substantially. Round gaps clearly had higher evaporation loss and lower soil moisture contents than similar sized but elongated gaps. A similar conclusion could be drawn on west-east positioned gaps compared with north-south gaps, the latter being the wetter gap. Evidently, gap shape and orientation are important parameters regulating microclimatic conditions and water dynamics in gaps and gap edges.

INTRODUCTION

Modelling radiation and the water balance in gaps

Canopy gaps as created by selective logging differ is size, shape, orientation to the sun and undamaged vegetation in parts of the gap. This variation in gaps generates a range of microclimatic conditions and associated soil water dynamics. Moreover, these different type of gaps also induce a series of conditions for forest regeneration, not only inside the perpendicular projection of the gap perimeter, but also in the adjacent gap edge area or microclimate influenced area (MIA *sensu* Popma *et al.* 1988). Since at the moment, natural forest regeneration after logging is the common practice in Guyana, knowledge on the impact of different gap sizes and shapes on forest regeneration is sought after.

Field measurements of microclimate and soil moisture in different gaps provided a first glance at the possible effects of gaps (Chapter 3). In a 3200m^2 gap, the MIA, determined by the maximum weekly air temperature, extended 19m into the forest edge. Air temperature is directly influenced by the amount of radiation in a gap. Although the amount of potential radiation in the gap centre increased with increasing gap size, the maximum temperature did not increase above a gap size of 570m^2. Besides temperature, gap size influenced humidity, wind speed and soil temperature and the latter was also strongly affected by soil cover and soil moisture. No gap size effects were found for soil moisture, neither between gap centres of different sized gaps, nor between gap centre, gap edge and forest. Only weak patterns were

observed of drier topsoil (0-20cm) moisture gaps than in forest and drier overall (0-100cm) moisture conditions in the forest than in the gap.

However, the variety of gap sizes and gap shapes, the spatial variability inside gaps and the determination of the MIA exceed the logistics of gathering field data. Moreover, field measurements are limited to the moment of collection and future projections of microclimatic conditions and soil water dynamics, essential in forest regeneration, are hazardous. Modelling the microclimate and water balance of a forest / gap system provides a tool to overcome these problems. The model FORGAP was specially written for this purpose (Chapter 4).

How is the water balance affected by gap size, gap shape and gap orientation?

The hypotheses, as postulated in Chapter 3, were also tested in this model study, since it is expected that modelling provide a more comprehensive insight than field measurements into the possible patterns of microclimatic conditions and the water balance in a wide variety of gaps, either model reconstructions of 'real' gaps or hypothetical gaps.

- Gradual changes of microclimatic and soil moisture conditions were expected from small to large gap sizes and from the centre of a gap into the forest understorey. Soil moisture conditions are wetter in large gaps than in small gaps or forest. These gradients will change in time due to the regeneration of the vegetation in the gap.
- Near the edges of large gaps, microclimatic and soil moisture conditions will prevail that are similar to those in small gaps. A large irregular shaped gap has microclimatic conditions and a water balance similar to that of a small gap. Likewise, ‘forest-islands’ inside a gap notably reduce the effects on microclimate and water dynamics of an otherwise large gap.
- The daily movement of the sun through the hemisphere has larger consequences on microclimate and water balance than the yearly fluctuation between the two tropics.
- The influence of a gap on the microclimate and soil moisture is directly linked to the height of the vegetation. Regenerating vegetation in a gap reduces these effects. In other words, the effect of a gap on the microclimate and water balance show the largest decrease in gaps with the largest height increment, usually the largest gaps.

These hypotheses were tested in a selection of the experimental gaps of the Pibiri Gap experiment (PGE, van Dam *et al.* 1999) and microclimatic conditions and the water balance was calculated for a number of years. In addition, the model was used on hypothetical gaps. In these so-called scenario studies, changes in microclimatic conditions and changes in the water balance was studied to assess the effect of:

1) Gap shape: are there differences in microclimate and soil moisture between circular or elongated shaped gaps? What is the influence of an irregular shaped edge of a gap on the amount of radiation and the water balance along this edge and in the resulting gap area?
2) Gap orientation: what are the effects on microclimate and water balance of the yearly movement of the sun (North-South oriented gap) or the daily variation in solar altitude (West-East oriented gap)?
3) Remaining vegetation in a gap: what is the influence of a ‘vegetation-island’ or 'forest-fragment' on the microclimate and water balance of a gap?
4) Multiple gaps in close proximity of each other: do many small gaps have a water balance that is comparable to a larger gap?

In a normal logging operation, elongated gaps or irregular shaped gaps are more common than the circular experimental gaps of the PGE and this gap shape and orientation can have large influences on the amount of radiation in a gap and the resulting water dynamics. In addition, single trees or forest fragments are sometimes left behind in an otherwise large gap and these forest fragments can decrease the amount of radiation and corresponding water dynamics. Likewise, usually more than one gap in a relatively small area (1 ha) is created. Although a

forest buffer separates these gaps from each other, the water balance can be comparable to a large gap.
The time-span of forest regeneration has been a debate among scientists (Dirzo *et al.* 1992, Martínez-Ramos *et al.* 1988, Martínez-Ramos and Alvarez-Buylla 1998) and even less is known about the influence of gap age on the microclimate and water dynamics. Although adequate field measurements are lacking, an attempt is made evaluate the effect of gap age:
5) How do microclimatic conditions and water dynamics change after 15 years?

The '97/'98 El Niño event
From July 1997 to March 1998, Guyana suffered from a severe drought due to an El Niño event. As a result, no rain was recorded for 3 consecutive weeks in March 1998. Calculation with FORGAP provided an exceptional opportunity to study the effects of prolonged drought on the water balance. Prolonged drought can severely damage the vegetation and limited the germination and survival of seedlings. Most plants in a tropical rain forest require a gap to germinate, since in a gap higher levels of solar radiation are found than in the forest understorey. The effect of a drought on the evaporation loss and soil moisture conditions in different sized gaps is not known.

METHODOLOGY

FORGAP input and output

Macroclimate input
Air temperature, air humidity, solar radiation, wind speed and rainfall were measured in a permanent climate station in the largest 3200m^2 gap (Chapter 2). Global radiation was measured as well and was used to calculate the cloud factor (Appendix 4.3). The macroclimate data of 1997 was used to calculate the water balance during a year. The initial settings at 1 January 1997 were determined by first running the model in 1996 for 2.5 months. The starting date of this initialisation run was 19 October 1996, which was the planting date of the experimental seedlings.

In some instances, the PGE climate station made no recordings due to technical malfunctioning. FORGAP cannot run with an incomplete meteorological input file. Therefore, the missing data, usually only a few hours or a few days, have been replaced by:
1) Substitution by linear regressions between a climate variable and another. This method was applied on regressions between radiation, temperature and humidity.
2) Substitution of the average value per hour of the same hours 1 week before and 1 week after the period of missing data. This method was used for wind and air pressure and for radiation, temperature and humidity if method 1 could not be used.
3) Substitution of the average value per hour of the same hours of other years, including the data collected in '91/'93 in the FRMH climate station. This method was applied on rainfall.

The scenario studies of long term modelling were with an average macroclimatic year. Data of temperature, humidity, air pressure, radiation, rainfall and wind speed were used of 1991, 1992 and 1993 (Jetten 1994a) and 1996, 1997, 1998 and 1999 (this study). A distinction was made in this dataset between hours with and hours without rainfall, since for example temperature during rainfall is lower than during dry periods. Initially, two average macroclimatological years were constructed: one containing the average macroclimatic parameters during a dry hour and one during rainfall. The average rainfall per hour was based upon all years in the dataset. The final average macroclimatic year combined the two initial ones, whereby one of the two was selected, based upon the occurrence of rainfall.

Vegetation data
Tree height of the undisturbed forest in the study area varied between 20 and 44 m (n=160) and the average height of 28m (σ 4.52) was used in FORGAP. The sapling growth model, litter mass, litter fall, decomposition and cell openness as given in Chapter 4 were used.

Maps and time series reports
FORGAP produced a large amount of maps and time series on radiation, evapotranspiration, and soil water dynamics like infiltration and percolation. A selection of FORGAP output was made. Model output was assessed for:

- potential radiation on the vegetation, the saplings in the gap and gap edge area and the soil,
- microclimate influenced area, defined by a 5% increase of potential radiation on the saplings compared to the radiation on the saplings of closed forest,
- potential evapotranspiration,
- interception evaporation including stem evaporation, litter interception evaporation and evaporation of ponded water,
- actual transpiration and soil evaporation,
- throughfall, stemflow and net rainfall,
- soil moisture conditions and occurrence of a matrix potential in the top 40cm of the soil between 0 and –10cm, -10 and –100cm, -100 and –1000cm, -1000 and –10,000cm and above –10,000cm and
- percolation below the root zone.

Effect of gap size on the water balance

The effect of gap size on the microclimate and water balance was modelled for 6 experimental gaps of 60, 210, 370, 570, 1280 and 3200m^2. The edges of these experimental gaps were measured in 1996 and FORGAP input maps were created of these gaps. Gap closure was not modelled, since it was relatively small (Rose 2000). In the first year after gap formation, canopy openness decreased 0.8% in the 3200m^2 gap and 4.4% in the 210m^2 gap.

The water balance of the gaps and the forest was calculated for 1997. From July 1997 to March 1998, Guyana was under the influence of extreme dry weather due to an El Niño event (Chapter 2). The effect of the '97/'98 El Niño event on evapotranspiration loss and soil moisture conditions was studied in greater detail.

Scenario studies with FORGAP

FORGAP was used to study the effects of hypothetical gaps.

- *Effect of gap orientation.* Two hypothetical rectangular gaps (1020m^2) were used, that were positioned either in a North-South direction (NS gap) or in a West-East (WE gap) direction. FORGAP results of these two gaps were compared to the output of a simulation run with a hypothetical circular gap of 1040m^2 (CIR gap).
- *Effect of gap shape.* The largest 3200m^2 gap had an irregular shaped edge and the water balance of these 'extensions' in the edge was compared the water balance in the centres of more circular gaps. The water balance was calculated of a model gap that had a forest fragment or forest island of 50m^2 (ISL gap) in the centre of the CIR gap that reduced the gap area to 990m^2.
- *Effect of multiple gaps.* At the research site at 2K, a logging operation in 1986 created several gaps within a 1 ha area (Ek 1997). The gap sizes were between 50 and 800m^2. FORGAP was used to calculate the water balance of this 1 ha area to study the effects of multiple gaps within a relative small area.

- *Effect of long-term calculations.* The average climate year was used to create a continuous climate input file of 15 years. FORGAP calculated the water balance for 15 continuous years in a 210, 570 and 3200m^2 gap.

FORGAP RESULTS

Radiation and the water balance of forest and gaps, 0.5–1.5 year after logging

Radiation

Annual potential radiation on the 28m tall vegetation (R_{veg}) was 8053 MJ.m^{-2}.yr^{-1}. In the centre of a gap, potential radiation on the saplings (R_{sap}) decreased with decreasing gap size from 7132 MJ.m^{-2}.yr^{-1} in the 3200m^2 gap to 3002 MJ.m^{-2}.yr^{-1} in the 60m^2 gap (Figure 5.1A). Likewise, the potential radiation at the gap edge decreased with decreasing gap size and a sharp transition occurred at the gap edge. The radiation on the saplings at the edge of the 3200m^2 gap dropped from 4519 MJ.m^2.yr^{-1} in the gap to 1581 MJ.m^2.yr^{-1} under the forest trees. Radiation on the soil (R_{soil}) decreased from 5990 MJ.m^2.yr^{-1} in the centre of the 3200m^2 gap to 2619 MJ.m^2.yr^{-1} in the centre of the 60m^2 gap and continued to decrease under the forest to 888 MJ.m^2.yr^{-1}. The irregularly shaped edge of the 3200m^2 gap created areas at the gap edge with an increase in shade during the year (Figure 5.2A). As a result, the amount of radiation in these areas was similar to that in 200m^2 gaps and the amount of radiation in the gap centre of the 3200m^2 was less than would have been for a more circular gap of 3200m^2. Clearly, the shape of the gap edge has a large influence on the actual microclimate that is present in a gap.

Evapotranspiration

Similar patterns as described for the potential radiation were discerned for the potential and actual evapotranspiration (Figure 5.1C). Potential evapotranspiration (E_P) decreased from 977mm (41% of annual rainfall P) in the 3200m^2 gap to 469mm (20% of P) in the 60m^2 gap. E_P was 1356mm for closed forest (56% of P). The amount of actual transpiration by the vegetation depends on the soil moisture and will be reduced if the amount of soil moisture becomes low. However, potential transpiration of the vegetation (E_{Tp}) was hardly limited and actual transpiration (E_{Ta}) was on average 92% of potential transpiration in the forest (E_{tp} 914mm) and 95% in the gap (E_{tp} 620mm) (not shown in Figure 5.1). A part of rainwater is intercepted by the leaves of the vegetation and evaporates after the rainstorm. This canopy interception evaporation (E_I) was not much different between different gaps, but large differences were found between gaps and forest. In the forest, E_I was 362mm (15% of P), while in the gaps, E_I was on average 15mm (0.6%). Clearly, the much larger storage capacity of the forest, with a leaf area index of 5.9 m^2.m^{-2} compared to 0.3 m^2.m^{-2} in the gaps, explains this difference. As was observed with radiation, soil evaporation (Figure 5.2B) and transpiration (Figure 5.2C) along the irregular shaped edge of the 3200m^2 gap was similar to the evapotranspiration of a 200m^2 gap.

After interception on the leaves, rainwater drains to the soil, mostly as throughfall, but a small portion as stemflow. The branches and tree trucks have a certain storage capacity, like leaves, and after the rainstorm, this water will evaporate. This evaporation from the stems of the vegetation (E_{st}) was remarkably large. In the forest, 34mm (1.4% of P) evaporated from the stems, while in the gaps, E_{st} was only 2mm (Figure 5.1C). Like transpiration, actual soil evaporation (E_{Sa}) is affected by the soil moisture content of the soil.

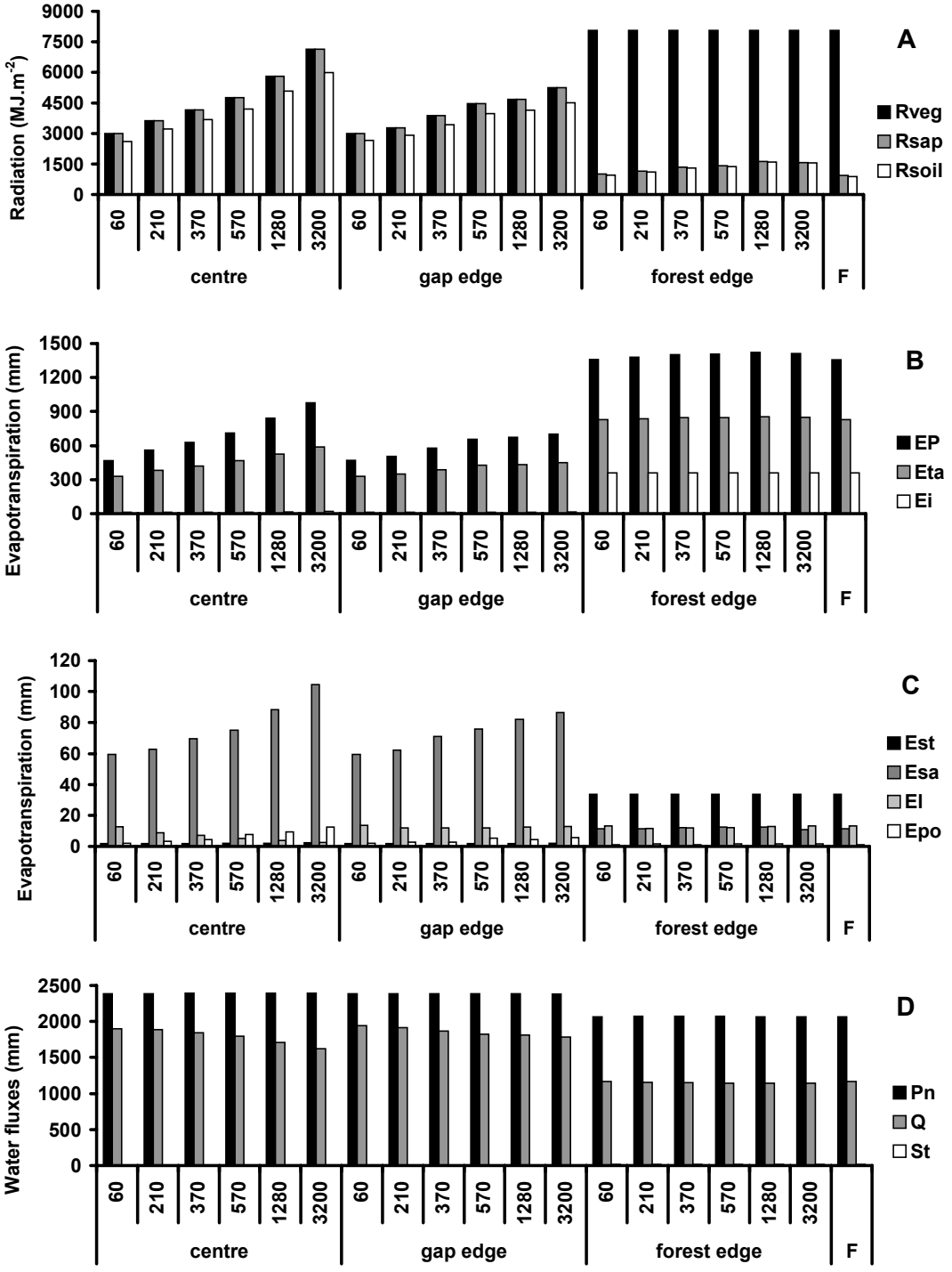


Figure 5.1 FORGAP results of A) radiation, B & C) evapotranspiration, D) throughfall, stemflow and percolation below 120cm depth in different gap sizes, 0.5–1.5 year (1997) after logging (July 1996) and at different locations in the gaps. (Rveg, Rsap, Rsoil: potential radiation on the vegetation, saplings and soil. Note that in the gaps, Rveg = Rsap. EP: potential evapotranspiration, Eta: actual transpiration, Ei: evaporation of intercepted water on the vegetation, Esa: actual soil evaporation, Est: evaporation of water on the stems of the vegetation, El: evaporation of water on the litter layer, Epo: evaporation of ponded water, Th, throughfall, Pn: net precipitation, Q; percolation below 120 cm, St: stemflow; 0mm in gap centre and gap edge, 16mm in forest edge. Note that Pn = Th + St – El and that the bulk precipitation in 1997 was 2410mm. F = Forest)

Potential soil evaporation is the potential amount of open water evaporation, which is clearly much more than the actual amount of water that can evaporate from the top layer (0-15cm). In the centre of the 3200m^2 gap, actual soil evaporation was 33% of potential soil evaporation (E_{Sp} 319mm, not shown in Figure 5.1) and actual soil evaporation was even more reduced in the forest, where only 11mm soil evaporation was found (27% of E_{sp}). This was not surprising, since the amount of radiation and wind in the forest was much less than in the gap. A third interception reservoir is the litter layer on the soil, which also stores a small amount of rainwater and from which water evaporates after a rainstorm. This soil litter interception evaporation (E_L) was less than 1% of year precipitation and apparently was of minor influence on the water balance of the forest. E_L increased slightly from the gap centres to the gap edges, where a thicker litter layer was present.

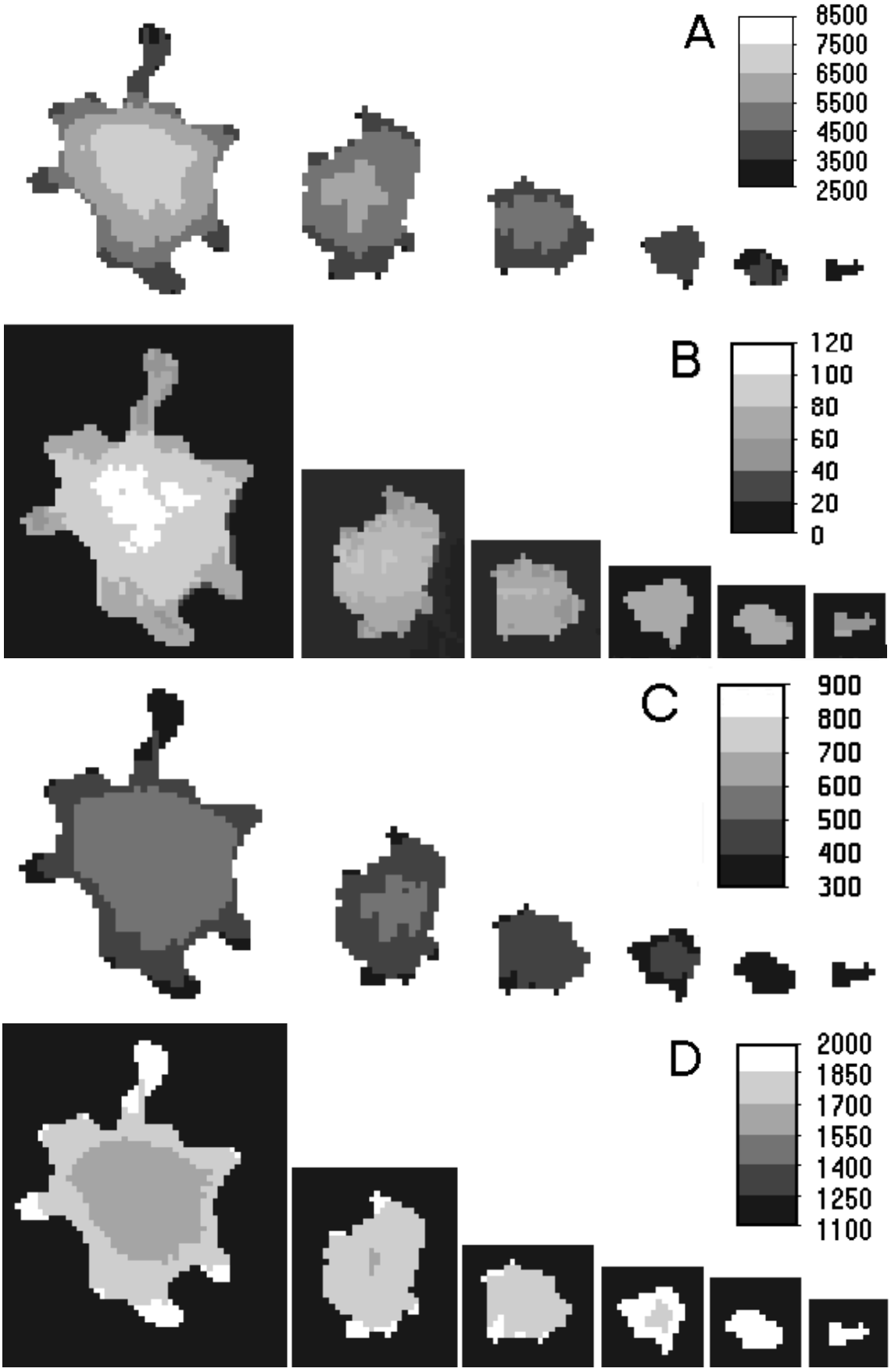
If the amount of rainfall in one time step exceeds the infiltration capacity, water will pond on the soil and a temporarily storage is created and this water will evaporate after a rainstorm until the next time step, when infiltration continues. This evaporation of ponded water (E_{po}) was negligible small in the forest, 1 mm, but increased to 12mm (0.5% of P) in the centre of the 3200m^2 gap. In the gap, there was more radiation and wind than in the forest, which increased the amount of E_{po}. In the forest, more water was available for infiltration in the time step following the ponded conditions.

Throughfall, stemflow and percolation

In the gaps, throughfall (T_h) – the amount of water after interception of gross precipitation on the vegetation – and net precipitation (P_n) – throughfall plus stemflow – were not different from each other, because litter interception and stemflow (S_t) were marginally small (Figure 5.1D). As a result, T_h in the gaps was almost 100% of P. Throughfall under closed forest was 2071mm, which was 86% of P, a percentage that was also found by field measurements (Jetten 1994a, Sluiter and Smit 1999). Percolation of soil water (Q) below the rooting zone of 140cm increased from 1624mm (67% of P) in the 3200m^2 gap centre to 1900mm (79% of P) in the 60m^2 gap centre, which was 40% more than the amount of Q under closed forest (1164mm). Percolation loss along the irregular gap edge of the 3200m^2 gap was similar to the percolation loss at the gap edge of a 200m^2 gap (Figure 5.2D). Stemflow (S_t) was absent in the gaps and was less than 1% of P in the forest (16mm).

Soil moisture conditions in the top 40cm of soil

The driest soil conditions occurred at the gap edges of the largest gaps, where the regenerating vegetation in the gap edge extracted some additional water from the soil compared to the undisturbed forest. Very wet conditions between saturation and –0.1cm matrix suction (pF-2) did not occur, somewhat drier conditions of –0.1 to -10cm (pF-2 to pF2) were more common in gap centres than at gap edges or in the forest (Figure 5.3). Very dry topsoil moisture conditions were only found in the gap centres of the 1280m^2 and 3200m^2 gaps, primarily caused by soil evaporation. In the gap centres and gap edges (eg in Figure 5.3), the most common soil moisture status was between –10 and –100cm, while at the gap edges under forest (ef in Figure 5.3) and in the forest, the frequencies of pF1 to pF2 and pF2 to pF3 were almost equal. A general conclusion is that in gaps larger than 1300m^2, dry soil moisture conditions are more frequent.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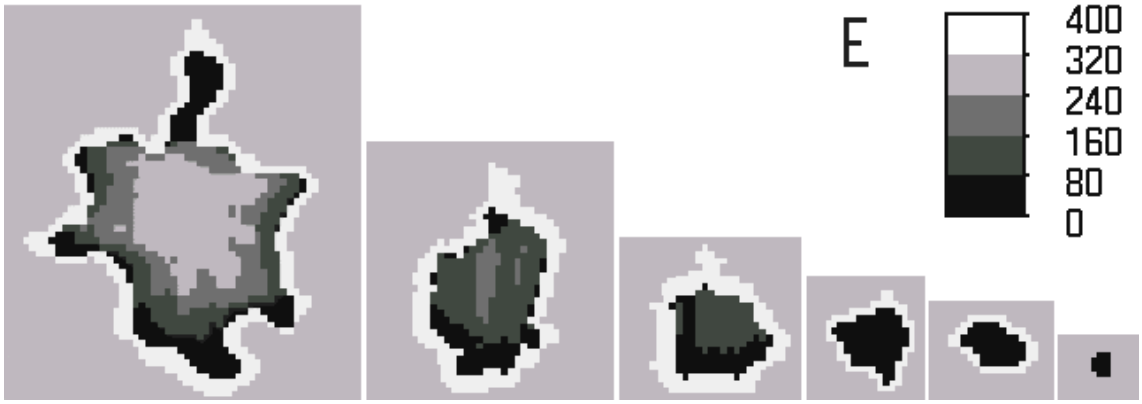

Figure 5.2 FORGAP results in a 3200m^2, 1280m^2, 570m^2, 370m^2 210m^2 and 60m^2 gap, 0.5–1.5 year after gap creation (1997) for – previous page – A: potential radiation on the vegetation (MJ.m^{-2}.yr^{-1}); B: actual soil evaporation (mm); C: actual transpiration of the vegetation (mm), D: percolation loss below the rooting zone (mm) and – this page – E: no. of hours in a year than the soil suction is lower than –1000cm.

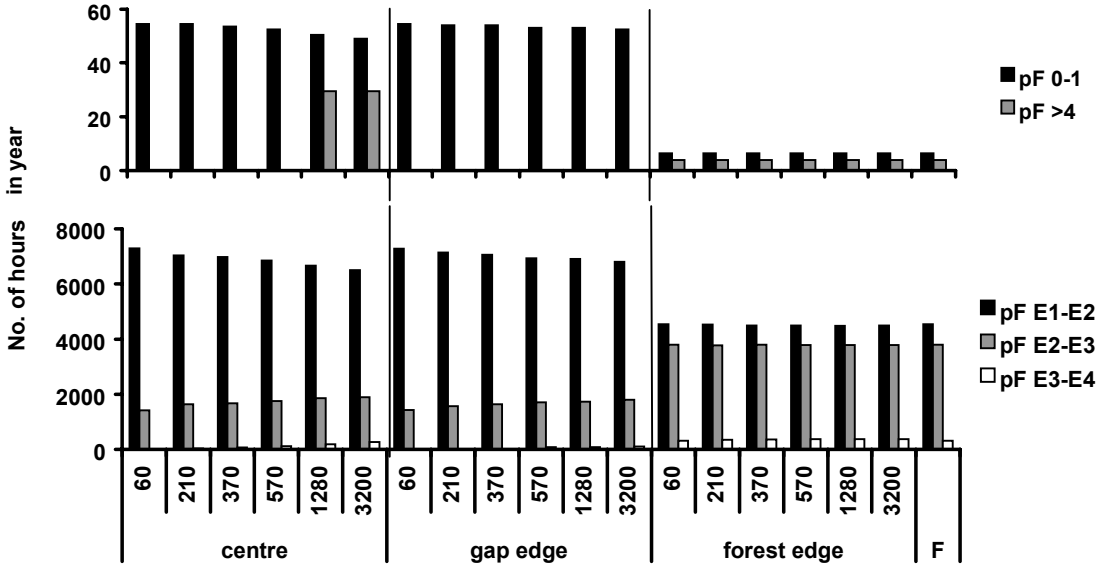

Figure 5.3 FORGAP results of the number of hours in a year (total hours is 365×24=8760) that a soil matrix suction was between two pF values (|x| cm suction head is log(x) pF value) in the top 40 cm of soil in forest and in different gap sizes, 0.5–1.5 year (1997) after logging (July 1996) and at different locations in the gaps. (Top chart represents wet conditions (pF 0-1) and dry conditions (pF>4), while the lower chart represents the intermediate conditions. (F = forest.)

Soil moisture and El Niño

In March 1998, rainfall was absent for 3 weeks after a period of already reduced rainfall due to the '97/'98 El Niño event (Figure 5.4A). Evapotranspiration loss continued during this period (Figure 5.4B) and pressure head *H* in the top 15cm of the soil dropped to –69,200cm in a 3200m^2 and to -43,100cm in the forest (Figure 5.4C1). The larger decrease in the gap was the result of a larger soil evaporation loss from the topsoil. This pattern was reversed in deeper layers, where pressure heads were lower in the forest than in the gap due to larger transpiration losses in the forest (Figure 5.4C2-4). Percolation below 140cm depth stopped during and after these three weeks without rainfall (Figure 5.4D). In the same period in 1997, percolation in the

gap was 1.3mm.d^{-1} and in the forest 0.7mm.d^{-1}. When rainfall was restored in the beginning of April 1998, all rainwater was immediately used for evapotranspiration and only the pressure head in the topsoil increased after the first rain showers (31/3/98). The pressure head in the layers below had a delayed response and continued to decrease: 15-40cm until 5/4/98, 40-80cm until 7/4/98 and 80-140cm until 10/4/98. Consequently, percolation loss did not increase before 11/4/98.

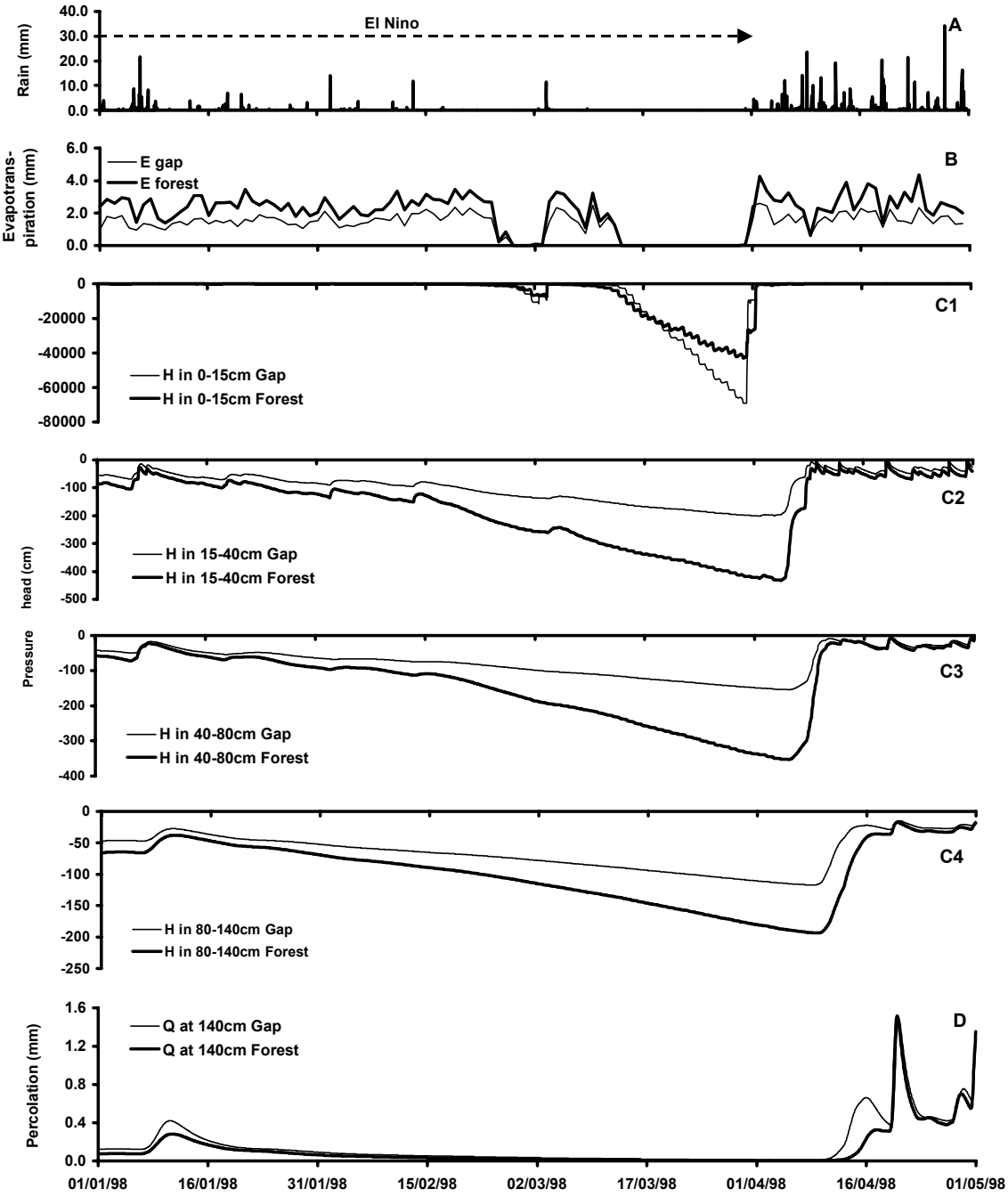

Figure 5.4 FORGAP results during the latter part of El Niño and in the first month after the dry period (1/1/98 – 1/5/98) in the centre of a 3200m^2 gap and in the forest: A) Rainfall, B) day totals of evapotranspiration loss, C) Soil matrix pressure head per depth layer: C1 0-15cm, C2 15-40cm, C3 40-80cm and C4 80-140cm and D) Percolation loss below 140cm.

Microclimate influenced area (MIA)
The smallest 60m^2 gap had a MIA that was 3.4 times larger than the perpendicular projection of the canopy trees that made the gap (sensu Brokaw 1982). The MIA of the 210 and 370m^2 gap were 2.2 and 1.9 times larger than the original gap size. The MIA's of the 570, 1280 and 3200m^2 gap were, respectively 1.6, 1.4 and 1.3 times larger than the actual gap size. The MIA of the 3200m^2 gap had a maximum extent of 8m into the forest understorey, while in the 60m^2 gap this was only 2m. The difference in gap size / MIA ratio can be explained by the differences in size of these two gaps. The MIA determined by the measured weekly maximum temperature in the 3200m^2 gap was almost similar, since no increase in temperature was found beyond 10m from the gap edge. Similar comparison between measured and calculated MIA of the other gaps is not possible, due to lack of field data.

FORGAP results versus field measurements

FORGAP did not only gave more detailed insight into the microclimate-influenced area than field measurements, the model also highlighted the potential differences between gap of different sizes and the effects of irregular gaps. Differences in soil moisture distribution within gaps and between gaps of different sizes were better visible and less blurred by the spatial heterogeneity in the experimental gaps. Notwithstanding that this heterogeneity is an essential element of the forest ecosystem, it makes comparison between different locations more difficult.

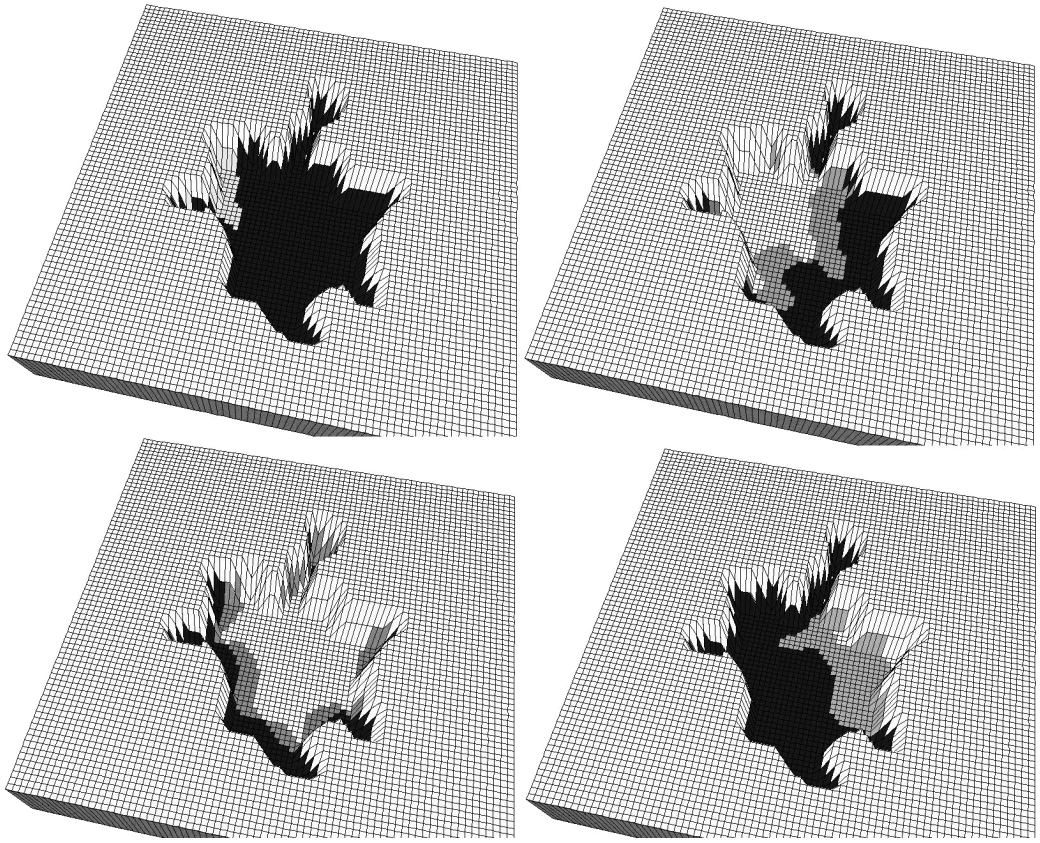

Figure 5.5 Example of radiation and shading effects in a 3200m^2 gap on 1 January at 8, 10, 13 at 16h. Black areas: shade, light gray: illuminated, dark gray: partly shaded during previous hour. (looking from South to North).

For example, the large variability in soil physical properties, soil cover and rooting patterns prohibited the distinction of soil moisture patterns, which were better explained by the model results. FORGAP enabled the study of daily patterns of for example solar radiation in gaps (Figure 5.5) and between gaps, which was not possible with field measurements.

Scenario studies

Gap orientation and gap shape The North-South (NS) and the West-East (WE) oriented gaps received, respectively, 86% and 94% of the amount of radiation compared to the circular gap (CIR), while the circular gap with a 50m^2 forest fragment or island in the centre of the gap (ISL) received 90% of the amount of radiation in the CIR gap (Figure 5.6). The WE gap had 10% more radiation than the NS gap. These patterns of radiation were also found for evapotranspiration fluxes and soil moisture dynamics. Thus it seems that gap orientation had only a limited effect on the water balance.

The edge of the 3200m^2 gap was irregular shaped, with many 'extensions' protruding up to 20m into the forest, while the other gaps were more circular. As was already mentioned above, the edge area of the 3200m^2 gap received less radiation and had lower evaporation than the centre of the 1280m^2 gap, while all other gap edge area received more radiation and had more evaporation than the gap centre of the next smaller gap size (Figure 5.1). Radiation, evapotranspiration and soil moisture conditions in the 'extensions' of the 3200m^2 were similar to conditions in the 200m^2 gap and are therefore a significant change in the water balance of the entire gap.

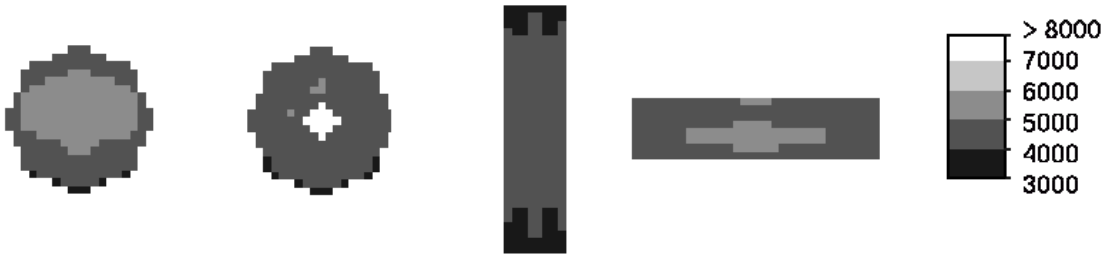

Figure 5.6 Effect of gap orientation and forest fragments on the potential radiation (MJ.m^{-2}.yr^{-1}). From left to right: perfect circular 1040m^2 gap and a circular 1040m^2 gap with a 50m^2 forest fragment in the centre, a North-South and West-East oriented 1040m^2 gap (looking from South to North).

Multiple gaps In a 'normal' forest logging operation, more than one gap is created within a relatively small area. Although the presence of a lot of small gaps could have the same effect as one large gap, the model results with FORGAP in a 1 ha forest with 12 small gaps with gap sizes of 20 to 800m^2 did not induce the radiation levels, evapotranspiration fluxes and soil moisture conditions towards of a much larger gap (Figure 5.7). Gap edge effects on radiation, evapotranspiration and soil moisture conditions did not extent far from the gap edge, but forest edges of large gaps (> 500m^2) that were within a few metres from each other experienced microclimatic conditions similar to small gaps (< 100m^2). For example, the forest edges of the two lower-left gaps in Figure 5.7 had radiation levels equal to the gap centre of the small gaps in the centre of Figure 5.7. The saplings at 2m into the forest between the gaps had grown 2.3 times more than at the opposite site of the lower-right gap, where no other gap was positioned. The MIA of these gaps together was 1.8 times larger than the combined gap sizes.

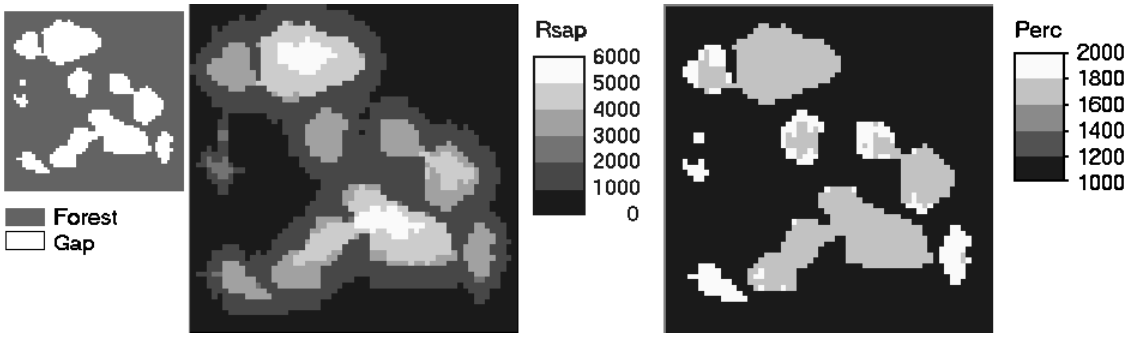

Figure 5.7 Effect of multiple gaps in an area (as displayed in the left corner) on the radiation on the saplings (Rsap: $MJ.m^{-2}.yr^{-1}$) and percolation below the rooting zone (Perc: mm).

Long term modelling

Long term modelling of radiation, evapotranspiration and soil moisture in gaps of different size was dominated by the regrowth of the vegetation in the gap. The largest increase of the vegetation in the gap was within the first 10 years after logging (Figure 5.8). The regrowth of the vegetation in the $3200m^2$ gap was almost equal throughout the whole gap. A gradual decrease in height can be seen at close proximity to the gap edge. The 'extensions' of the gap edge clearly had a much lower regrowth. The regrowth in the two smaller gaps was less uniform throughout the gap than in the $3200m^2$ gap, but showed a continuous gradient of decreasing vegetation height towards the gap edge.

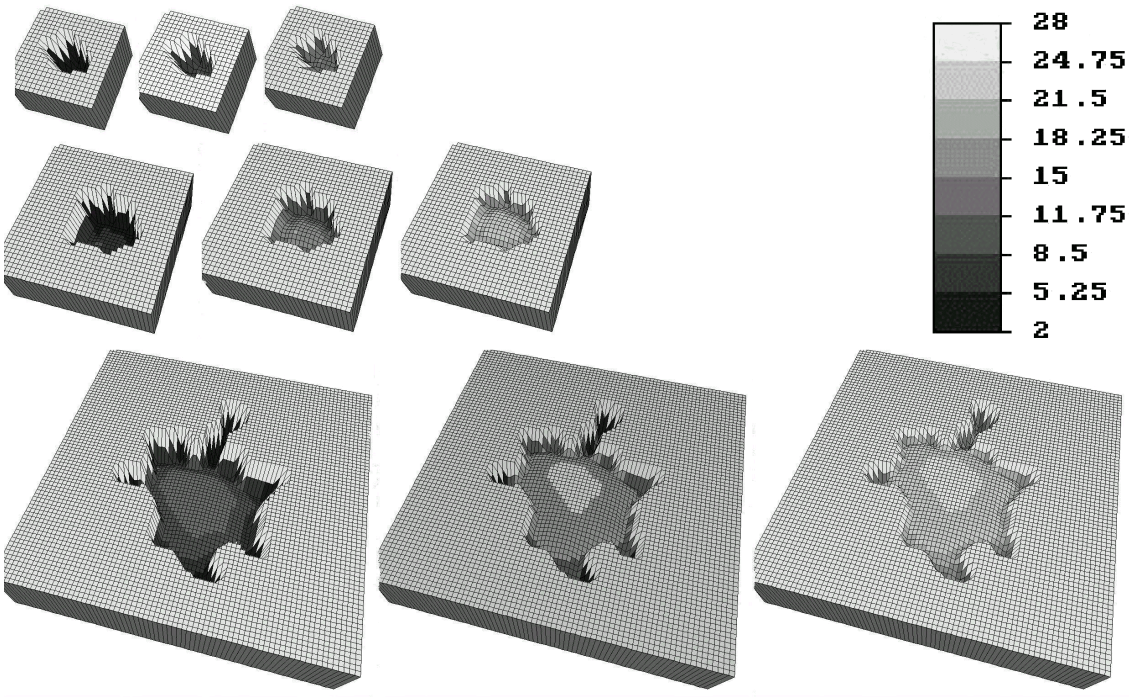

Figure 5.8 Sapling height (m) in a 210, 570 and $3200m^2$ gap (top-down) after 5, 10 and 15 years (left-right) with a surrounding forest of 28m. (Eye position in the South, looking North)

The potential radiation on the vegetation in the 3200m^2 gap was 82% of the radiation sum of the forest, while the 210m^2 gap received only half that amount. As a consequence, the actual transpiration of the vegetation in a 210m^2 gap was 57% of that in the 3200m^2 gap. Throughfall in the gaps did not show large differences between gaps, but percolation was more than twice as large in the 210m^2 gap as in the 3200m^2 gap. Despite this, dry soil moisture conditions in the 210m^2 gap were very rare, while in the 3200m^2 occurred for more than half the number of times as in closed forest. There were clear gradients of sapling height, actual transpiration, interception evaporation, percolation and dry soil conditions from gap centre to gap edge, with a sharp transition going into the forest. Radiation on the saplings and on the soil and throughfall had a gradual transition between gap and forest.

After 15 years, the vegetation in the gap had attained a height of 26.4m and the radiation on the vegetation in the gap was almost at the same level throughout the gap. The radiation started to decrease at 6m close to the gap edge. Spatial patterns of radiation, evaporation and soil moisture became more pronounced after 15 years of simulation and North-South gradients could be distinguished. The northern part of a 3200m^2 gap received 17% more radiation than the southern part the gap, which resulted in an 8% taller vegetation in the northern part of the gap. Therefore the northern part of the gap had 9% more transpiration, but 1% less soil evaporation than the southern part of the gap. The lower soil evaporation in the northern part of the gap was caused by twice as many occurrences of soil moisture suctions below –1000cm in the northern part of the gap compared to the southern part of the gap. Although a WE oriented gap received more radiation than a NS oriented gap (Figure 5.6), apparently, the influence of solar declination throughout the year was an important parameter, as was already weakly noticeable in the circular gap of Figure 5.6.

DISCUSSION

Modelling the water balance in different sized gaps with FORGAP

Interpretation of FORGAP results: spatial variability of soil and vegetation attributes

Soil hydraulical properties, leaf area index and litter cover were based upon field information or literature. These attributes usually have a large spatial variability and vegetation attributes usually also have a large seasonal variability. For example, soil properties like infiltration rates and hydraulic conductivity have a short distance variation with a relative variance between 30 and 50% within 2m (Jetten 1994a). Vegetation properties like canopy openness or LAI above a point change throughout the year, when the vegetation grows or dies. Such variations can be modelled by running the model with a wide variety of possible solutions. However, differences between positions in a gap or between gaps of different size would be difficult to interpret. Instead, average values are more useful because they are best estimates of the parameters and potential differences between sites become apparent.

Differences between gap sizes and within gaps

Gradients of increasing solar radiation, evapotranspiration fluxes, drier topsoils and wetter subsoils were found from small to large gaps and from the gap edge to gap centres, but these gradients were not present over the whole range of gap sizes. In gaps up to 200m^2, radiation and evapotranspiration differences between gap centre and gap edge were small. Radiation is one of the main parameters in the model. It is the driving force of the evapotranspiration fluxes and sapling growth in the gaps. Not surprisingly, any pattern that was found for radiation was also found for the evapotranspiration fluxes and related to that, the growth of the saplings and the soil moisture conditions in the gaps. However, the difference between evapotranspiration fluxes in gaps and forest were not of the same magnitude as the differences in radiation between gaps and forest. In the centre of the largest gap, radiation was almost equal to the amount of radiation

on the forest (89%), while the amount of actual evapotranspiration in the centre of the largest gap was much lower than the forest (61%). This is caused by the much smaller vegetation in gaps than in forest, which reduces transpiration and interception loss.

Against expectations, litter interception loss was small. This can be explained by the relative small amount of litter on the soil. In the Colombian Amazon, total litter mass was 6.73 $kg.m^{-2}$ (Tobón Marin 1999), which is much more than the 0.60 $kg.m^{-2}$ of the research area. Surprisingly, evaporation from the tree stems was relatively large. It must be noted however, that the derivation of stem evaporation was based upon data from forest trees (Jetten 1996) and in gaps, stem density is larger than in forest, but stem roughness and therewith the storage capacity is probably less. The precise storage capacity of the stems of regenerating plants in not known.

There was a clear distinction of interception loss between gaps and forest, but differences between or within gaps were less apparent. There was only 1% difference in throughfall between the largest and the smallest gap. Consequently, differences in soil moisture conditions between different gaps cannot be explained by differences in the amount of net rainfall. Since the hydrological parameters were equal for all gaps, differences between gaps in soil moisture conditions and percolation loss were only related to the soil evaporation and sapling transpiration flux.

Soil water extraction by the vegetation that surrounds the gap was not modelled, because roots did not occupy neighbouring grid cells. It is likely that the smallest gaps experience soil moisture conditions that approach the conditions in the forest, instead of the conditions as shown in Figure 5.1, since the vegetation that surrounds these small gaps will most likely extract water from the gap (assuming a grid cell of 2×2m, as was used in the model runs). Therefore, the simulated soil moisture content of the gap edge of these small gaps was wetter than can be expected, although these differences between centre regions of a gap and gap edges were also not found in soil moisture measurements (Chapter 3). The gradient of drier soil moisture conditions at the forest edge compared to the forest was simulated correctly by the model, since the vegetation in the forest edge extracted more water than the vegetation in the undisturbed forest. However, differences in soil moisture conditions between forest edge area and forest were smaller than expected.

Microclimate Influenced Area

The single multiplication factor of 3.4 for the microclimate influenced area (MIA), as proposed by Popma *et al.* (1988), was not found with the FORGAP simulations. The shading of the gap at low solar altitudes of the smallest gap limited the MIA to 2 times the actual size of the gap, as was found for gaps between 200 and 400m^2. The gaps of Popma *et al.* (1988) were between 12 and 223m^2 and their research site were located at Los Tuxlas, Mexico, at a latitude of 18°. Since the PGE study area is located at 5° latitude, the sun will be at high solar altitude during most parts of the day and throughout the year. These high solar altitudes prevent the extent of the MIA deeper into the forest. Although the influence of the sun can be noticed at distances further away in the early morning and late afternoon, the amount of radiation at these hours is still small and does not contribute to an increase in MIA. The extent of the MIA is depended on latitude, topography, gap size and shape, orientation to the sun and height of the surrounding vegetation. These factors will result in a MIA of which the extent into the forest fluctuates along the gap edge. Apparently, the gap size – MIA multiplication factor increases from the low to higher latitudes.

El Niño

During the El Niño event, soil evaporation strongly decreased the amount of water in the soil. In gaps, soil evaporation loss from the top 15cm of soil was even larger than transpiration losses in forest. These very dry soil conditions can seriously affect plant growth. However, it is not known to what depth direct soil evaporation decreases the amount of soil moisture. Possibly, direct soil evaporation is only limited to the top 5cm under normal climatic conditions. A mulch could be formed that limits the drying out of deeper layers. On the other hand, during prolonged drought, direct soil evaporation could decrease soil moisture conditions much deeper than 15cm. Nevertheless, topsoil moisture conditions in larger gaps can decrease the change of survival of very small seedlings.

Scenario studies

The largest part of a North-South oriented gap (NS) did not receive any radiation in the early morning or late afternoon, while in a West-East oriented gap (WE) during the same periods of the day, radiation was present. Consequently, a WE gap received more radiation on an annual basis than a NS gap. The daily fluctuation of radiation in a gap was more important than the north-south movement of the sun during a year. However, the influence of gap orientation was small and most likely irrelevant for forest regeneration within normal logging operations.

The irregular shaped 3200m^2 gap had approximately 500m^2 of smaller gaps that were attached to the gap as 'extensions' protruding into the forest. In these 'extensions', microclimate and soil moisture conditions prevailed that were more associated with the size of the extension, up to 200m^2, than with the size of the entire gap. Didham and Lawton (1999) pointed out the importance of the shape of the gap edge and the extent to which disturbances can penetrate into the undisturbed forest. They noted that microclimatic conditions and soil moisture in the forest edge changed over time, when the vegetation in the gap and forest edge regenerated, as was shown by the decrease in maximum air temperature in the gaps (Chapter 3).

The effect of forest fragment reduced the amount of solar radiation and associated evapotranspiration fluxes. The forest fragment acted as a buffer to large-scale disturbances of the microclimate and the water balance. These forest fragments can reduce the overall effect of an otherwise large gap and it is therefore important that the vegetation in a gap remains as undamaged as possible during and after logging.

The influence of multiple gaps in a relatively small area was small. If the forest edges of the gaps were overlapping within a few meters of each other, a slight increase in transpiration was found compared to forest edges of a single gap. This relative small influence can be explained by the fact that the gaps in this area were only small to medium sized.

The FORGAP simulation runs of 15 continuous years are somewhat difficult to interpret, since they are mainly influenced by the regrowth of the vegetation in the gap, which is based upon a vegetation growth equation based upon 2.5 years of regeneration in gaps. The actual pattern of regrowth after 15 years, including the death and survival of light-demanding or shade-tolerant species in different sized gaps, is unknown. The growth model does not distinguish between species, nor does it incorporate competition or death. Moreover, the growth model is only related to transpiration, while soil nutrients and water also influence growth rates. Also, in FORGAP, water uptake by the vegetation occurs according to a constant distribution of the roots throughout the soil profile, which does not change through time. This distribution does not compensate for below ground competition between roots. Therefore, monitoring of growth rates of different tree species in different sized gaps remains essential in understanding which gap sizes influences the regeneration of which tree species. FORGAP cannot provide these answers.

However, the model simulations of 15 year showed that the regrowth in large gaps does not proceed equally over the gap, but increased growth can be expected in the northern area of the

gap. Of course this is directly related to the latitude of the research area and this result will be even more pronounced at higher latitudes.

CONCLUSIONS

Solar radiation was the most important factor in explaining differences between the water balance of different sized gaps or within gaps. Differences between gaps and forest were also generated by differences in vegetation attributes. An irregular gap edge could significantly decrease the effective area of a gap and the corresponding water balance. At 5° latitude, gap orientation was not so important.

The 3D approach of FORGAP improved existing models, since shading effects in gaps cannot be simulated with these models. Moreover, the microclimate-influenced area in the forest edge cannot be determined in such detail as with FORGAP. Especially in large logging gaps, the forest edge is an important area where forest regeneration also takes place and more attentions should be addressed to forest edges and radiation extinction in future research. More information is also needed on root growth into gaps and water extraction from the surrounding forest to improve the model.

The results of the evapotranspiration losses and soil water dynamics during the dry weather of El Niño pointed out that these climatic anomalies could have serious consequences for the forest regeneration in gaps, if gaps are created during these dry conditions.

Acknowledgements
The author wishes to thank Victor Jetten, Hans ter Steege and Peter Burrough for their comments.

Littertrap

6 LITTERFALL AND NUTRIENT INPUT IN GAPS OF VARYING SIZE

with Jakolien Leenders and Saskia Visser

Abstract
The major sources of nutrients for a tropical rain forest are enclosed in litterfall. Selective logging creates gaps in the forest in which the amount of litterfall and the nutrients contained in the litterfall are reduced. This could lead to potential nutrient stress for the regenerating vegetation in the gaps. A hypothesis is tested up on litterfall distribution in gaps of different size.

Annual litterfall in the undisturbed forest of the PGE research area was on average 9.3 $t.ha^{-1}$, which consisted of 5.3 $t.ha^{-1}$ leaf litter, 2.3 $t.ha^{-1}$ small woody litter and 1.7 $t.ha^{-1}$ other small litter. In March 1998, as a result of the dry period of the '97/'98 El Niño event, litterfall increased two-fold. Litterfall in gaps decreased sigmoidally with the distance to the gap edge up to 15 m from the gap edge, beyond which litterfall decreased only marginally. In the gap centre of the largest 3200m^2 gaps, annual total litterfall was 0.5 $t.ha^{-1}$. Consequently, nutrient addition to the centre of this gap also reduced by 95%.

Three years after gap creation, the regenerating vegetation in a 3200m^2 gap, predominantly pioneer species, produced more litterfall than the litterfall from the surrounding forest. This pattern was also found in older gaps, where eventually an equal amount of litterfall as in the surrounding forest was produced in a 13-year-old gaps. The recovery of litterfall occurs faster in larger gaps than in small gaps, because the regeneration of the vegetation, and consequently the litter turnover, is faster in larger gaps than in small gaps. Similar patterns as with litterfall quantities were observed for nutrient input in gaps. Consequently, it is estimated that potential nutrient stress as a result of a decrease in litterfall only occurred between 1 and 3 years after gap creation.

INTRODUCTION

Litterfall in logging gaps on infertile soils

The most important source of nutrients for a tropical rain forest on infertile soil is litterfall. The amount of nutrients that arrive in these ecosystems through atmospheric deposition or weathering is disproportionately small to the amount of nutrients contained in litterfall. For example, the annual litterfall in a mixed Greenheart forests on haplic Ferralsols in the interior of Guyana is on average 9.0 $t.ha^{-1}.yr^{-1}$ (Brouwer 1996, Thomas 1999), which contains almost 50 times more nitrogen than the amount of N added to the soil through atmospheric deposition (Brouwer 1996). Not surprisingly, many studies of litterfall in undisturbed Amazonian forest have stressed the importance of litterfall in the nutrient cycle (Brouwer 1996, Duivenvoorden & Lips 1995, Luizão 1989 & 1995, Puig & Delobelle 1988, Scott *et al.* 1992, Thomas 1999). Litterfall consists of leaves, twigs, branches, flowers, seeds and fruits, commonly referred to as 'small litterfall', since whole trees or large branches are excluded. The organically bound nutrients in plant litter become available for the forest after conversion into mineral nutrients through the processes of decomposition and mineralisation. A decrease in litterfall will inevitably result in a decrease in available nutrients, after the litter mass on the soil has decomposed. Trees on infertile soils are continuously competing with each other for these

scarce nutrients. Especially young seedlings and saplings are vulnerable for the amount of easily obtainable nutrients. A decrease in nutrient availability resulting from a decrease in litterfall could therefore affect the regeneration of tree species.

In Guyana, large tracts of the tropical rain forest are selectively logged, whereby only the commercially valuable trees are removed. Selective logging disturbs the nutrient cycle in various ways, because nutrients are lost from the boles that are removed and litterfall is decreased due to the removal of the tree that produce the litter. Locally, the gaps created by logging result in a drastic decrease in litterfall (Thomas 1999) and thus in nutrient input to the soil. Although there are numerous studies on natural tree fall gaps (Brokaw 1982b, Denslow 1980, Hartshorn 1990, Whitmore 1989), logging gaps (Brown 1993, Ek 1997, Rose 2000) and the importance of these gaps in forest regeneration and biodiversity, there has been only one reported study directed at the effects of logging gaps on litterfall (Thomas 1999). Logging gaps vary in size, depending on the amount of trees that were felled. While the amount of litterfall in very small gaps may hardly be disturbed, litterfall in large gaps can seriously be reduced. The amount of accessible nutrients after decomposition of the litter layer will decrease in time, which ultimately decreases the regrowth of the vegetation in the gap.

This study focuses on the effects of logging gaps of different sizes on litterfall and the nutrient supply through litterfall in these gaps. Litterfall in gaps are expected to show a spatial pattern, which will be explained below. In addition, seasonal fluctuations of rainfall or irradiance can result in temporal patterns of litterfall. Several authors have reported the seasonal dependency of litterfall related to the dry season (Cuevas and Media 1986, Dantas and Philipson 1989), the wet season (Duivenvooren and Lips 1995, Puig and Delobelle 1988) or light as a long-term evolutionary driving force (ter Steege and Persaud 1991, van Schaik *et al.* 1993). It is expected that flowers, fruits and seeds will have a stronger seasonal pattern than leaves and woody parts.

A hypothesis of litterfall distribution in gaps

The travel distance of litterfall in forest depends on the following variables:
1) *The shape and weight of the litter* Light flat-shaped leaves will glide further away than heavy round-shaped branches and flat-shaped leaves are more susceptible to wind.
2) *Wind* Wind speed inside a closed forest decreases with height. Wind has more grasps on a leaf that is abscised in the top of a tree than deep inside the canopy. Likewise, trees at the edge of a gap are more affected by wind than trees in closed forest (Sizer *et al.* 2000).
3) *Obstructions* Obstructions like other trees, branches and leaves reduce the potential travelling distance of the litter.
4) *Location of abscission* The height of abscission of leaves, branches or other plant parts, i.e. where it detaches from the tree, affects the potential travelling time of the litter.

As a result of the combination of the variables explained above, we hypothesize that litterfall dispersal of a single tree can be described by a Gaussian-shaped distribution, as is commonly used for seed dispersal (Janzen 1970). This hypothesis is based upon the assumption that the maximum amount of litterfall of a single tree is located directly under the crown of the tree and that the amount of litterfall decreases with increasing distance from the tree. This decrease can be described with a sigmoidal function. Litterfall of a forest is the sum of these sigmoidal functions of all trees. The solid lines in the grey areas in Figure 6.1 schematically show the litterfall distribution around single trees in a forest.

In a gap, the litterfall depends on the litterfall distribution of the trees on the edge of the gap and since there are no other trees that restrict the distribution of litterfall, the travel distance of the litter will increase than under closed forest (dashed line Figure 6.1). In other words, the amount of litterfall at a certain position in a gap is related to the distance to the gap edge, notwithstanding the large natural variability of the variables wind and obstructions. In small gaps, litterfall distributions of all trees at the gap edge will contribute to the litterfall in the gap.

In large gaps however, the litterfall at a certain point in the gap might well be related to distance to the nearest gap edge. Total litterfall under the trees at the gap edge will be less than the total litterfall in undisturbed forest, since there are fewer trees that contribute to the total litterfall. Litterfall in gaps will become less depended on litterfall from the gap edge, when the vegetation in the gap has accrued biomass and starts to produce its own litter. (gap centre small curves Figure 6.1).

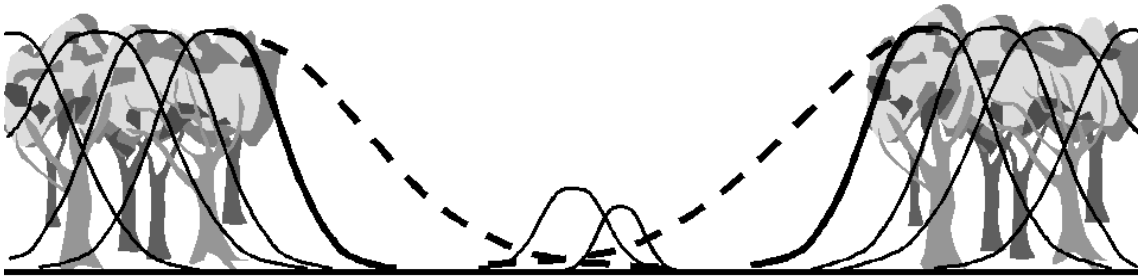

Figure 6.1 Hypothetical litterfall in forest (grey area) and gap (open area). The solid lines represent the hypothetical amount of litterfall around a single tree (forest) or saplings (gap). The litterfall of a tree at the gap edge (thick solid line) is not hindered by the presence of others trees, so the litterfall is dispersed further (dashed line).

This hypothetical distribution of litterfall in gaps can be modelled. A litterfall model for gaps can be used to calculate the amount of nutrient input through litterfall at any point in a gap, which provides insight into areas with potential nutrient stress for regenerating tree species. A model of litterfall in gaps should be ecologically meaningful, i.e. when the model parameters can be explained in ecological terms like a logistic model:

$$LF_d = a / (1 + e^{(b - c \cdot d)}) \quad (1)$$

in which LF (t.ha^{-1}) is the amount of litterfall at distance d (m) from the edge and a, b and c are model parameters, representing the amount of litterfall of the undisturbed forest (a), the inflection point of the curve (b) and the steepness of the curve (c). The parameters of the logistical model were estimated through curve fitting with annual litterfall distribution in gaps. The following hypotheses can be derived from the general hypothesis above:

1) The amount of litterfall decreases with increasing gap size and with increasing distance from the gap edge. These gradients in litterfall will result, after decomposition of the litter layer, in gradients of nutrient availability.
2) Over time, when the vegetation in the gap has accumulated biomass, the vegetation in the gap starts to produce its own litter, whereby the litterfall gradients in the gaps will change. It is expected that the largest shifts occur in the largest gaps, where the largest increase in biomass is expected.
3) Litterfall in gaps can be described by a sigmoidal model that relates gap size or, more specific, the distance to the gap edge to the amount of litterfall.

To test the hypotheses, litterfall was collected in logging gaps of different size and age over a period of three years in the tropical rain forest of Guyana. Besides the litter quantity, nutrient content of the litter was also analysed to calculate total nutrient fluxes.

El Niño and litterfall

From July 1997 to March 1998, an El Niño event caused a severe drought in Guyana and surrounding countries (Chapter 2). Soil moisture conditions throughout the research area decreased (Chapter 3 and 5) and the vegetation reacted to this drought. Small seedlings died, larger saplings suffered from severe drought stress and large trees abscised their leaves. During our litterfall experiments, special attention was given to the effect of El Niño on litterfall.

METHOD

Litterfall was collected in the gaps of the Pibiri Gap Experiment (PGE, see van Dam *et al.* 1999 and Chapter 2), the Forest Reserve Mabura Hill (FRMH, Brouwer 1996) and at the 2K research site (Ek 1997) in three separate experiments, as is described below. The study sites are located in a mixed tropical rain forest on haplic Ferralsols. The climate is characterised by two wet and two dry seasons, with an annual rainfall of 2700mm (Jetten 1994a) (see Chapter 2 for a complete description of the study areas).

Litter collection

Experiment 1 From October 1996 until October 1999, litterfall was collected in 34 one-m^2 traps that were placed in an undisturbed forest plot and in 9 PGE gaps with gap sizes of 140, 210, 240, 570, 700, 960, 2680, 2950 and 3200m^2. Litter traps in these gaps were placed along a gap-centre to gap-edge line, whereby the largest three gaps had 4 litter traps and the other gaps were equipped with 3 litter traps. In the first year, litter was collected weekly and sorted into leaves, woody parts, seeds plus fruits (combined) and flowers. In the later years, the seeds, fruits and flowers fractions were grouped to one 'other' fraction. Litter was oven-dried at 60° C for a week and weighed.
Experiment 2 From August 1998 to October 1999, litterfall was collected in 46 0.25-m^2 traps located in the FRMH and 2K study areas. The traps were distributed over the 4 gaps and nearby undisturbed forest plots of these two study sites (FRMH gap sizes 740 and 3440m^2, 2K gap sizes 200 and 800m^2). The traps were located under the dense vegetation that was present in the gaps. Litter was collected fortnightly and sorted for leaves, woody parts and other litter. Litter was oven-dried at 60° C for a week and weighed.
Experiment 3 From August 1998 to October 1999, litterfall was collected in 16 0.25 m^2 traps placed under the regenerating vegetation in the 3200m^2 PGE at 10 cm above the soil. Litter was collected fortnightly and sorted for leaves and other litter. Litter was oven-dried at 60° C for a week and weighed.

Litter traps were positioned in the gap centre, at the gap edge and in the forest edge area and in addition, the 3200m^2 gap had an extra litter trap between centre and edge trap. In 1997 and 1998, hemispherical photographs were taken above the traps of Experiment 1 using a Nikon Fujix digital camera and a Sigma 8 mm fish-eye lens. The photographs were analysed for canopy openness with WINPHOT (ter Steege 1997).

Rainfall measurements, chemical and statistical analysis

The amount of litterfall per week is not constant throughout a year, but a seasonal pattern of litterfall is reported for the study area (Brouwer 1996, ter Steege and Persaud 1991, Thomas 1999). To test this seasonal pattern, rainfall was measured manually in the nearby PGE field camp and with a tipping bucket attached to an automated weather station (see Chapter 2). Rainfall and weekly litterfall was tested for temporal auto correlation and cross-correlation analysis was made between litterfall and rain using Statistica (StatSoft Inc 1993). Significant differences between litter collection in gap of different sizes or age were tested with an ANOVA. The curve fitting was performed with CurveExpert (D. Hyams & Microsoft 1993).

In 1997, monthly samples were taken from the different litter fractions collected in the PGE litter traps for chemical analyses. The samples were shipped to the Netherlands, where they were ground and digested, using an adapted Kjeldahl procedure (Allen 1989). Litter samples were put in a mixture of concentrated sulphuric acid and 30% peroxide, with selenium as a catalyst. The destruates were analysed for P, K, Ca, Na, Mg, and Al using an Inductively Coupled Plasma Emission Spectrophotometer (Spectroflame, Spectro) and colorimetrically for

N with Flow Injection Analysis (Skalar). Although aluminium is not a nutrient, in fact it is toxic for most plants, it is studied along with nutrients. It is expected that in gaps, due to acidification (Chapter 9), large amounts aluminium become mobile that can pose a potential treat to the regeneration of tree species that are not adapted to high concentrations of Al. Input of Al through litterfall provides insight into the origin of aluminium.

LITTERFALL DISTRIBUTION IN GAPS

Litterfall quantities in forest and gaps

Forest litterfall and seasonal patterns

Annual total litterfall in the undisturbed forest was 9.3 $t.ha^{-1}.yr^{-1}$. Litterfall in the PGE forest (experiment 1) had an irregular temporal pattern (Figure 6.2), with the largest litterfall of 55 $g.m^{-2}$ in one week at the end of the dry period of the '97/'98 El Niño event. In March 1998, as a result of the dry period of the '97/'98 El Niño event, twice as much litter compared to the same period in other years fell on the soil, mainly consisting of leaves. Leaf litterfall was on average 9.8 $g.m^{-2}.wk^{-1}$ (σ 6.97), woody parts 4.2 $g.m^{-2}.wk^{-1}$ (σ 3.70) and other small litter 3.0 $g.m^{-2}.wk^{-1}$ (σ 3.99). A seed rain of *Mora gonggrijpii* caused the large flush of other small litter fraction around June 1997 (Figure 6.2). In one week, one litter trap collected 118 $g.m^{-2}$ of seeds and cotyledons. One seed of *Mora gonggrijpii* has an average dry weight of 52 g (ter Steege 1994). The average annual rainfall during the research period was 2660mm. Rainfall and leaf litterfall showed a significant ($p<0.05$) 1-2 week autocorrelation, while woody litterfall was not temporally auto correlated. The other small litterfall fraction showed a 1-5 week autocorrelation. Besides the obvious effect of El Niño, when a large flush of leaf litterfall was recorded during the driest period (peak leaf litterfall on 2 April 1998 in Figure 6.2), leaf and woody litterfall were only cross-correlation with the rainfall of the preceding week.

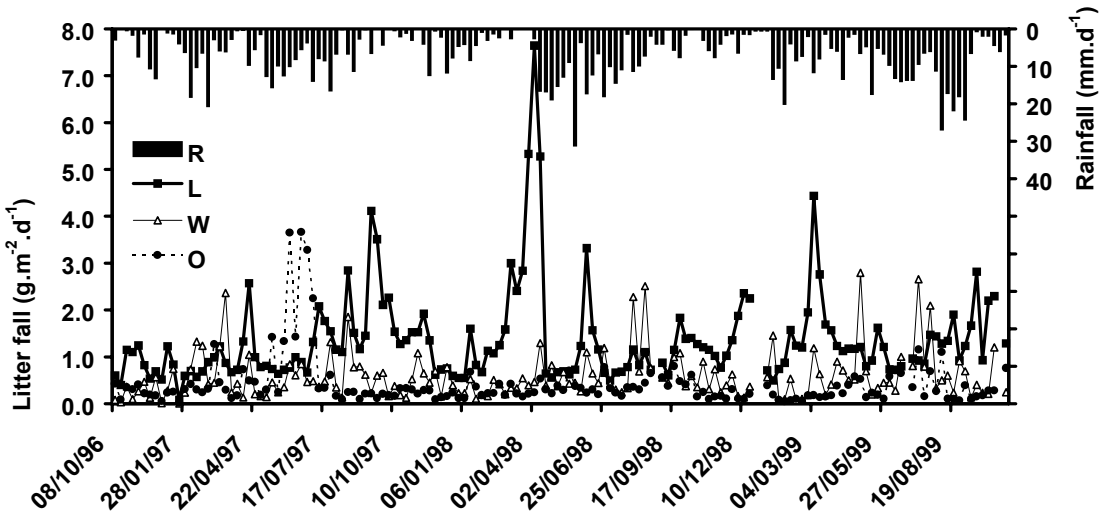

Figure 6.2 Weekly forest litterfall and daily rainfall in the PGE research area from October 1996 to October 1999. (R: rainfall, L: Leaf litter, W: woody parts, O: Other small litter)

Gap size and litterfall

Annual total litterfall in the undisturbed forest was 19 times greater than total litterfall in the gap centre of the 3200m^2 gaps (Table 6.1). Leaf litter was 57% of total litterfall, twigs and branches comprised 25% of total litter and the flowers, fruits and seeds were 18% of total litterfall. Total

litterfall increased from 14.2% in the gap centre to 24.7% near the gap edge in the gap and to 90.8% near the gap edge under a closed canopy (forest edge in Table 6.1).

Table 6.1 Average annual litterfall ($t.ha^{-1}.y^{-1}$) in the PGE litter traps from October 1996 to October 1999 (c: gap centre, ce: in between gap centre and edge, ge: near gap edge in gap, fe: near gap edge under closed canopy).

	forest	200m²			800m²			3200m²			
		c	ge	fe	c	ge	fe	c	ce	ge	fe
Leaves	5.325	2.068	2.838	4.904	0.591	1.121	5.138	0.386	0.281	1.220	4.554
Woody	2.315	0.210	0.433	1.632	0.036	0.084	1.548	0.030	0.017	0.174	2.101
Other	1.680	0.462	0.714	2.811	0.100	0.119	0.946	0.074	0.060	0.198	1.740
Total	9.320	2.741	3.984	9.347	0.727	1.324	7.632	0.489	0.359	1.592	8.395

Leaf litterfall had the largest contribution to total litterfall at every point in a gap and in the undisturbed forest, followed by woody parts and finally other small litter (Figure 6.3). At 10m into a gap, the average leaf litterfall was only 14 % of forest leaf litter, woody parts were 3% and other small litter was 10% of forest litterfall. At 10m into the forest, the average leaf litterfall was 94% of forest litterfall, woody parts were 89% and other small litter was 95% of forest litterfall. In the first 1.5 year after gap creation, seed and fruit fall in the gaps up to 5m from the gap edge was 23.2 % of seed and fruit fall in the undisturbed forest. Seed and fruit fall beyond 5m from the gap edge dropped sharply to 6.9% of the seed and fruit fall in the forest.

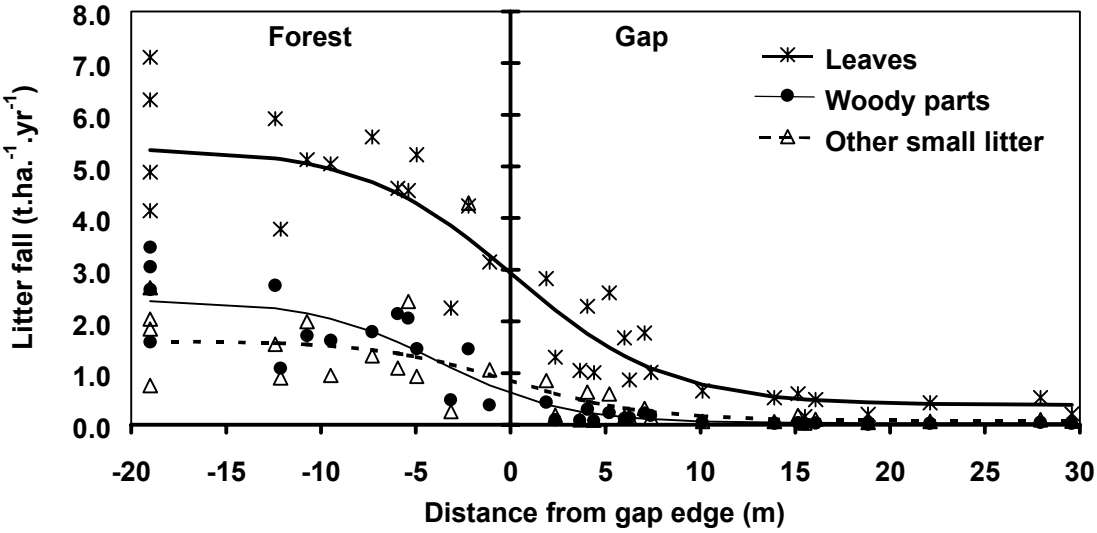

Figure 6.3 Average yearly litterfall (October 1996 to October 1999) of leaves, woody parts and other small litter in all gaps in relation to the distance to the gap edge. The lines represent the curve fits according to model equation 1; R^2: leaves 0.94, woody parts 0.91 and other small litter 0.84 (see Table 6.2 for model parameters).

Gap age and litterfall

Litterfall in the 1, 2 and 3-year-old PGE gaps was significantly less than forest (Scheffé test, $p<0.05$), although no differences were found between gaps (Table 6.2). Litterfall in the 7-year-old 3200m² gap was still less than forest litterfall, but not significantly different (Scheffé test, $p<0.05$), while litterfall in the 7-year-old 800m² was significantly less from forest. Litterfall in the 13-year-old gaps were not significantly different from forest litterfall. Leaf litterfall in the 7-year-old 800m² gap was 68% of forest litterfall and in the 3200m² gap was 77% of forest

litterfall. Leaf litterfall in the 13-year-old, 200 and 800m^2 gaps was 104 and 118% of forest litterfall, respectively. The forest plots in the PGE, FRMH and 2K study sites received similar amounts of leaf litter, but the 2K plots received less of the other small litter fractions.

Table 6.2 Leaf litter and other small fall (t.ha^{-1}.yr^{-1}) in the centre of gaps of different age and size. m: mean litterfall with one se: standard error. Letters indicate significant differences between gaps of different size (Scheffé test, $p<0.05$) per litter fraction and gap age.

Study area & age		PGE: 1 yr		PGE: 2 yr		PGE: 3 yr		FRMH: 7 yr		2K: 14 yr	
	size group	m	se	m	se	m	se	m	se	m	se
Leaf	**forest**	3.86^a	0.47	5.32^a	0.57	5.03^a	0.51	4.93^a	0.37	4.97^a	0.25
	200m^2	1.44^b	0.23	2.47^b	0.28	2.08^b	0.57			5.19^a	0.33
	800m^2	0.40^b	0.05	0.38^b	0.04	0.81^b	0.13	3.37^b	0.35	5.87^a	0.33
	3200m^2	0.25^b	0.04	0.25^b	0.10	0.55^b	0.15	3.78^{ab}	0.35		
Other	**forest**	3.80^a	0.58	3.39^a	0.54	3.34^a	0.53	3.21^a	1.38	1.89^a	0.21
	200m^2	0.80^b	0.33	0.65^b	0.24	0.35^b	0.06			2.17^a	0.44
	800m^2	0.15^b	0.10	0.07^b	0.01	0.14^b	0.03	0.95^b	0.18	3.04^a	0.60
	3200m^2	0.04^b	0.02	0.07^b	0.01	0.18^b	0.03	1.41^{ab}	0.25		

Note: For comparison, the gaps of the three study sites, PGE, FRMH and 2K are grouped to size: small 200m^2, medium 800m^2 and large 3200m^2 gaps.

Litterfall in the 1-year-old PGE forest was not significantly different from any PGE gaps, because the PGE forest litterfall was relatively low in that year. Other litterfall was not significantly different between any site of any age. Statistical comparison between the PGE, 2K and FRMH bi-weekly collections could only be made for the total annual amount of litter, because litterfall in the different plots was not collected on the same day, but with one or two days in between. This time lag can create differences in litterfall that are not related to differences between research site or gap size.

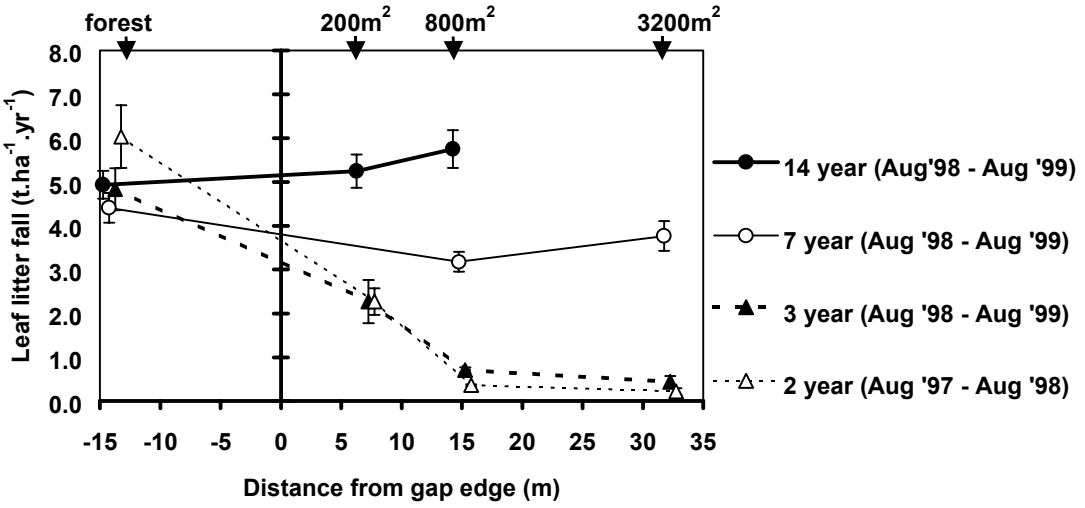

Figure 6.4 Annual leaf litterfall (+/- 1 standard error) in the gap centres of the 200, 800 and 3200m^2 gaps, expressed in the distance to the gap edge, at 2, 3, 7 and 14 year after gap creation. (N varies for each observation; PGE site: 2 and 3 year, gaps N=3 and forest N=7; FRMH site: 7 year, gaps N=10, forest N=5; 2K site: larger gap N=11, small gap and forest N=5)

The results as presented in Table 6.2 and Figure 6.4 indicate the importance of litterfall originating from the regenerating vegetation in the gap. At 25 m from the gap edge in the centre of the 3200m^2 gap, leaf litterfall collected under the regenerating vegetation (experiment 3) was 5.7 times more than leaf litter collected in the traps at an open location (experiment 1) and leaf litterfall under the vegetation in the gap decreased towards the gap edge (Figure 6.5). The other small litterfall fraction had a similar pattern to leaf litterfall.

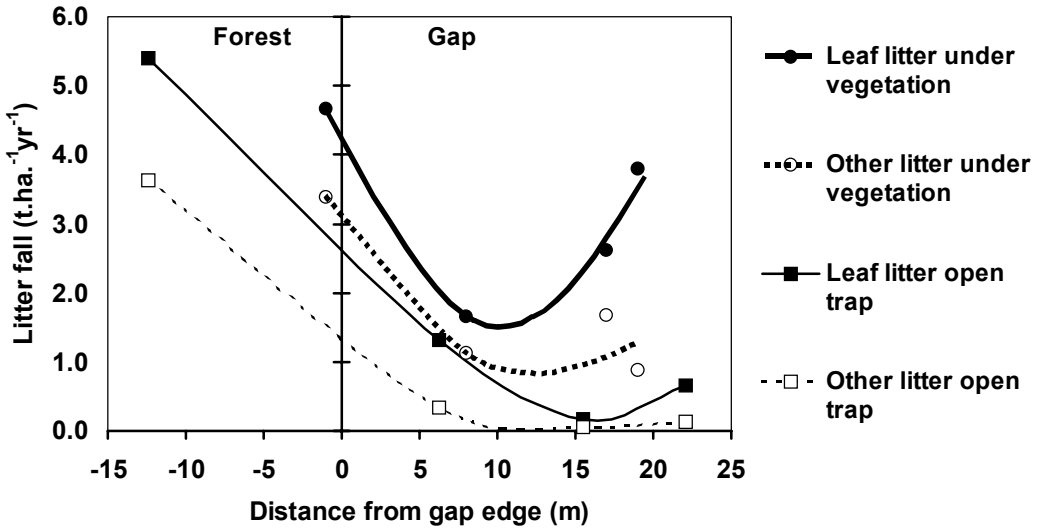

Figure 6.5 Leaf and other small litterfall collected in traps under the regenerating vegetation at 10 cm from the ground and in 'open' traps at 1 m above the ground in a 3200m^2 gap, 3 years after gap creation. The lines represent smoothed fits through the data points.

A model of litterfall in gaps

The logistical model proved reliable in predicting litterfall in gaps. The correlation coefficient of the leaf litterfall model fit of the three consecutive years of litter collection was always higher than 0.88 (Table 6.3). The parameters of the model give insight into temporal changes. Throughout the collection period, the inflection point[1] (*b*) of leaf litterfall was almost at the gap edge, although a small movement was detected from the gap into the forest, while the curve steepness (*c*) decreased (Table 6.3 upper part).

Table 6.3 Litterfall modelling in gaps per collection period. Logistic model: $LF_d = a/(1+\exp(b-c \cdot d))$, with LF_d de litterfall (kg.ha^{-1}.yr^{-1}) and d the distance to the gap edge (m).

	Leaf litterfall				Woody litterfall				Other small litterfall			
All traps	**a**	**b**	**c**	**R^2**	**a**	**b**	**c**	**R^2**	**a**	**b**	**c**	**R^2**
96/97	4.829	-0.098	-0.254	0.91	2.651	1.157	-0.202	0.86	1.659	-0.477	-0.409	0.73
97/98	5.967	-0.026	-0.192	0.90	3.025	1.397	-0.183	0.87	1.438	-6.335	-3.410	0.71
98/99	6.151	0.022	-0.174	0.88	2.409	1.325	-0.397	0.90	1.084	-0.363	-0.380	0.59
96-99	5.613	-0.044	-0.204	0.94	2.557	1.134	-0.247	0.91	2.020	0.760	-0.180	0.84
Per gap size over period 96-99												
200m^2	5.649	-0.255	-0.170	0.92								
800m^2	5.396	0.180	-0.314	0.87								
3200m^2	5.613	-0.120	-0.210	0.81								

[1] Note that a negative value of *b* indicates a position inside the gap.

The inflection point of woody litterfall was inside the forest, but moved towards the edge in the course of the collection period. Although the inflection point of other small litterfall was positioned in the gap and further away from the gap edge than leaf litter, other small litterfall decreased rapidly with increasing distance from the edge. The curve fitting of the leaf litterfall of the separate 200, 800 or 3200m^2 traps gave slightly different model parameters (Table 6.3 lower part). The curve fitting of the leaf litterfall modelling with all litter traps underestimated the leaf litter in the small gaps and overestimated the leaf litter in the medium sized gaps, which is not surprising, since more trees at the gap edge will contribute to litterfall in the gap centre of a 200m^2 than in a 3200m^2 gap.

In the litterfall model given above, litterfall is expressed as a function of distance to the gap edge, thereby relating the distance to gap size. The canopy openness above a litter trap is another gap related variable. The canopy openness[2] in 1997 in the centre of the 200m^2 gaps was between 5.21 and 14.53%, in the 800m^2 gaps 14.71 – 19.52%, in the 3200m^2 gaps 34.82 – 38.69% and in the forest 3.23 – 5.76%. The sigmoidal model (equation 1) was based upon a hypothesis on litterfall dispersal in relation to the distance to the gap edge. The openness of the canopy also includes the variability of the openness of the forest that surrounds the gap and a sigmoidally shaped relationship is not an appropriate model. Therefore, a simple exponential decline of litterfall quantity versus increasing canopy openness LF_{co} (t.ha^{-1}.yr^{-1}) was used: $LF_{co} = a \cdot e^{-b \cdot co}$ in which a is the leaf litterfall of the forest at 0% canopy openness a, b the rate of decline and co is the canopy openness (%). In 1997, coefficient a was 4.678 and coefficient b was 0.070, while in 1998 a was 7.013 and b was 0.074. The large difference of parameter a in 1997 and 1998 was caused by the differences in leaf litterfall in the forest and small gaps, which in 1998 was on average 1.3 t.ha^{-1}.yr^{-1} more than in 1997 (Figure 6.6).

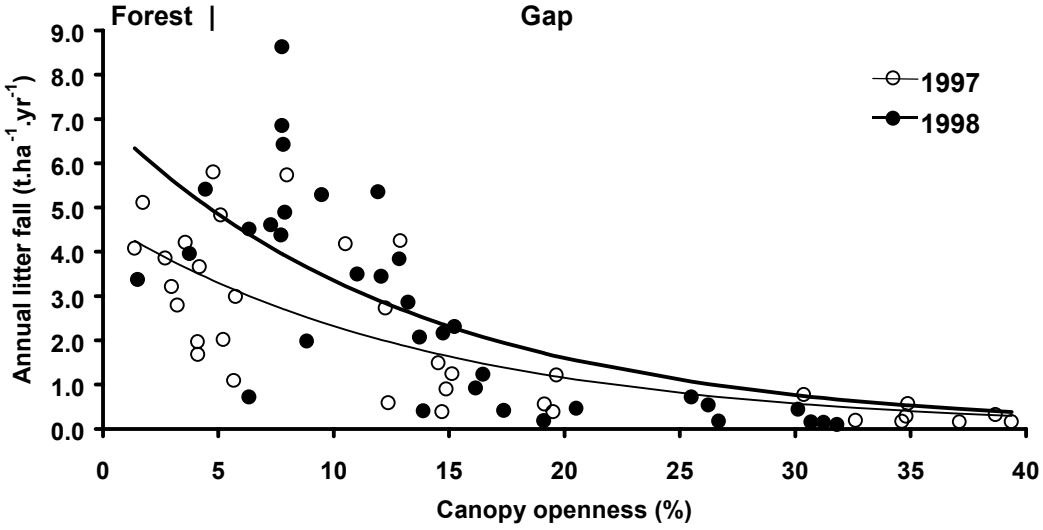

Figure 6.6 Year sum of leaf litterfall against canopy openness above the PGE litter trap. The lines represent an exponential model, see text for equation. (R^2 1997: 0.75, 1998: 0.70)

The dry period of the El Niño event, followed by a very wet period is though to have caused these different litterfall quantities. A transition in litterfall was found around 15% canopy openness, which could indicate a reduced influence of the surrounding forest. Litter traps with canopy openness over 15% only received litter from the nearest gap edge.

[2] Between 1997 and 1998, the average canopy openness decreased from 15.0% in 1997 (range 1.4-39.4%) to 14.6% in 1998 (range 1.5-31.8%). The canopy openness of the largest gaps decreased due to regrowth in the gap and the canopy openness of the smallest gaps and the traps located in the forest increased due to natural tree fall.

Nutrient content in litterfall

Chemicals in litterfall in gaps of different size

Total nutrient input in litterfall depends on total litterfall per fraction and the nutrient concentrations per litter fractions. Not surprisingly, the highest concentrations for the macro-nutrients N, P and K were found in flower parts, seeds and fruits, which serve to attract animals for pollination or dispersal or which are a food source for a future seedling (Table 6.4). Except for Ca and P, leaves had higher concentrations of elements than woody parts. There was little difference between fractions for aluminium.

Table 6.4 Mean concentration and standard deviation ($g.kg^{-1}$) of litter fractions as collected in all PGE traps in 1997.

Fraction	no	N	σ	P	σ	K	σ	Ca	σ	Na	σ	Mg	σ	Al	σ
Leaves (L)	6	13.26	0.76	0.10	0.06	2.25	0.16	5.35	0.62	2.72	0.45	2.52	0.20	0.99	0.51
Woody parts (W)	6	11.25	1.97	0.09	0.05	1.78	0.26	6.93	1.48	1.21	0.32	1.84	0.47	0.80	0.41
Flower parts (F)	6	14.62	2.12	0.61	0.27	6.15	3.37	4.73	0.91	1.56	0.32	1.97	0.27	0.56	0.26
Seed, fruit parts (S)	6	10.60	2.30	0.55	0.22	5.27	1.26	3.64	0.95	2.23	0.69	1.87	0.82	0.68	0.23
Other (O=F+S)	12	12.61	2.98	0.58	0.23	5.71	2.47	4.19	1.05	1.90	0.62	1.92	0.59	0.62	0.24

Total nutrient input in gaps and forest was based upon the average yearly litterfall from October 1996 to October 1999 and the average nutrient concentration (Table 6.5). The relative contribution of leaf litterfall in gaps to the total nutrient input in gaps was 74%, compared to only 5% for twigs and branches and 21% for other litter, mainly flower parts.

Table 6.5 Bulk nutrients ($kg.ha^{-1}.y^{-1}$) in sorted litter in undisturbed forest and in the gap centres of the PGE gaps, based on litterfall quantities from October 1996 to October 1998.

		N	P	K	Ca	Na	Mg	Al
forest	**Leaves**	70.59	0.51	11.99	28.51	14.46	13.39	5.26
	Woody	26.05	0.20	4.13	16.05	2.79	4.26	1.85
	Other	21.19	0.98	9.60	7.03	3.19	3.22	1.04
	total	117.84	1.68	25.71	51.59	20.44	20.88	8.16
200m²	**Leaves**	27.42	0.20	4.66	11.07	5.62	5.20	2.04
	Woody	2.36	0.02	0.37	1.46	0.25	0.39	0.17
	Other	5.83	0.27	2.64	1.94	0.88	0.89	0.29
	total	35.62	0.48	7.67	14.47	6.75	6.48	2.50
800m²	**Leaves**	7.84	0.06	1.33	3.17	1.61	1.49	0.58
	Woody	0.41	0.00	0.06	0.25	0.04	0.07	0.03
	Other	1.26	0.06	0.57	0.42	0.19	0.19	0.06
	total	9.50	0.12	1.96	3.83	1.84	1.74	0.68
3200m²	**Leaves**	5.11	0.04	0.87	2.06	1.05	0.97	0.38
	Woody	0.34	0.00	0.05	0.21	0.04	0.05	0.02
	Other	0.93	0.04	0.42	0.31	0.14	0.14	0.05
	total	6.38	0.08	1.34	2.58	1.22	1.17	0.45

Total nitrogen input in the $200m^2$ gap centre was 30.2% of undisturbed forest N input, and in the 740 and $2940m^2$ gaps, 8.1 and 5.4%, respectively. A similar pattern was observed for the other nutrients, except for phosphorus. The larger nutrient supply in the smallest gap was directly related to the larger supply of woody parts and other small litter, which did not reach the gap centre of the larger gaps.

Nutrient input through litterfall in gaps of different age

Nutrient input in gaps is strongly influenced by the type of litter. In the FRMH and 2K gaps, litterfall is largely from the vegetation in the gap itself. The nutrient content of leaves or other litter parts of these predominantly pioneer species was not measured. Instead, an estimate of the nutrient input in the gaps was based upon the concentrations of N and P of litter collected in the PGE litter traps (Table 6.4) and the average concentration of N and P of the pioneer species *Cecropia obtusa*, *Goupia glabra*, *Peltogyne venosa* and *Eschweilera sagotiana* as published by Raaimakers (1995) and Brouwer (1996). The average nitrogen concentration in these pioneer leaves is 17.8 $mg.g^{-1}$ and in stem parts 8.2 $mg.g^{-1}$, while the average phosphorus concentration in leaves and stems is 0.6 $mg.g^{-1}$. The nutrient composition of the litter at 2K and at the FRMH is not known, but the vegetation in the 2K 800m^2 was dominated by *C. obtusa* while in the FRMH 3440m^2 *G. glabra* was common (pers. obs.). Nutrient input in gaps of different age was estimated by assuming that 50% of the litterfall in the gaps originated from pioneer species and 50% from climax vegetation.

Table 6.6 Nutrient input of N and P ($kg.ha^{-1}.yr^{-1}$) in gaps of different size and age.

		Nitrogen					Phosphorus				
		1yr	**2 yr**	**3 yr**	**7yr**	**14 yr**	**1yr**	**2 yr**	**3 yr**	**7yr**	**14 yr**
Leaf	**forest**	51.18	70.54	66.70	65.37	65.90	0.39	0.53	0.50	0.49	0.50
	200m^2	19.09	32.75	27.58		80.50	0.14	0.25	0.21		1.87
	800m^2	5.30	5.04	10.74	52.27	91.05	0.04	0.04	0.08	1.22	2.12
	3200m^2	3.32	3.32	7.29	58.63		0.03	0.03	0.06	1.36	
Wood	**forest**	42.75	38.14	37.58	36.11	21.26	0.34	0.31	0.30	0.29	0.17
	200m^2	9.00	7.31	3.94		21.10	0.07	0.06	0.03		0.73
	800m^2	1.69	0.79	1.58	9.24	29.56	0.01	0.01	0.01	0.32	1.02
	3200m^2	0.45	0.79	2.03	13.71		0.00	0.01	0.02	0.47	
Total	**forest**	93.93	108.68	104.27	101.48	87.16	0.73	0.84	0.80	0.78	0.67
	200m^2	28.09	40.06	31.52		101.61	0.22	0.31	0.24		2.60
	800m^2	6.99	5.83	12.32	61.51	120.62	0.05	0.04	0.09	1.53	3.14
	3200m^2	3.77	4.10	9.32	72.34		0.03	0.03	0.07	1.84	

DISCUSSION

The '97/'98 El Niño event and forest litterfall

Litterfall in the PGE forest was influenced by short-term climatic fluctuations. There was more leaf litterfall in the PGE forest during drier periods than during wetter periods, which is a common phenomenon for most forest types in Guyana (Brouwer 1996, Thomas 1999). Likewise, flowering and fruiting increased, which can be triggered by dry weather conditions (Augspurger 1982, Cooper 1982, Opler *et al.* 1976, ter Steege and Persaud 1991). Leaf litterfall was strongly influenced by the drier periods associated with the '97/'98 El Niño event, when litterfall increased more than 4-fold compared to the average annual litterfall. The annual total litterfall in the PGE forest of 9.3 $t.ha^{-1}.yr^{-1}$ was well within the range of other litterfall studies in South-American undisturbed forest of 7.3 $t.ha^{-1}.yr^{-1}$ in Brazil (Klinge and Rodrigues 1968) and 10.3 $t.ha^{-1}.yr^{-1}$ in Venezuela (Cuevas and Medina 1986).

Litterfall in gaps

The amount of leaf, woody and other small litterfall decreased with increasing distance from the gap edge. Deposition of woody parts, seeds and fruits was almost absent more than 5m from the gap edge. Litterfall in the PGE gaps was less than in the PGE forest and the disturbance only affected the gap area up to 6m into the forest, where less litterfall was found. In a 10m wide edges of forest fragments in central Amazonia, Sizer *et al.* (2000) found a 2.5 times higher amount of litterfall compared to undisturbed forest in the first 6 months after edge creation, which they contributed to greater wind force and prematurely loss of leaves due to severe changes in microclimatic conditions. After these 6 months following edge creation, Sizer *et al,* (2000) found that litterfall was lower than the forest, which was still less than the forest almost 4 years after edge creation. Litterfall in the PGE gap edges was not measured in the first 6 months after gap creation, but a similar increased litterfall might have occurred. Clearly, litterfall is only disturbed in the gap itself and its immediate surrounding, but has little influence on the total average litterfall of a larger area (1 ha). Thomas (1999) reported in a mixed Greenheart forest in Guyana that the total annual litterfall of 1 ha forest was not significantly different between pre- and post-logging of a 4.9 tree.ha^{-1} selective logging operation, although litterfall decreased significantly for those litter traps near or in the logged gaps.

Litter that originated from the forest that surrounded the gap dominated litterfall in young gaps, i.e. younger than 2 years. Litterfall in older gaps was also influenced by litter that originated from the vegetation in the gap itself. The oldest gaps at the FRMH and 2K sites had an equally annual litterfall than forest litterfall. The larger amount of litterfall in the 3200m^2 FRMH gap as compared to the 800m^2 FRMH gap can be explained by the taller vegetation in the 3200m^2 gap. The vegetation in this large gap consisted mainly of pioneer species (pers. obs.), which have a higher leaf turnover rate. Three years after gap creation, litterfall in the centre of the 3200m^2 PGE gap was dominated by litterfall from the regenerating vegetation in the gap. The influence of these, predominantly, pioneer species on the litterfall decreased towards the gap edge, which was related to the decrease in vegetation height or biomass towards the gap edge (Leenders and Visser 1999, Appendix 3D). These pioneer species are still present in the 13-year-old gaps and produced an equal amount of litter than the forest (Figure 6.4). Already at 7 years after gap creation, leaf litterfall in the 3200m^2 gap was more than in the 800m^2 gap. It was estimated that leaf litterfall in the 800m^2 gaps attained a similar amount as in the forest after 11 years, primarily because of the high leaf turnover rate of the pioneer species in the gap. As was expected, litterfall in gaps could be divided into two source groups: litter that originates from the forest, the *forest litterfall*, and litter that originates from the vegetation in the gap, the *gap litterfall*.

The logistical model was fitted successfully through the litterfall data of all gap size together. However, this resulted in an underestimation of the litterfall in the 200m^2 gaps and an overestimation of the 3200m^2 gaps. The results of the model fits per gap size suggests that litter traps in the smallest gaps received litter from all gap edges, while the bulk of the litter collected in the litter traps in the largest gaps originated only from the nearest gap edge. Furthermore, the data suggest that this nearest-gap-edge dependency starts at a distance of 15 m from the gap edge, which corresponds to the centre of an 800m^2 gap.

The result of seed and fruit dispersal in gaps provides an interesting thought on colonalisation of tree species in relation to seed weight. Tree species with heavy seeds drop their seeds directly under the crown of the tree and their seeds are only dispersed further away from the parent tree in sloping terrain or displacement by mammals. In Guyana, 87-90% of all woody species are animal dispersed (van Roosmalen 1985) or more importantly, 51% of the timber species of Guyana – most of which have heavy seeds – are mammal-dispersed (Hammond *et al.* 1996). For example, 95% of the seeds of the climax tree species *Chlorocardium rodiei* are dispersed

within 10m from the adult tree (Zagt and Werger 1997). The tree species with heavy seeds have a preference for their regeneration for small gaps (10-500m^2; Hammond and Brown 1995). Moreover, recent canopy openings are usually avoided by animals (Schupp *et al.* 1989). In the PGE gaps, seed and fruit fall was almost absent at more than 5m from the gap edge. These results suggest that tree species with heavy seeds did not disperse through wind or gravity to the centres of gaps larger than 80m^2. Notwithstanding some additional dispersal by animals, these findings suggests that species with heavy seeds will have a very limited dispersal in large gaps and the regeneration of these species in large gaps almost completely depends upon the presence of their seeds at the time of gap creation.

Nutrient input in forest and gaps

In the first years after gap creation, nutrient input in gaps through litterfall is limited. There is a potential nutrient stress for the regenerating vegetation in the gaps. Nutrient input in gaps through litterfall decreased with increasing distance from the gap edge. However, in gaps older than approximately 13 years, nutrient input in gaps was more than in undisturbed forest. This is caused by a higher leaf turnover rate of the, predominantly, pioneer species in the gap and a higher leaf nutrient content of these pioneer species. On the other hand, the demand for nutrients in these gap centres is also larger because of the faster regrowth of the vegetation, so no accumulation of nutrients is likely to occur. Nutrient addition to the soil in the undisturbed PGE forest was well within a range of other litterfall studies on Ferralsols (Brouwer 1996, Coomes 1997, Duivenvoorden and Lips 1995, Luizão 1989 & 1995, Puig and Delobelle 1988, Scott *et al*. 1992).

Since leaf litterfall had the largest contribution to total litterfall, the nutrient input in gaps was dominated by the chemical composition of leaves. Three years after gap creation, the species composition of the regenerated vegetation in the largest PGE gaps was dominated by pioneer species (Rose 2000) and the nutrient addition in these gaps shifted from forest litterfall to gap litterfall. This clearly shows that when assessing the nutrient input in gaps through litterfall, the species compositions of the litter must be taken into account. As a result of decomposition of the litter layer in the gaps, a potential nutrient stress might have developed in the first 2 years after gap creation, but gradually restored, when the contribution of gap litterfall increased.

CONCLUSIONS

Litterfall in gaps decreased with increasing distance from the gap edge and the decline in litterfall compared to mean forest litterfall started in the gap edge. The results of the litterfall modelling suggests that at a distance further than 15m from the gap edge, the bulk of litterfall originated from the nearest gap edge, while at distances closer than 15m from the gap edge, litterfall originated from all gap edges.

The recovery of litterfall in gaps was faster in largest 3200m^2 gaps than in smaller 800 or 200m^2 gaps, because the litter turnover in large gaps was faster than in small gaps. In large gaps, predominantly pioneer species were regenerating, that have a higher litter turnover rate.

Nutrient stress due to a reduced litter input in gaps can occur between 1 and 2 years after gap creation, when the litter turnover of the vegetation in the gap is still small and the litter layer on the soil has almost completely decomposed.

Acknowledgements
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Litterbags

7 DECOMPOSITION IN TROPICAL RAIN FOREST GAPS IS NOT INFLUENCED BY GAP SIZE

with Raymond Sluiter and Niels Smit

Abstract
Decomposition rates of leaves, woody and flower parts were not different between gaps of different sizes, but decomposition rates of these litter fractions in forest environments were faster. Flower parts decomposed faster than leaves, followed by woody parts. In the forest, 48.2% of the initial weight of *Chlorocardium rodiei* leaves remained after 382 days, while in the gaps 63.1.7% was still present. The difference in weight loss between gaps and forest was not found in nutrient loss from the *C. rodiei* leaves. Element concentration decreased in time for N, P, K, Ca, Na and Mg, but all in different orders of magnitude, initial concentration loss and total concentration loss. A single exponential model of litter weight loss due to decomposition, which can be used in a nutrient modelling study, described the weight loss adequately.

The difference in weight loss between gaps and forest en the lack of difference between gaps of different size can be attributed to 1) the prevailing microclimatic conditions in the gap, which desiccated the litter layer, thus limiting microbial attack and 2) damage to the belowground biomass and mycorrhizal infections as a result of logging, which play an important role in the decomposition process. Furthermore, it was concluded that a limited damage to the vegetation in a logging gap can minimize the effect of a gap on the decomposition process, when the microclimatic and edaphic conditions are less disturbed.

INTRODUCTION

Decomposition in tropical rain forest and gaps

Decomposition and the nutrient cycle
Decomposition of dead plant material into smaller fragments is the first step in the conversion of organically bound nutrients to mineral nutrients that can be used by plants. As such, decomposition of plant litter in a tropical rain forest on infertile soils is an important process in the nutrient cycle, since almost all plant available nutrients in these ecosystems originate from plant debris. Decomposition of plant litter has been widely studied (Anderson and Swift 1983, Andrén and Paustian 1987, Burghouts *et al.* 1992, Cooper 1982, Esser and Leith 1989, Golley 1983, Swift and Anderson 1989) and the fastest decomposition rates have been found in undisturbed tropical rain forest (Kiffer *et al.* 1981, Olson 1963). Moreover, many of these authors have stressed the importance of decomposition in nutrient cycling. A disturbance of the decomposition of the litter layer in a tropical rain forest will affect the nutrient cycle. Especially young plants that are competing with each other and with mature trees for the scarcely availably nutrients can be seriously hampered in their survival and growth as a result of a decrease in available nutrients. Disturbances in tropical rain forests are widespread and vary from clear felling with slash-and-burn practices to harvesting of non-timber forest products. In the tropical rain forest of Guyana, selective logging creates gaps in the canopy that vary in size, depending on the size and the number of trees that were felled. The presence of these gaps disturbs the nutrient cycle because of changes in microclimatic conditions and soil moisture dynamics

(Becker *et al.* 1988, Brown 1993, Chapter 3) and litterfall (Thomas 1999, Chapter 6). However, the influence of gaps of different size on the decomposition rate of different litter fractions is poorly understood.

Decomposition in gaps
The decomposition rate of plant litter is influenced by the quality of the decomposing resource, the edaphic and environmental conditions and the decomposer community (Swift *et al.* 1979). Gaps are warmer and less humid than the surrounding forest. Although the subsoil in gaps is usually wetter than in the forest (Jetten 1994a), the increased soil evaporation in gaps dries out the topsoil, where most of the decomposer community live. The decomposer community consists of soil biota, including micro-flora (fungi and bacteria) and soil micro-, meso- and macro-fauna that form an integrated system for the decomposition of plant debris (Tian 1998). This community will be especially affected by dry soil conditions, since water is needed as a transport medium. There are a few reported studies of the effect of gaps on decomposition (Brouwer 1996, Denslow *et al.* 1998, Luizão *et al.* 1998, Zhang and Zak 1995). Decomposition studies in Central and South America found little significant differences between gap size or canopy openness and decomposition rate (Denslow *et al*. 1998, Luizão *et al.* 1998). On the other hand, in natural tree fall gaps in China, Zhang and Zak (1995) reported significant lower decomposition rates in large gaps compared to small gaps and undisturbed forest.

Objectives and hypotheses

In logging gaps, the nutrients that are released through decomposition are of crucial importance for the regenerating vegetation in the gaps. Nutrient stress and competition for nutrients between different plant species contribute to the future species composition of the forest. The contradicting findings in literature on the effect of gaps on the decomposition rate, emphasised the need for further studies into the effects of logging intensity, expressed as gap size or canopy opening, on the decomposition process. Therefore, this study was designed to assess the effects of logging gaps on the decomposition process with special attention on the microclimatic parameters that influence decomposition rates.

It is assumed that with increasing gap size, the decomposition rate of leaves and other litter parts decrease. Moreover a gradient of decreasing decomposition rates with increasing distance from the gap edge is present. These gradients are expected for both weight loss of the litter and nutrient release from the litter. Although there are large differences between the rates of release of different chemical elements from the litter, it is expected that for most elements, similar patterns can be observed as for weight loss. The decrease in decomposition rate with increasing gap size is based upon changes in edaphic and microclimatic conditions in different gap sizes like an increase in radiation and temperature and a decrease in the moisture content of the litter. These hypotheses were tested in decomposition experiments in tropical rain forest logging gaps of varying size in the interior of Guyana in 1997 and 1998.

METHODS

The study site is located 50km South of the Mabura Hill township, in the interioir of Guyana. The research was carried out in a mixed tropical rain forest, in which *Chlorocardium rodiei* is a dominant tree species. The haplic Ferralsols of the study sites are well-drained with sandy to sandy-clay-loam texture. Annual rainfall is 2700mm with two relatively wet and two relatively dry seasons (Jetten 1994a) (see Chapter 2 for a complete description of the study areas).

Litter weight and nutrient loss with litter bag experiments

Litter weight loss and changes in litter nutrient quantities in time were studied with litterbags (Swift and Anderson 1989). Two litter bag experiments were carried out in the PGE undisturbed forest and gaps (40, 60, 210, 400, 570, 1280 and 3200m^2). The litterbags were placed in 15 plots that were located on a transect from the gap centre into the forest. The number of plots in a gap depended on the gap size, with only one plot in the smallest gaps and 4 plots in the largest gap. The distance each plot to the gap edge was measured and hemispherical photographs were taken to calculate canopy openness with WINPHOT (ter Steege 1997).

The first litterbag experiment studied the decomposition rates of freshly fallen *Chlorocardium rodiei* leaves. Over a period of 3 weeks, leaves were collected from cloths that had been spread on the forest floor. To ensure that the initial physical and chemical condition of the leaves was comparable, very soft or brittle leaves were discarded as well as leaves with green parts. Leaves were air-dried in an air-conditioned room (26 °C, 80% humidity) to ensure a standard initial moisture condition of the leaves. A separate set of these air-dried leaves was used to calculate the initial oven-dried weight (48h at 70°C) of the leaves in the litterbags. A good correlation between air-dried and oven-dried weight loss was found: $W_{oven\text{-}dry} = 0.9339 \cdot W_{air\text{-}dry}$ (N = 30, R^2 = 0.99). Leaves were cut into small 2×2 cm pieces and, on average 0.54 g leaves were put into 7×8 cm nylon bags with a 1 mm mesh. The litterbags were placed on top of the litter layer on the forest floor, where they were secured with small metal pins. Litter that fell on top of the litterbags was not removed. The litterbags were installed on 13 and 14 August 1997 and harvested after 31, 84, 230, 276 and 382 days. The collection dates were based upon an expected exponential weight loss pattern (Brouwer 1996, Wieder and Lang 1982, Andrén and Paustian 1987) and an important change in microclimatic conditions: the '97/'98 El Niño event. At each harvest, five randomly selected litterbags were removed from each plot. The leaves were oven-dried (48h at 70°C) and sand, roots and fungal infections were removed before weighing. The leaves were stored in sealed polyethylene bags and transported to the Netherlands for chemical analysis.

A second litterbag experiment studied the weight loss of woody litter and flower parts. The woody parts consisted of branches, twigs and tree bark. These litter fractions were collected in litter traps (Chapter 6). Woody and flower parts were oven-dried (48 h at 70ºC) and on average 0.53 g woody parts and 0.36 g flowers were put in separate 7×8 cm nylon bags with a mesh size of 800µm. The mesh size of this experiment was smaller than the mesh size of the first experiment due to availability of the mesh at the start of the experiments. The litterbags filled with woody or flower parts were placed next to the leaf litterbags on 13 and 14 August 1997. At 84, 295 and 382 days after placement, 5 bags of woody parts and 5 bags of flower parts per location were randomly collected. The contents of these litterbags were oven-dried (48 h at 70ºC) and weighed. Although the mesh size of the litterbags was different, a T-test of weight loss of leaves buried at the same location in 800 µm bags and 1000 µm bags did not show any significant differences (p=0.261, t=-1.144).

Modelling litter weight loss

The litterbag methods provided data for modelling weight loss due to decomposition, which is needed to model the nutrient cycle in gaps (a decomposition model is used in FORGAP, Chapter 4). Several models have been proposed to describe the disappearance of litter over time (Wieder and Lang 1982, Andrén and Paustian, 1987). The three most common ones are:

Linear model:	$M_t = M_{t0} - c \cdot t$	or	$W_t = 100 - c \cdot t$	(1)
Single exponential model:	$M_t = M_{t0} \cdot e^{-c \cdot t}$	or	$W_t = 100 \cdot e^{-c \cdot t}$	(2)
Double exponential model:	$M_t = Mr_{t0} \cdot e^{-cr \cdot t} + Ml_{t0} \cdot e^{-cl \cdot t}$	or	$W_t = 100 \cdot (e^{-cr \cdot t} + e^{-cl \cdot t})$	(3)

in which M_t is the weight (g) at time t (time unit, usually d: day), M_{t0} the initial weight (g) that can be split into a refractionary or insoluble part Mr and a labile part Ml, c the decomposition constant (time unit^{-1}) with cr the refractionary constant and cl the labile constant and W_t the remaining weight in % of the initial weight at time t. Andrén and Paustian (1987) also proposed a consecutive double exponential model, where the refractionary part of the litter is first converted to a liable state, after which it is removed completely. Wieder and Lang (1982) argued that the linear model could not explain the constant biological activity with a decreasing substrate, despite their usual good fit. The double exponential model requires a detailed sampling of the litter weight loss throughout the decomposition experiment, which was not feasible in this study. Therefore, only the single exponential model was tested in this study.

Litter turnover experiment

Quantitative decomposition rates can be evaluated with the litter turnover rate method (Nye 1961). The litter layer on the soil is a steady-state input-output system: it receives fresh litter through litterfall and soil litter is removed through decomposition. The ratio of litterfall (L_f in t.ha^{-1}.yr^{-1}) and litter layer mass (L_m in t.ha^{-1}) is the litter turnover rate or k-factor (yr^{-1}):

$$k = L_f / L_m. \quad (4)$$

The value of k represents the number of litter layers that are decomposed in one year. It is opposite to the half-life coefficient $k^*=L_m/L_f$, which describes the time-span, in years, in which one litter layer is decomposed. Litter turnover is determined by measuring litterfall over a prolonged period of time and by measuring the amount of litter on the forest floor in the vicinity of the litterfall collections at several points in time during the litterfall collections. The litter turnover method does not provide detailed information on the pattern of litter weight loss through time or the loss of nutrients in the litter, but it indicates the overall decomposition rate of the study site, without interfering with local microclimatological conditions. The litter turnover method is very useful in comparing between different forest types.

The litter turnover rate was determined over a period of 1.5 years. Litterfall was measured in 34 one-m^2 litter traps that were placed in the undisturbed forest and in 9 PGE gaps (gap sizes: 140, 210, 240, 370, 570, 700, 960, 2680, 2950 and 3200m^2). The traps were placed along a transect from the gap centre into the forest. Litterfall was collected weekly from October 1996 until May 1998 (see also Chapter 6). The environmental settings of the litter traps were described in the same way as the litterbag plots, namely distance to the gap edge and canopy openness. Litter was sorted into leaves, woody parts and other small litter. These fractions were oven-dried (one week at 60°C) and weighed. The litter layer was sampled around the litter traps on 16 October 1997 and 4 May 1998. All litter on the soil within a metal ring with a diameter of 30 cm was removed. Per collection, three random samples around a litter trap were taken. Soil litter was not collected at locations where there was a large degree of topsoil disturbance due to walking or where large amounts of felling debris were piled up as a result of the removal of the crowns and logs from the gap. Roots and soil were removed from the collected litter before sorting. The litter was sorted into recognisable leaves up to 0.5 cm, recognisable woody parts and other small litter. Sorted litter was oven-dried (48 h at 70ºC) and weighed. Litter turnover rate per sorted fraction was calculated as the year sum of litterfall (t.ha^{-1}.yr^{-1}) prior to a litter layer collection, divided by the litter layer mass (t.ha^{-1}).

Grouping of decomposition plots

The litterbag experiments were carried out on 15 plots with different edaphic and microclimatic conditions. At each harvest, only five litterbags per plot were collected, which is a small amount for an appropriate statistical analysis. Therefore, litterbag decomposition plots were grouped

according to the size of the gap, the canopy openness (*co*) and the distance to the gap edge (*dte*). Gap size had the highest weighting factor in the formation of the litterbag decomposition groups. The litterbag decomposition plots were grouped into forest plots (*co* 3-6%, *dte* < -13m), small gaps (40-60m^2, *co* 3-4%, *dte* 2 to 3m), medium gaps (210-570m^2, 8-16%, *dte* -2 to 13m) and large gaps (1280-3200m^2, *co* 14-44%, *dte* -14 to 21m).

Litter turnover was determined at different locations than the litterbag plots. Litter turnover was not measured in small gaps (<100m^2), but microclimatic conditions of the gap edge plots of the 200m^2 gap resembled the microclimatic conditions of the 50-100m^2 gaps. Therefore, litter turnover plots were grouped into forest plots (*co* 1-12%, *dte* < -5.0m); gap edges or small canopy openings (*co* 4-15%, *dte* -3.2 to 1.9m), medium gaps or medium canopy openings (*co* 5-19%, *dte* 4.1 to 15.2m) and large gaps or large canopy openings (*co* 19-39%, *dte* 7.4 to 22.1m).

Microclimate, soil moisture, chemical and statistical analysis

In addition to the litterbag decomposition plots, weekly measurements of minimum and maximum temperature were made (see Chapter 3). The microclimate data from the PGE permanent climate station (van Dam 1999 and Chapter 2) and the program FORGAP (Chapter 4) was used to calculate soil radiation, soil evaporation and soil moisture of the decomposition plots. In 1998, a moveable climate station was installed that measured the microclimate for 10 days near a decomposition plot, before it was moved to the next plot (see also Chapter 3). Due to technical malfunction of the climate station, not all plots were visited. Linear regressions were calculated between the permanent and mobile climate stations to compute the microclimate of all decomposition plots.

The leaves in the litterbags were digested with a modified Kjeldahl procedure (after Allen 1989). The leaves were digested using a mixture of concentrated sulphuric acid and 30% peroxide, with Selenium as a catalyst. The destruates were analysed for PO_4, K, Ca, Na, Mg, and Al on an Inductively Coupled Plasma Emission Spectrophotometer (Spectroflame, Spectro) and colorimetrically for NH_4 with Flow Injection Analysis (Skalar). The litter was analysed for aluminium content, because it has been shown that in gaps, high concentrations of aluminium can occur (Brouwer 1996). Aluminium is toxic for most plants and analysing litter decomposition for Al gives insight into the origin of Al.

The results of the litterbags and the litter turnover experiments were tested for normality and all variables were log-transformed. Differences between grouped decomposition plots were tested in an ANOVA a Scheffé test for post-hoc comparison (Statistica, StatSoft Inc. 1993).

RESULTS

Microclimate

Although it was expected that air temperature in gaps was higher than in forest and increased with increasing gap size, the forest plots and the small gap plots had comparable air temperatures. The average daily maximum air temperature increased with increasing gap size from 29.7°C in the small gaps to 37.1°C in the large gaps (Table 7.1). At night, large gaps cooled down more than the forest. Soil temperature had a pattern similar to air temperature. Night humidity was near saturation for all plots and the average daily minimum decreased 96.1% in the forest to 63.0% in the large gaps. Gradients of increasing soil evaporation and radiation were found from the forest plots to the large gap plots. According to calculations with FORGAP (Chapter 4 & 5), the driest soil moisture conditions in the top 15 cm of the soil prevailed in the forest and a gradient was present between the gaps, with the wettest conditions

in the small gaps. We observed that the soil moisture conditions in the top 5 cm of soil, where most of the soil biota live, was regularly drier in the medium and large gaps than in the small gaps or forest. Moreover, the moisture condition of the litter layer of the forest was almost always wetter than in the gaps. Only after recent rainfall was the moisture condition of the litter layer equal between forest and gaps.

Table 7.1 Daily mean minimum and maximum air temperature (AT), soil temperature (ST), relative humidity (RH), and total daily mean soil evaporation (ES) and radiation on the soil (RS) Microclimate and, mean soil moisture (SM) per gap group and in the forest during litterbag decomposition experiment (15 Aug. 1997 – 31 Aug. 1998).

	min AT[1]	max AT[1]	min ST[2]	max ST[2]	min RH[2]	max RH[2]	sum ES[3]	sum Rsoil[3]	mean SM[3]
	°C	°C	°C	°C	%	%	mm.d^{-1}	MJ.d^{-1}	%
Forest	24.1	29.5	24.1	26.2	96.1	99	0.10	2.07	12.43
Small	23.4	29.7	23.2	25.0	no data	no data	0.18	7.64	15.09
Medium	23.0	33.8	24.0	31.0	80.1	97.6	0.23	11.27	14.62
Large	22.6	37.1	25.4	36.0	63.0	98.6	0.32	16.03	13.86

1) Measured next to decomposition plots with min/max thermometer.
2) Calculated from regression analysis between permanent climate station and moveable climate station.
3) Calculated with FORGAP.

There were distinct differences in soil moisture content during the course of experiments (Figure 7.1). The average soil moisture content in the largest gap prior to the first harvest was 14.6%, followed by an average 10.1% in the second period, 10.9% in the third period, 19.0% in the fourth period and 17.2% in the last period. The topsoil moisture condition in the forest, as calculated with FORGAP in the month prior to the fourth collection on 16 May 1998, increased from 8 to 20%. A similar pattern was observed for the topsoil moisture content in the gap plots, although the topsoil moisture conditions in the gaps prior to the wet period was drier than under forest. There were only small differences (< 1% θ) in topsoil moisture content between forest and gaps during the wet period.

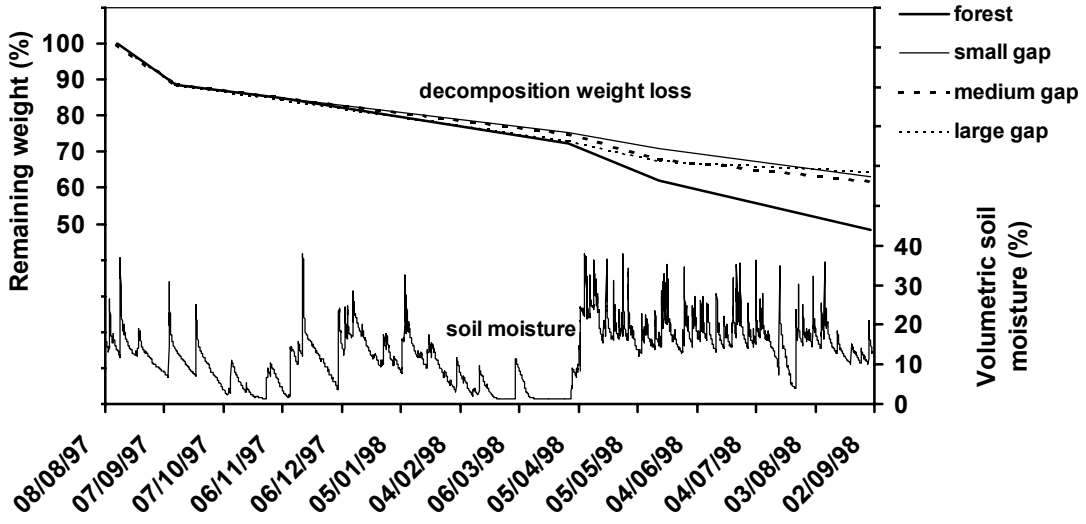

Figure 7.1 Soil moisture content under forest (right axis), calculated with FORGAP, during the decomposition experiment and remaining weight in the leaf litterbags in the gaps and forest (left axis).

Litter bag experiments

Litter weight loss
The largest weight loss of *Chlorocardium rodiei* leaves was in the first month after placement (Figure 7.1). After this first month, the rate of litter disappearance slowed down and became constant in the gaps and the forest, but increased again in the forest between the third (230 days) and fourth (276 days) collection of litter bags. The large amount of rainfall in April 1998 and consequently higher soil moisture content may have increased the decomposition rate in the forest, but apparently not in the gaps.

Against expectations, no significant differences were found of leaf litter loss from the litter bags after 382 days between different gap sizes, but the forest litter bags had a significantly lower amount of remaining weight compared to all gap size groups (Scheffé-test, $p<0.05$) (Table 7.2). The average remaining leaf weight after 382 days of all plots was 60.9% (σ 10.4%). The remaining weight of the woody fraction after 382 days was 59.8% (σ 14.7%). Flower parts had an average remaining weight of 50.6% (σ15.5%). The larger standard deviation of the woody and flower fractions compared to the leaf fraction could be the result of a higher variability in the initial material in the litterbags. After 382 days, there was a significant difference in weight loss between woody parts and flower parts (Scheffé test, $p<0.05$; not shown in Table 7.2).

Table 7.2 Decomposition results of leaves, woody parts and flower parts per gap group after 382 days: Mean (m) and standard error (se) of the remaining weight, as % of initial weight. The letters indicate significant differences (post-hoc Scheffé-test, $p<0.05$), but different litter fractions were not tested against each other.

	Forest		**Small**		**Medium**		**Large**	
	m	***se***	***m***	***se***	***m***	***se***	***m***	***se***
Leaves	48.2 [a]	2.8	63.1 [b]	2.9	61.7[b]	1.5	64.5[b]	2.6
Woody parts	56.1	4.9	66.2	3.7	60.2	2.8	58.5	4.2
Flower parts	39.4	4.0	58.3	5.0	54.1	1.9	48.5	3.9

The woody and flower parts weight loss decreased with increasing gap size, whereby the flower parts had the largest weight loss and had the largest distinction between gap sizes (Figure 7.2). However, these differences were not significant (Table 7.2). Woody and flower parts were not collected after one month, but the amount of weight loss after two months of the woody parts did not indicate a rapid decrease in the first month. Woody parts decomposed slower than flower parts in all decomposition plots. The remarkable increase in remaining weight of the flower fraction at the end of the experiment can only be explained by a relatively larger content of less decomposable flower parts in those bags.

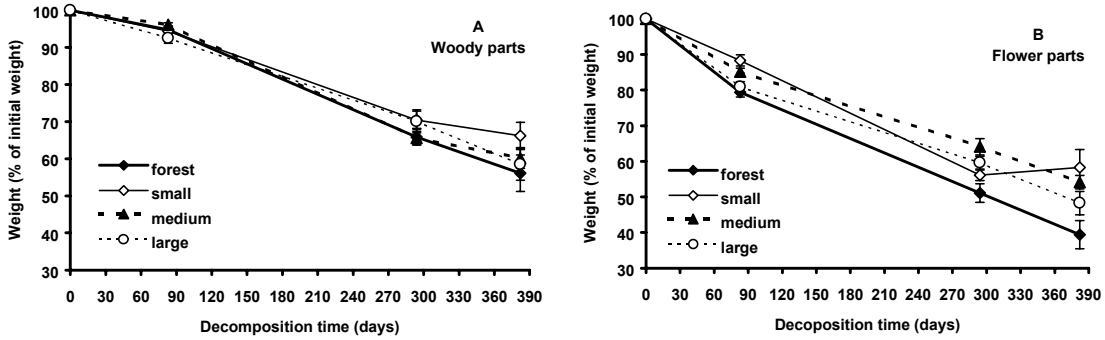

Figure 7.2 Weight loss as % of the initial weight of A: Woody parts and B: Flower parts per time step per gap group of the. The markers indicate the mean value with ± 1 standard error. Horizontal axis gives the days after placement: 13/8/97.

Neither an increasing nor a decreasing gradient from the gap centre into the gap edge area of decomposition rates of leaves and woody parts was found (Figure 7.3). The decomposition rates of leaves and flower parts in areas inside or close to a gap were, although highly variable, of the same magnitude compared to the decomposition rates in undisturbed forest with a 'closed' canopy. The woody fraction was not analysed in relation to the distance to the gap edge, since litter bags with woody parts were only located near the gap edge.

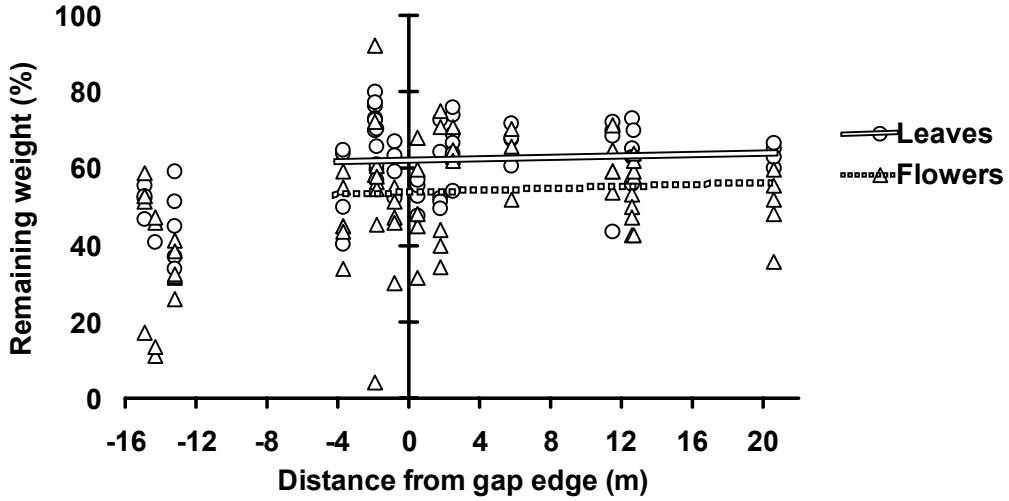

Figure 7.3 Remaining litter weight (in % of original weight) of leaves and flower parts in relation to the distance to the gap edge. The lines represent linear regression through the data points located in the gap or gap edge area, but not in the forest (> -5 m). The regressions are not significant: R^2 leaves=0.007, R^2 flowers=0.006.

Change in nutrient composition of leaf litter

Concentrations of N, P, K, Ca, Na and Mg in the leaves decreased in the course of the litterbag experiment, but Al concentrations increased (Figure 7.4). The strongest decline was observed for Na and K, while all elements, except Na, showed a large temporal variability. In all plots, the amount of Sodium in the leaves dropped to 20% of the initial concentration after the first month and was almost absent at the end of the experiment. There were no consistent patterns between gaps of different size or the forest and no significant differences (Scheffé test, $p<0.05$; Table 7.3). For example, nitrogen levels had the lowest concentrations at the end of the experiment in the forest plots and the highest in the small gap plots while magnesium concentrations were highest in the forest and lowest in the small gaps.

Table 7.3 Decomposition results per gap group of the mean (m) and standard error (se) of the remaining quantity as % of initial quantity of N, P, K, Ca, Mg, Na and Al after 382 days. The letters indicate significant differences between decomposition sites per element (post-hoc Scheffé-test, $p<0.05$).

	ini. conc.	**Forest**		**Small gap**		**Medium gap**		**Large gap**	
	mg/g	***m***	***se***	***m***	***se***	***m***	***se***	***m***	***se***
N-NH4	15.03	62.0[a]	3.7	85.5[b]	4.8	72.2	2.6	77.6	3.3
P-PO4	0.36	38.2	5.7	40.6	4.1	31.2	3.1	37.1	3.7
K	0.98	21.3	2.9	18.9	2.3	16.3	1.8	16.9	2.2
Ca	4.12	83.2	6.6	77.4	10.8	89.7	7.1	83.7	4.6
Mg	2.79	41.7	4.5	26.2	5.9	32.9	3.3	30.0	3.7
Na	3.01	2.2	0.6	1.7	0.4	1.7	0.3	2.2	0.2
Al	0.26	282.0[b]	36.5	1078.6[a]	320.4	339.7[b]	46.7	270.7[b]	58.7

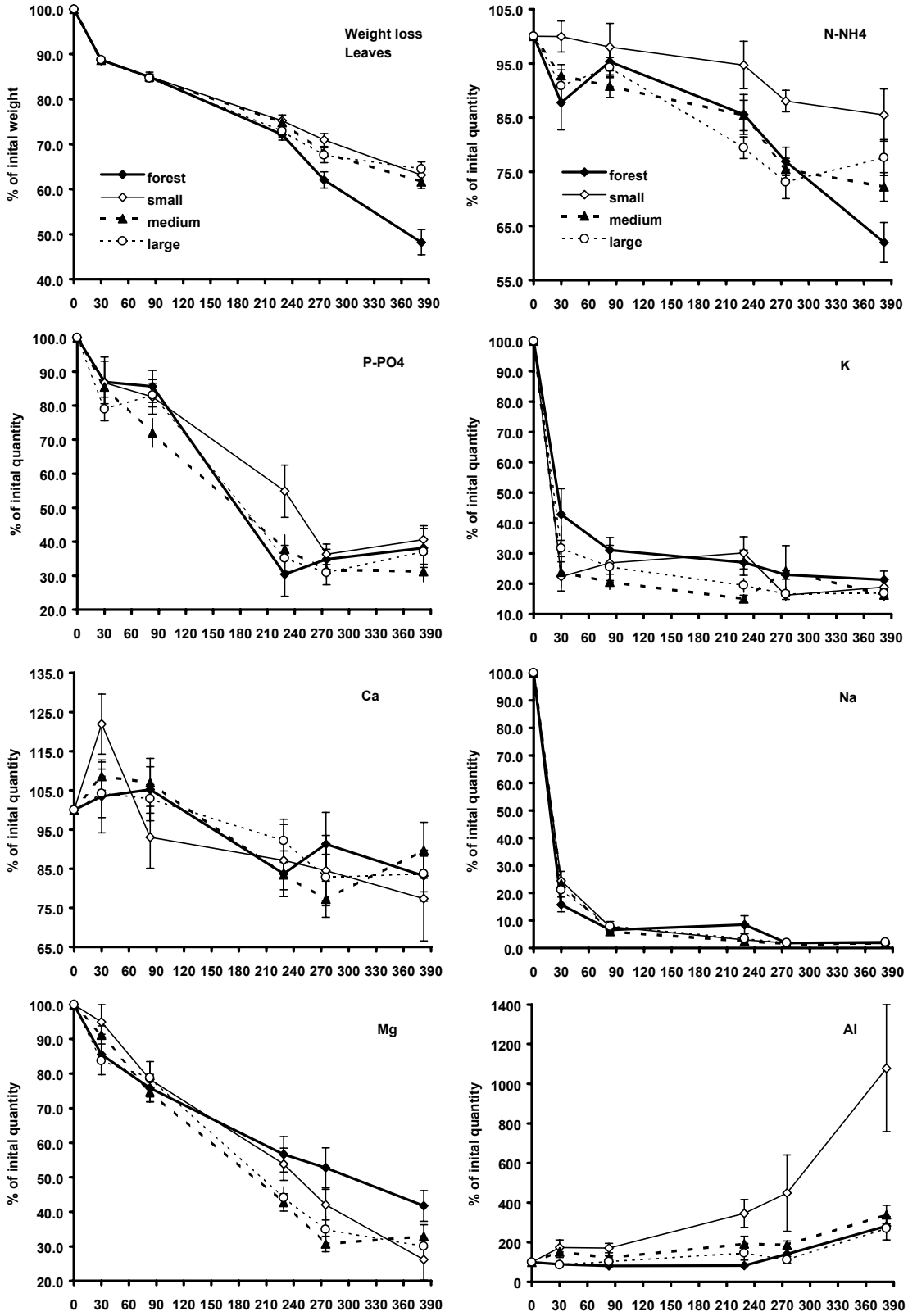

Figure 7.4 Decomposition results of *Chlorocardium rodiei* leaves per time step per gap group of the % remaining weight and the % of remaining quantities of N, P, K, Ca, Mg, Na and Al. The markers indicate the average value with ± 1 standard error. Horizontal axis gives the days after placement: 13/8/97.

Phosphorus quantities dropped to 30-36% of initial levels in the first 275 days, after which all plots, except the medium gaps, showed an increase of 3-6% over initial levels. Loss of potassium, like sodium, occurred mainly in the first month. Magnesium and calcium also decreased over time, but at a constant rate. Aluminium quantities increased up to 1079% in the small gaps and up to, on average, 184% in the other plots, which indicated that Al is not removed from the litter. The high Al content in the small gaps at day 382 was based upon 3 samples out of 11. The average relative quantity of the other 8 samples was 329.2 (% of initial quantity, σ 103.59).

Modelling leaf decomposition

The single exponential model described the weight loss of leaves, woody and flower parts moderately well (Table 7.4). All litter fractions had the largest decomposition rate in the forest, but no differences were found between gaps of different sizes. The highest goodness of fit was found for leaf decomposition in forest. The coefficient *A* of the models indicated that the flower parts had the largest decomposition rate followed by leaves. The models were used to calculate the remaining weight of *Chlorocardium rodiei* leaves after one year, which resulted in 51.8% in the forest and 62.2% in the gaps.

Table 7.4 Results of the decomposition regression modelling per litter fraction for the remaining weight in the litterbags: $RemainingWeight_t = 100 \cdot e^{-c \cdot t}$, with t in days.

	Forest		**small gap**		**medium gap**		**large gap**	
	c	**R^2**	***c***	**R^2**	***c***	**R^2**	***c***	**R^2**
Leaves	0.0018	0.816	0.0013	0.648	0.0013	0.667	0.0013	0.498
Woody parts	0.0016	0.436	0.0011	0.668	0.0014	0.741	0.0014	0.584
Flower parts	0.0025	0.672	0.0017	0.614	0.0016	0.581	0.0021	0.327

Litter turnover experiment

The leaf litter layer mass decreased in the gap with increasing distance from the gap edge (Figure 7.5). This pattern was not observed for woody parts and other small litter. Similarly, the litter layer mass decreased with increasing canopy openness (data not shown). The average total litter layer mass of the forest was 5.98 $t.ha^{-1}$ (σ 2.27), and the small, medium and large gap groups had a total litter layer mass of 4.00 (σ 1.56), 3.39 (σ 1.73) and 4.09 (σ 2.12) $t.ha^{-1}$, respectively. Only total litter layer mass in the forest was significantly larger than in the medium gap group (Scheffé test, $p<0.05$, N=129). Woody and other small litter layer mass had no gap size group related pattern (Figure 7.6).

Total litterfall in the forest was 10.14 $t.ha^{-1}$ (σ 2.96)[1] and the small, medium and large gaps had a total litterfall of 6.26 (σ 1.95), 2.23 (σ 1.33) and 0.60 (σ 0.47) $t.ha^{-1}$, respectively (Figure 7.6). Leaf litterfall decreased with increasing gap size (see also Chapter 6), while woody and other small litterfall was almost absent in the gaps. Total litterfall decreased significantly from the forest plots to the medium gap group (Scheffé test, $p<0.001$, N=129), but litterfall in the medium and large gap groups were not significantly different from each other.

These patterns of litterfall and littermass resulted in contrasting patterns of litter turnover. The litter turnover rates of woody parts and other small litter clearly decreased from forest to the large gaps group, but the leaf litter turnover rate was highly variable between gap groups. Nonetheless, the total litter turnover rate decreased from 1.81 in the forest to 0.19 in the larger gap group (Figure 7.6 & Table 7.5).

[1] Note than in Chapter 6, total annual litterfall was 9.3 $t.ha^{-1}.yr^{-1}$. The difference is caused by a difference in measuring period; Chapter 6: 1996-1999, this chapter: 1997-1998, period of littermass collections.

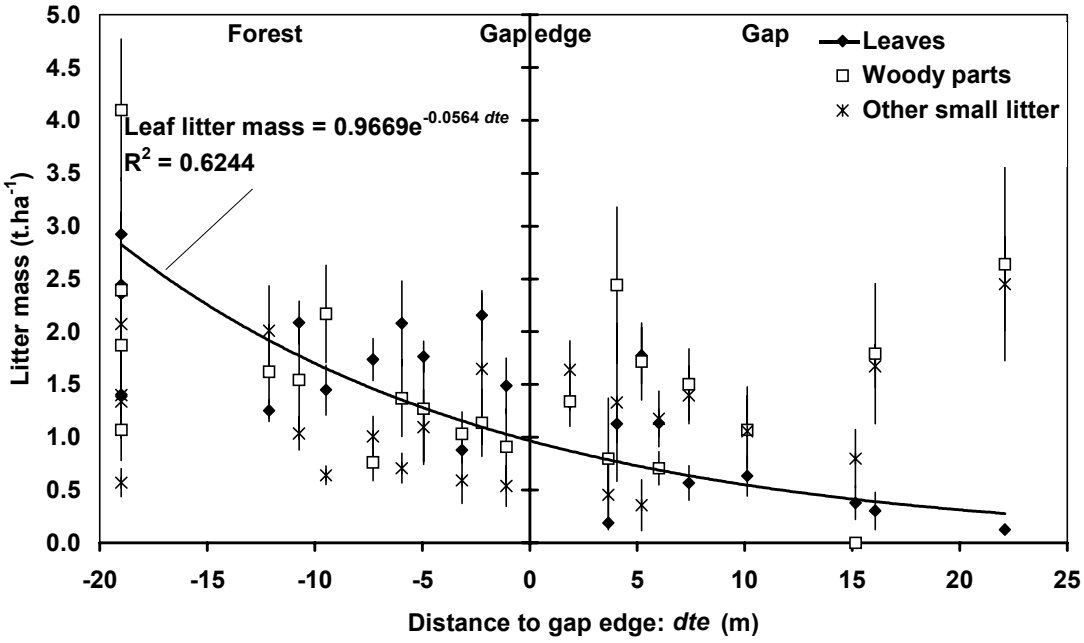

Figure 7.5 Litter layer mass as function of the distance of the plot to the gap edge.

The average total litter turnover in the gaps was 0.82 (σ 0.66) and in the forest 1.80 (σ 0.55) (Table 7.5). This means that one litter layer in the forest is decomposed in 6.7 months and in the gaps in 14.6 months. Significant differences of total litter turnover were found between all litter turnover groups. The differences in total litter turnover between gaps and forest were caused by the differences in litter turnover of woody parts and other small litter, which was much smaller in gaps for woody parts anfd other small litter than for leaves. The high turnover rate of the other small litter fraction (k-factor 3.5) was caused by an exceptionally large seed rain of 118 g.m^{-2} in one week. The seed rain was collected below a *Mora gonggrijpii*, which has an average dry seed weight of 52 g (ter Steege 1994).

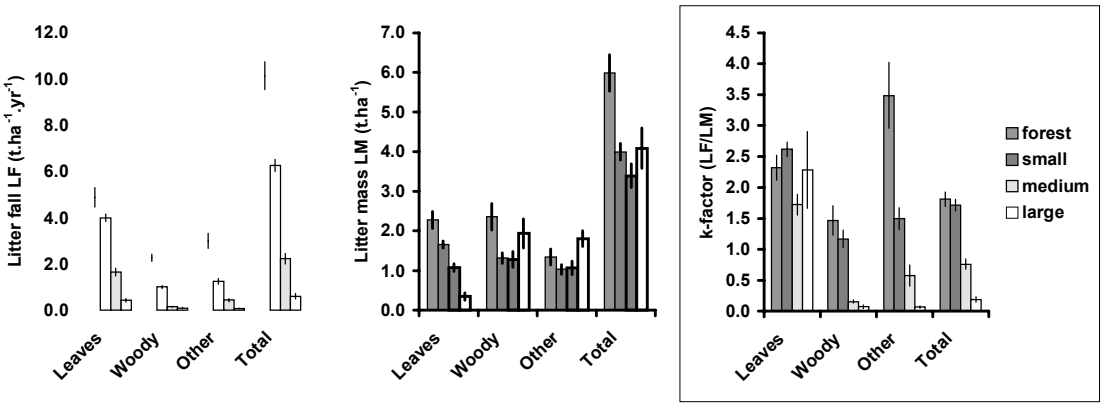

Figure 7.6 Litterfall (A), littermass (B) and litter turnover k-factor (C) of leaf-, woody-, other small litter and total litter in undisturbed forest and small, medium and large gaps. (error bars indicate 1 standard error)

Table 7.5 Litter turnover rates (k-factor) of leaves, woody parts and other small litter per gap group: Mean (m) and standard error (std err). The letters indicate significant differences (post-hoc Scheffé-test, $p<0.05$ at least), but different litter fractions were not tested with each other.

	forest		small gap		medium gap		large gap	
	m	***se***	***m***	***se***	***m***	***se***	***m***	***se***
Leaves	2.32^{a}	0.20	2.62^{ab}	0.12	1.72^{b}	0.17	2.29^{ab}	0.62
Woody parts	1.47^{a}	0.24	1.17^{b}	0.14	0.15^{b}	0.03	0.08^{ab}	0.03
Other small litter	3.49^{a}	0.53	1.50^{ab}	0.18	0.58^{b}	0.17	0.07^{b}	0.02
Total litter	1.81^{a}	0.12	1.71^{a}	0.09	0.76^{b}	0.08	0.19^{c}	0.04

DISCUSSION

Logging gaps and litter weight loss

Litter weight loss from litterbags

Litter decomposition rates were not affected by gap size, but the presence of a gap did decrease the decomposition rate. Similarly, no gradients were present of decomposition rates in relation to the distance to the gap edge or canopy openness. Flower parts had the highest decomposition rates in forest, followed by leaves and woody parts.

The difference in decomposition rates between gaps and forest can be explained by differences in environmental conditions and disturbances of soil fauna and flora due to logging. Microclimatic conditions in gaps dried out the litter layer and the top 5 cm of the soil. These dry conditions were less favourable for soil fauna and flora involved in the decomposition process. In gaps, the microclimatic conditions during a day was sufficient enough to evaporate all intercepted water by the litter within one or two hours after a rainstorm. In the forest, rainwater that was intercepted by the litter layer could take more than a day to evaporate. These wetter conditions in the forest increased the decomposition rate. The influence of the microclimate on the decomposition rate became evident in the very wet period at the end of the decomposition experiment. The strong increase in rainfall and consequently rise of the soil moisture content caused an increase in the decomposition rate of the leaves in the forest, but not in the gaps, where evaporation between rain storms immediately dried out the litter layer, thereby reducing the rate of decomposition. The larger evaporation in gaps is a combination of higher radiation levels, higher temperature, lower air humidity and more wind near the soil surface, which constantly displaces the leaf litter, thereby exposing the underlying leaves to direct evaporation.

Other differences between the forest and the gaps are related to logging. Mycorrhizal infections play an important role in the decomposition process in tropical forest (Janos 1980a, St.John and Uhl 1983, Swift and Anderson 1989) and forest succession (Alexandre 1989, Janos 1980b). In a logging gap, whether a small or a large one, the bulk of the roots in the gap were killed due to the felling of the parent trees and it is likely that also the mycorrhizal infections were affected. In Cameroon, spore numbers and mycorrhizal colonisations were much lower in skid trails and landings compared to primary forest (Onguene 2000). As a result, a large portion of the roots and mycelia involved with decomposition are absent in logging gaps compared to undisturbed forest and it may take several years before the mycorrhiza infections and root activity are restored. This hypothesis is supported by the fact that fungi had infested, to various degrees, the litterbags in the forest plots, but were almost absent in the gap plots. An overall dry litter layer throughout the gap and reduced mycorrhiza activities around the logged trees in the gaps were probably the main reasons for the lack of differences in decomposition rate between different gap sizes, but also can explain the larger decomposition rate in forest.

Similar findings as in our study can be found in literature, where decomposition rates were not affected by differences in canopy openness (Denslow *et al.* 1998) or in different sized gaps as well as the position in the gap (Luizão *et al.* 1998). Despite the fact the gaps of different size can have large differences in air temperature, evaporative drying rates, moisture content or even total invertebrate density (Didham 1998), their decomposition rate showed no differentiation. Although the moisture content of the littermass was not measured in our study, we hypothesize that the decomposition of plant litter is more influenced by the moisture content of the litter than of the soil.

Some comments on litter bags experiments

The litterbag method provides detailed insight into litter weight loss and changes in nutrient quantities through time and is especially useful for comparing decomposition rates between different plant species, between plant parts or between different sites. However, the litterbag method has several disadvantages. Firstly, the mesh size of the litterbags may exclude certain soil biota (Tian 1998). Secondly, litterbags have been reported to create their own moisture and microclimatic conditions that may not reflect the actual conditions of the study site (Tanner 1981). The effect of the 1000 μm mesh litter bags on the decomposition rate of *Chlorocardium rodiei* leaves was tested in a separate experiment (see Sluiter and Smit 1999), as well as the effect of cutting the leaves into smaller fragments. Litterbags significantly increased decomposition rate compared to leaves that were put into a 1 by 1 cm metal mesh box. Leaves in the litterbags were wetter for longer periods. Also, the decomposition rates of cut-leaves were significantly higher than decomposition rates of whole leaves. Cutting the edges of the leaves increased nutrient leaching and increased the fungal ingrowths into cut-edges of the leaves (pers. obs.).

The contents of the litterbags filled with woody or flower parts consisted of a wide variety of tree species and the decomposition rate of these tree species is likely to differ. A litterbag decomposition experiment with an unknown mixture of litter made the comparison between sites more difficult, although from the results it can be concluded that the decomposition rate of flower and woody parts was lower in gaps than in forest.

Litter turnover experiment

The litter turnover experiments gave decomposition rates of the entire litter layer, which is almost impossible to achieve with a litterbag experiment, because of the large variety of different types of litter from different tree species. The littermass collections were made at 16 and 22 months after gap creation. The ongoing decomposition in the gaps after gap creation had already diminished the litter layer substantially, while during the same period there was a limited supply of new litter through litterfall. The gap edge received more litter than the gap centre (see also Chapter 6), resulting in a decreasing litter layer with increasing distance from the gap edge. This gradient was apparent for the leaf litter, but not for the woody and other small litter fraction. The woody and other small litter fraction consisted mainly of twigs, branches, bark, and woody cotyledons of large seeds, which are all plant parts that decomposed slower. Since there was almost no new woody litter arriving in the gap centres of the large gaps, the turnover rate of woody litter became almost zero and significant differences between forest and gaps were found. This was in contrast to the turnover rate of leaf litter, where no significant differences were found.

The high leaf litter turnover rate in the large gaps can be explained by the fact that predominantly very light leaves, in which heavy woody parts are lacking, can reach the centre of the largest gaps and these leaves are easily decomposable. The 2.3 yr^{-1} leaf turnover and 1.8 yr^{-1} total small litter turnover of the forest, as found in this study, are within the range of turnover values reported in literature of South America (Brouwer 1996, Cornforth 1970, Fittkau

and Klinge 1973, Luizão *et al.* 1998, Puig and Delobelle 1988, Scott *et al.* 1992). The turnover rate of the woody fraction, 1.47 y^{-1}, is surprisingly high. Delaney *et al.* (1998) found a turnover rate of wood of 0.01-0.06 per year. They indicated that most of the dead wood was in the standing dead category, which is important to incorporate in any study. Therefore, the woody turnover rate as reported in our study must be regarded as the turnover rate of the small woody fraction and not the total woody fraction, which would include complete dead trees. The other small litter fraction decomposed faster than woody parts, which could be explained by the higher nutritious value of the other small litter fraction, consisting of flowers, seeds and fruits, and higher lignin content of the woody parts. Several authors have suggested that the chemical composition of litter is more important than soil moisture or temperature (Alvarez-Sánchez and Becerra Enríque 1996, Brouwer 1996). The composition of the litter can be essential for the regenerating vegetation in gaps. Especially in large gaps, the regenerating vegetation consists to a large extent of pioneer species. The decomposition rate of the litter of pioneer species can be much faster than that of a climax species like *C. rodiei* (Brouwer 1996, Ewel 1976), although slow decomposing pioneer species have also been reported (Mesquita *et al.* 1998). In the PGE forest, leaves of the pioneer species *Goupia glabra* were almost completely decomposed after 1 year, while the firm leaves of the climax species *Chlorocardium rodiei* had only 52% weight loss after 1 year (van Dam unpubl.). The difference in nutrient release through decomposition between pioneer and climax species in gaps is unknown, but since the decomposition rate of litter of pioneer species is usually faster than of climax species, this litter composition can be of crucial importance for the nutrient availability of the regenerating vegetation in gaps.

Nutrient release from decomposing leaf litter

Nutrient loss from the *Chlorocardium rodiei* leaves showed large variation between different elements or between gap size groups. No other pattern was found than that the concentrations of all elements except aluminium decreased in time. Aluminium remained behind in the leaves and thus Al concentrations increased. The major weight loss of the *C. rodiei* leaves was in the form of carbon. Besides carbon, loss of nitrogen and to a lesser extent the loss of calcium, magnesium and sodium contributed to the weight loss of the *Chlorocardium rodiei* leaves.

The loss of N, K, Ca, Mg and Na in *C. rodiei* leaves in the forest were of the same magnitude as the loss of these elements from leaves of same species in comparable forest and soil type reported by Brouwer (1996), despite the large difference in climatic conditions due to the El Niño event in our study. Apparently, the very wet climatic conditions in the last months of our decomposition experiment enhanced the decomposition rate. The decomposition rate as found by Brouwer was more constant in time, but resulted in similar weight loss after one year. Luizão *et al.* (1998) reported a decrease of N, P, K, Ca and Mg concentrations in leaves of 4 different tree species with a known range in decomposition rate. In their study, gap size had significant effect on nutrient quantities, but none was ranked in the same order.

Singh (1969) attempted to correlate various chemical constituents of tropical tree species with their rate of breakdown and concluded that numerous chemical characteristics had an effect on decomposition. For example, species with high initial nitrogen content decomposed more rapidly than species low in nitrogen (Ewel 1976). In Guyana, contrasting findings were reported, since the initial N content in 5 different tree species gave a negative correlation with decomposition rate (Brouwer 1996). The physical structure of the leaves was probably more important than the chemical content. Species rich in lignin content decompose slowly (Blow 1955). The lignin content of *C. rodiei* leaves is 4.0% (Raaimakers in Brouwer 1996), which is much less than other values in tropical forest (range 10 – 40%) (Anderson *et al.* 1983, Palm and Sanchez 1990), and a clear correlation between decomposition rate and lignin content has not been found.

These findings suggest that the rate of decomposition is more influenced by the physical nature of the litter than by the chemical composition. Our experiments showed that the turnover

rate of *C. rodiei* leaves in forest, 0.52 yr^{-1}, was relatively slow compared to the turnover rate of the leaf litter layer of the forest of 2.32 yr^{-1}. A one-year decomposition experiment with *G. glabra* and *C. rodiei* leaves gave a similar decomposition rate for *C. rodiei* leaves as presented in this study, but more that half of the *G. glabra* leaves had decomposed completely (van Dam unpubl.). The smooth leathery surface of the firm and thick *C. rodiei* leaves provides a strong physical barrier against insect attack and mycorrhiza infection. The ingrowths of fungi in the cut-edges of C. *rodiei* leaves increased the decomposition rate compared to intact leaves (Sluiter and Smit 1999), which indicated that mycorrhiza had difficulties with the surface of *C. rodiei* leaves.

Decomposition modelling

The lack of difference in the decomposition models in the gaps support the findings that the decomposition rates in gaps of different size were equal. Although the single exponential model is an oversimplification of the decomposition process, it gave good estimates of the decomposition rates in the different locations and for the different litter fractions. The rapid decrease of quantities of potassium and sodium (Figure 5) indicated that the decomposition rate in the first few weeks was not equal to the decomposition rate after a few months. Litter consist of a refractory component that decomposes very slowly and a faster decomposing labile part (Bunnel and Tait 1974). As suggested by various authors, this composite litter weight loss is best modelled by the double exponential model (Bunnel and Tait 1974, Andrén and Paustian 1987, Palm and Sanchez 1990, Gosz *et al.* 1973), in which the refractory and labile fractions are modelled separately or together. Alvarez-Sánchez and Becerra Enríque (1996) fitted an exponential model, a double exponential model and a negative exponential model through their leaf decay data at Los Tuxlas, Mexico. They concluded that the double and negative exponential model yielded the best fits. These models require a large amount of data and attempts to fit a double exponential model through the data of the litterbag experiment yielded many possible solutions.

CONCLUSIONS

Gaps reduced the decomposition rate compared to forest, but no differences were found between gaps of different size. The reduced decomposition rates in gaps are explained by the lack of living roots with mycelia associations and the desiccation of the litter layer. These reduced decomposition rates can lead to a potential nutrients stress for the regenerating vegetation in the gaps.

The logging gaps of the PGE were almost completely cleared of all vegetation that most likely resulted in a loss of living biomass in the soil as well. In a more normal felling operation, several trees are left standing, which reduces the evaporation from the litter layer and results in less damage to the roots. Such findings emphasize the need for a minimized damage to the vegetation in and around logging sites.

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In situ mineralisation experiment

8 THE RECOVERY OF MINERALISATION IN GAPS OF DIFFERENT SIZE

with Saskia Visser and Jakolien Leenders

Abstract
The effects gaps of different size and age were studied to determine how these gaps affect mineralisation and how long the influence of the gap persists. In addition, microclimatic and edaphic conditions that affect mineralisation were studied.

Soil N-content and soil moisture conditions were the most important variables that affected N-mineralisation rates within plots with similar environmental conditions, but different N-mineralisation rates between forest and gap are best explained by littermass, living root content, canopy openness and again soil moisture content.

Net N-mineralisation rates were 4 times lower in gaps over 200m^2 than in forest, but gaps smaller than 100m^2 had undisturbed mineralisation rates. The recovery of N-mineralisation rates occurred in the largest gaps prior to smaller gaps, because the largest increase in biomass and consequently litter production, decomposition and mineralisation was found in the largest gaps. Moreover, the environmental conditions in the soil in these larger gaps become more favourable for mineralisation after a number of years of regeneration in the gaps. However, it is expected that potential nutrient stress can occur in two-year-old gaps, when the vegetation is still low and the remaining litter layer is completely depleted. Species who can cope with these nutrient starved habitats can have a competitional advantage over less well-adapted species.

INTRODUCTION

Factors affecting mineralisation rates in forest and gaps

Nutrients become available to plants after the mineralisation of organically-bound chemical elements to their mineral form. As such, mineralisation is an inextricable component of the nutrient cycle in any terrestrial ecosystem. Nitrogen is one of the critical nutrients for plant growth that is obtained from the mineralisation of soil organic nitrogen to mineral forms of N ($N\text{-}NH_4^+$ and $N\text{-}NO_3^-$). An overview of the major components of the nitrogen cycle has been given in Chapter 2. A reduction in N-mineralisation rates due to a disturbance of one or more factors that affect the mineralisation process can decrease the nitrogen availability for plants and therewith affect an optimal performance of an ecosystem.

Mineralisation is influenced by the quality and quantity of the resource i.e. plant litter, the microclimate and edaphic conditions, the soil physical and chemical properties and soil moisture. In a tropical rain forest, canopy gaps created by selective logging, can change the nitrogen mineralisation rates, as gaps in the forest alter the nutrient cycle by:

1) changing microclimatic conditions and soil moisture (Becker *et al.* 1988, Chapter 3),
2) reducing litter input (Thomas 1999, Chapter 6),
3) decreasing decomposition rates (Chapter 7),
4) increasing nutrient loss through leaching (Brouwer 1996, Chapter 9) and
5) inducing low pH levels (pH<4, Brouwer 1996, Chapter 9) that can liberate toxic levels of aluminium from the soil complex.

Selective logging is common practice in the forests of Guyana, whereby different sized gaps are created in which different levels of disturbance to the nutrient cycle occur. After felling, regeneration of the forest takes place in these gaps and nutrient stress of macro-elements such as nitrogen and toxic levels of microelements such as aluminium may become limiting conditions for the regeneration of the forest in general and for future commercial tree species in particular. Mineralisation in tropical rain forest has been studied intensively in undisturbed forests (Barrios & Herrera 1994, Montagnini & Buschbacher 1989, Tanner 1977, Vitousek & Matson 1988), but only a few studies have been carried out in logging gaps (Marss *et al.* 1991, Vitousek & Denslow 1986). Moreover, little is known about mineralisation rates in gaps of different size and how mineralisation rates are restored in time.

Are mineralisation rates affected by gap size or gap age?

Mineralisation rates are variable in time, caused by differences in seasons, and in space, caused by differences in soil physical and chemical properties, litter quantity and quality and soil microbial biomass. Understanding which of these factors are most important in the mineralisation process is essential to explain differences between mineralisation in forest and in gaps. First, mineralisation in undisturbed forest in different seasons was studied as well as the factors that influence the mineralisation rate.

1) How are ammonification, nitrification and net N-mineralisation rates affected by seasons and are there differences between different years?
2) How are the N-mineralisation rates affected by resource availability, microclimatic and edaphic conditions?
3) Can factors affecting N-mineralisation explain differences in N-mineralisation rates between different sized gaps and between gaps and forest?

Second, the effect of gap size and age on the mineralisation process was studied.

4) Do N-mineralisation rates decrease with increasing gap size?
5) Are N-mineralisation rates restored to the level of the undisturbed forest when resource availability, microclimatic and edaphic conditions are restored as well?

We expect that immediately after gap creation, mineralisation rates in gaps will be affected by microclimatic and soil moisture conditions only, since the resource for mineralisation, the litter layer on the soil, is still intact, although large differences due to logging, like crown debris, can be present (Brouwer 1996). Most likely, microclimatic and topsoil moisture conditions are less favourable in large gaps than in smaller ones, since the higher solar radiation, air and soil temperature and lower air humidity dries out the litter layer and the topsoil (0-5 cm). Therefore, N-mineralisation rates are expected to decrease with increasing gap size.

Over time, the litter layer on the soil decreases with increasing gap size or with distance from the gap edge, since the amount of freshly fallen litter is less in large gaps than in small gaps (Chapter 6) and decomposition rates are not affected by gap size (Chapter 7). This combined effect of reduced resource availability and drier environmental conditions will decrease the mineralisation rate and it is expected that this reduction will be larger in large gaps than in small gaps. Mineralisation rates are restored, when sufficient littermass is being produced by the regenerating vegetation in the gaps. Since litterfall in gaps and gap size are inversely related, it is expected that N-mineralisation rates will be lower in large gaps than in small gaps.

A series of mineralisation experiments were carried out in logging gaps of different size and age the interior of Guyana from 1997 to 1998. To gain a better understanding of the factors that influence the mineralisation process, a multivariate analysis of these factors and N-mineralisation was performed. This information is needed to assess the results of the mineralisation experiments in different gaps and relate possible differences to environmental or edaphic factors.

METHODS

Mineralisation experiments and other measurements on microclimate, soil moisture, littermass and roots were carried out in undisturbed forest and in 7 gaps of the Pibiri Gap Experiment (PGE, van Dam *et al.* 1999, but see Chapter 2), in 2 gaps in the Forest Reserve Mabura Hill (FRMH, Brouwer 1996) and in 2 gaps at the research site at 2K (Ek 1997). All research sites were characterised by a haplic Ferralsol carrying a mixed Greenheart forest, in which *Chlorocardium rodiei* is the dominant tree species. A long wet season is common from May to August, followed by a strong dry season from September to November. Annual rainfall is 2700mm and average daily temperature is 25°C (Jetten 1994a).

General field and laboratory methodology

In situ N-mineralisation was determined as the difference between extractable N in incubated and initial soil samples. Soil samples were taken from two 20 cm PVC tubes with a diameter of 1.5 inches that were inserted vertically into the topsoil (10 cm) (adapted from Adams *et al*. 1989 and Raison *et al*. 1987). The tubes were covered with lids and a small hole in the part extending above the soil enabled the release of nitrogen gas. Soil samples from the tubes were transferred to a plastic bag, to avoid evaporation of soil moisture, where it was thoroughly mixed by hand and large roots were removed. One tube, i.e. the initial soil sample, was processed immediately and a second tube was processed after an incubation time, i.e. the incubated sample. Both tubes were treated similarly. Two soil sub-samples of approximately 10 g were put into two bottles: one containing 25 ml of 1M KCl extraction fluid and one with 25 ml of 0.01M $CaCl_2$. Another soil sub-sample was stored in a plastic bag to determine the soil moisture content. The bottles with the extraction fluids and soil samples were shaken for at least 1 hour after which the fluid was allowed to settle for a few minutes. The contents of the KCl and $CaCl_2$ bottles was filtered (SNS 592) and the clear fluid was stored in 12 ml laboratory tubes. Acidity was determined in the clear filtrated extraction fluid. The $CaCl_2$ extraction was treated for conservation with 0.6 ml HNO3 (25%) and the KCl extraction was acidified with 0.6 ml H_2SO4 (5%). The samples were transported to the laboratory in Utrecht, the Netherlands. The $CaCl_2$ samples were analysed on an Atomic Emission Spectrometer (SpectroFlame ICP-EAS) for concentrations of Al^{3+}, K^{+}, Fe^{2+}, Mn^{+}, Mg^{2+}, SO_4^{2-}, Zn^{2+}, Si^{2+}, and $Ca2^{+}$. The KCl samples were analysed colorimetrically (Skalar) for NH_4^{+}, NO_3^{-}, Cl^{-} and PO_4^{3-}.

Ammonification and nitrification (mg $N.kg^{-1}$ dry $soil.d^{-1}$) were calculated as the difference of extractable $N\text{-}NH_4^{+}$ or $N\text{-}NO_3^{-}$, respectively, for the incubated and the initial sample, divided by the number of incubation days (Barrios & Herrera 1994). There is some controversy in the literature about the calculation of net N-mineralisation. Raison *et al.* 1987 simply added ammonification and nitrification rates, whereas Cavelier *et al.* (2000) also include nitrite ($N\text{-}NO_2^{-}$) in the calculation of net N-mineralisation. Most authors, however, calculate net-mineralisation rate as the difference between incubated $N\text{-}NH_4^{+}$ plus $N\text{-}NO_3^{-}$ minus their initial content, divided by the incubation time (e.g. Barrios & Herrera 1994; Marrs *et al.* 1988). This method was used in our study.

Mineralisation experiments

Variability of N-mineralisation in undisturbed forest and a large gap
In an undisturbed 9 ha forest area in the PGE research area (see Appendix 2.3), ammonification, nitrification and net N-mineralisation were assessed in a nested variance sample scheme (Riezebos 1989) to ensure an adequate random sampling. The 9 ha area was subdivided into plots of 50 by 50m. In September 1997 (dry season), mineralisation was measured in 3 plots. In each plot, 2 random sub-plots of 5 by 5 m were selected, 15 m apart. In these sub-plots, 2 random pairs of samples were taken, 1.5 m apart. The pairs were 15 cm apart. The PVC tubes

were closed on both sides and incubated for 14 days. In June 1998 (wet season), the experiment was repeated in 5 plots (sub-plots distance 20m, sample distance 2 m, no lower sampling level). The PVC tubes were closed at the top and incubated for 7 days. The spatial variability of mineralisation in a 2-year-old 3200m^2 PGE logging gap was studied in July 1998 (wet season). Mineralisation samples were taken along two perpendicular transects that enabled the study of gap-centre – gap-edge gradients. Samples were incubated for 7 days and the PVC tubes were closed at the top. To increase the number of replicates, the experiment was repeated after one week.

Soil, litter and microclimatic factors that affect N-mineralisation
Factors that influence N-mineralisation were measured at the same locations where mineralisation experiments were carried out in the 5 PGE forest plots and in the largest PGE gap (3200m^2) in July 1998. Littermass, was collected in a metal ring (diameter 30 cm) and sorted into recognisable leaf parts up to 0.5cm, woody parts and a rest fraction. Litter was oven-dried (48 h at 70ºC) and weighed. Roots were sampled with a metal pipe (diameter 5 cm) with sharpened teeth at one end. This pipe was inserted 10 cm into the soil. The soil was sieved under a running tap and all roots were removed. Roots were sorted into living and dead roots according to colour, texture and brittleness. The roots were stove-dried (48 h at 70ºC) and weighed. Soil chemical data were obtained from the initial samples of the mineralisation experiments. Soil chemical attributes that were analysed were: soil N content; soil fertility, which is defined as the sum of cations K, Mg, Mn and Na; soil toxicity given by the Al concentration; and soil pH-KCl. Soil texture was analysed for samples that were taken in small 100 cm^3 metal rings next to the mineralisation tubes. No direct microclimate measurements were made, but microclimate was related to canopy openness, since canopy openness is well correlated with radiation, soil and air temperature (Whitmore *et al.* 1993, Chapter 3). Hemispherical photographs were taken at all mineralisation plots and canopy openness was calculated with WINPHOT (ter Steege 1997).

Effect of gap size and age
In October 1997 and in July and August 1998, mineralisation was measured in the centres of the, 15 and 26-month-old PGE gaps, respectively, with gap sizes of 40, 60, 210, 370, 570, 1280 and 3200m^2. In 1997, six samples per gap were incubated for 14 days, with both ends of the PVC tubes covered. In 1998, fifteen samples per gap, closed on the top only, were incubated for 7 days and 5 samples were grouped to give 3 samples per gap for analyses. A similar experiment was carried out in July 1998, in the undisturbed forest and in the 6.5-year-old FRMH gaps, which had areas of 740 and 3440m^2 (Brouwer 1996) and in the 13-year-old 2K gaps, 200 and 800m^2 in size at gap creation (Ek 1997).

Statistical analysis

All variables were analysed for normality per treatment since some of the data were collected at two very different sites, an undisturbed forest and a large gap and bimodal distributions were expected. Differences between experiments were tested with ANOVA and individual differences were tested post-hoc with an Scheffé test (Statistica, StatSoft Inc. 1993).

RESULTS

Variability of mineralisation in pristine forest and a 3200m^2 gap

In the undisturbed forest, ammonification, nitrification and net N-mineralisation rates were highly variable, both in time, between different seasons and years (Table 8.1) as in space,

within a supposedly homogeneous forest area of 9 ha. Significant differences in N-mineralisation rates occurred between forest plots that were only 100m apart (Scheffé test, $p<0.05$, N97=24, N98=20), but these differences between plots were not consistent between years, which indicated a large temporal variability as well. Significant differences between different seasons of all forest plots together were only found for nitrification in the dry season of 1999 with the other seasons (Scheffé test, $p<0.001$).

In contrast to the mineralisation experiments in the forest, the mineralisation experiment in the large 3200m^2 gap did not produce any significant differences (Mann-Whitney test) in ammonification, nitrification or mineralisation rate, neither from the gap centre to the gap edge, nor between the N-S or E-W oriented transects. Apparently, the factors controlling the mineralisation process were less heterogeneous in the gap than in the forest. Average ammonification rate in the gap was 0.13 mg $N.kg^{-1}.d^{-1}$ (σ 0.58, 54.8 $kg.ha^{-1}.yr^{-1}$), nitrification rate was 0.10 mg $N.kg^{-1}.d^{-1}$ (σ 0.10, 44.9 $kg.ha^{-1}.yr^{-1}$) and net N-mineralisation rate was 0.23 mg $N.kg^{-1}.d^{-1}$ (σ 0.59, 99.7 $kg.ha^{-1}.yr^{-1}$).

Table 8.1 Ammonification, nitrification and net N-mineralisation in Pibiri Forest plots ($mg.kg^{-1}.d^{-1}$, value between brackets in $kg.ha^{-1}.yr^{-1}$). Letters indicate significant differences between seasons (columns, Scheffé test, $p<0.001$; note that $p<0.05$ was not found).

year&season	n	N-NH4	σ	N-NO3	σ	net N-min	σ
1997 dry	24	0.33 (145)	0.65	0.73 (323) [b]	0.31	1.06 (468)	0.85
1998 wet	20	0.93 (404)	0.77	0.56 (249) [b]	0.46	1.48 (653)	0.96
1998 dry	17	0.85 (378)	0.75	0.69 (305) [b]	0.38	1.47 (656)	1.09
1999 dry	18	0.08 (36)	1.39	1.68 (748) [a]	1.26	1.79 (799)	1.33
Mean	79	0.53 (236)	0.96	0.90 (397)	0.81	1.42 (631)	1.07

Multivariate analysis of N-mineralisation

Littermass, roots, soil physical and chemical properties

The largest differences between gap and forest were found for littermass and the amount of living roots, which were larger in the forest than in the gap and canopy openness and dead root mass, which were larger in the gap than in the forest.

Mean forest leaf littermass was 1.98 $t.ha^{-1}$ (σ 0.74), compared to a mean gap leaf littermass of 0.32 $t.ha^{-1}$ (σ 0.30). However, total littermass, including woody debris, was less variable between gap and forest, since total littermass in the forest was 8.32 $t.ha^{-1}$ (σ 4.06) and in the gap 8.46 $t.ha^{-1}$ (σ 6.55). The average living root content in the top 5 cm of soil under forest was 7.09 $t.ha^{-1}$ (σ 4.96), which was 3.7 times more than the 1.90 $t.ha^{-1}$ (σ 1.37) in the gap. Not surprisingly, due to logging, dead root mass in the top 10 cm of soil was larger in the gap; 7.96 $t.ha^{-1}$ (σ 3.76), than in the forest; 0.92 $t.ha^{-1}$ (σ 1.34). Gravimetric soil moisture of the top 5 cm of soil in the gaps was less than in the forest: 13.5 $g.g^{-1}$ (σ 2.36) versus 20.5 $g.g^{-1}$ (σ 7.36). The texture in the gap was sand and had a clay content of 0.01% (σ 0.004). The texture in the forest varied from sand to sandy loam and an average clay content of 0.06% (σ 0.043) was found. The average pH-KCl under forest and in the gap were similar: 3.61 (σ 0.22) and 3.52 (σ 0.19) respectively. There were more exchangeable cations (Ca, K, Fe, Mg, Mn, Na) in forest soil than in the soil of the gap, but the N-content under forest 2.64 mg $N.kg\ soil^{-1}$ (σ 2.09) was lower than in the gap 3.15 mg $N.kg\ soil^{-1}$ (σ 1.62). The average canopy openness of the forest was 3.26 % (σ 0.78) and of the gap 15.74% (σ 9.58).

Principal component analysis
The factors controlling the mineralisation process as described above were subjected to a principal component analysis (PCA) to examine which factor had the largest influence on N-mineralisation. The data set was reduced to: leaf littermass, living root content, soil moisture, clay content, soil fertility expressed in N content and sum of cations, soil toxicity as Al content, pH-KCl and canopy openness.

The first PC axis, representing 29.8% of the variance, almost completely explains the N-mineralisation rate (factor loading: fl 0.77) (Figure 8.1). Factor loadings of more than |0.7| are found for leaf littermass, living root content and canopy openness (Table 8.2). The second PC axis explains 14.6% of the variance and is related to the soil chemical attributes N-content and Mineralisation rate is positively correlated to the amount of littermass, living root content and N content of o the soil, but negatively correlated to canopy openness and acidity A third axis represents 13.7% of the variance and is related to the exchangeable cations in the soil (not shown in Figure 8.1).

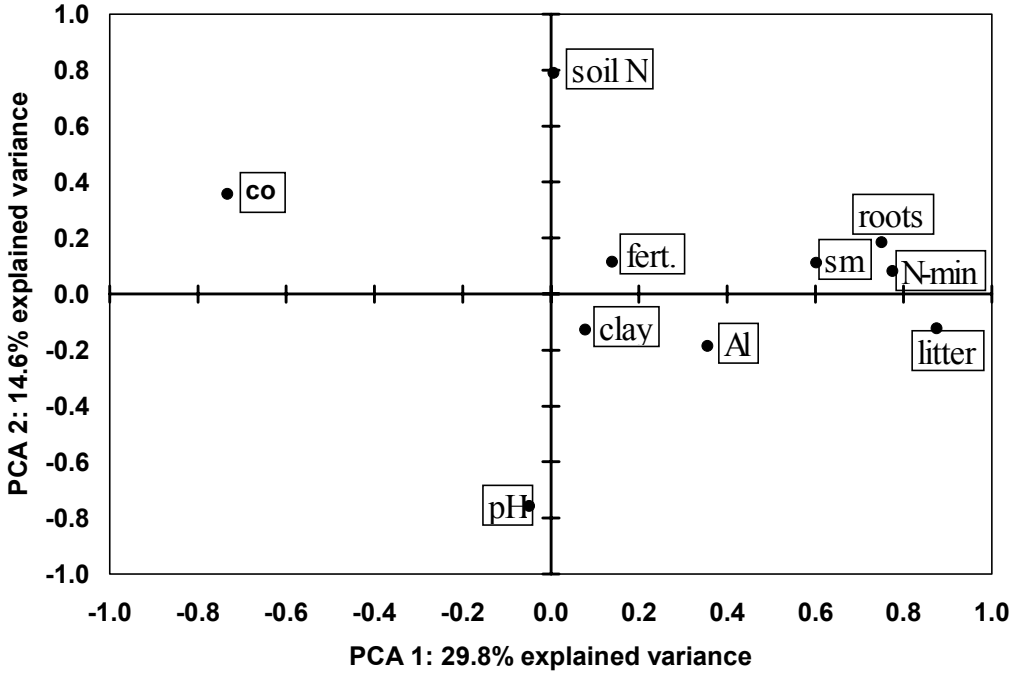

Figure 8.1 Factor loadings of first two PCA axes (co: canopy openness, fert.: fertility index, sm: soil moisture) for all data of forest and the 3200m^2 gap.

The data set was strongly biased by the large difference between the gap and the forest, which did not give insight into the factors that control the mineralisation process of the undisturbed forest. A PCA of the forest plots separately gave an explained variance of the first PC axis of 23.6%, and which was explained by total N-content and soil moisture content (Table 8.2). A PCA of the gap data had a first PC axis that explained 26.4% of the variance by soil chemical properties of soil N content, pH-KCl and soil moisture.

In conclusion, total N-content of the soil and soil moisture conditions were the most important variables that affected N-mineralisation rates within plots with similar environmental conditions, whether that was an undisturbed forest or a large logging gap. However, when comparing sites with different environmental settings, i.e. between forest and gap, littermass,

living root content, canopy openness and again soil moisture were the factors that had the largest influence on N-mineralisation rates.

Table 8.2 Factor loadings of principle component analyses of N-mineralisation rates (N-min), soil N content (N cont), acidity (pH), soil moisture (SM), canopy openness (CO), living root content (LR), clay content (Cl), soil fertility (Fert) and aluminium content (Al) in Forest and a 3200m^2 gap combined and separately. (%EW: % of explained variance per PC axis, factor loadings larger than |0.7| are printed bold)

	Forest and 3200m^2 gap, N=64			**Forest, N=40**			**3200m^2 gap, N=24**		
	PC1	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**	**PC1**	**PC2**	PC3
N-min	**0.77**	0.08	-0.30	-0.66	0.09	-0.04	0.54	0.43	-0.56
N cont	0.01	**0.79**	-0.40	**-0.81**	-0.11	0.29	**0.79**	-0.30	0.51
pH	-0.05	**-0.76**	-0.18	0.48	-0.67	-0.33	**0.81**	-0.27	0.49
SM	0.60	0.11	-0.63	**-0.74**	-0.35	-0.24	**0.70**	-0.09	-0.53
CO	**-0.73**	0.36	0.05	0.17	**0.81**	0.07	-0.46	-0.62	-0.42
LM	**0.87**	-0.12	0.06	-0.24	0.33	-0.54	0.39	-0.56	-0.22
LR	**0.75**	0.19	0.18	-0.28	**0.72**	0.15	-0.21	-0.63	-0.23
Cl	0.08	-0.13	-0.04	-0.05	-0.36	0.46	-0.06	-0.22	-0.25
Fert	0.14	0.11	**0.80**	0.50	0.36	-0.10	-0.37	-0.42	0.64
Al	0.36	-0.19	0.02	-0.26	0.07	-0.64	-0.14	0.52	0.31
%EV	29.8	14.6	13.7	23.6	21.5	12.0	26.4	19.5	19.5

Effect of gap size on N-mineralisation, ammonification and nitrification

Two years after gap creation, the average net N-mineralisation in the forest plots was 1.14 mg.kg^{-1}soil.d^{-1} (σ 1.13, N 61; 502 kg.ha^{-1}.yr^{-1}) and in the gaps larger than 200m^2, 0.30 mg.kg^{-1}soil.d^{-1} (σ 0.56, N 36, 131 kg.ha^{-1}.yr^{-1}) (Figure 8.2).

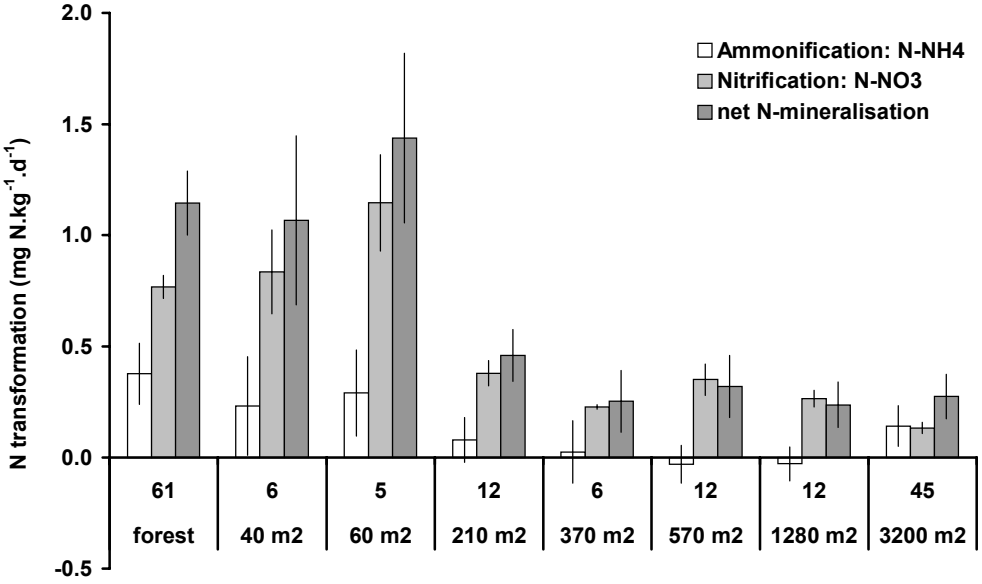

Figure 8.2 Ammonification (N-NH4), nitrification (N-NO3) and net N-mineralisation (N-min.) rates in forest and PGE gaps of different sizes. The bars represent the average value of the experiments in 1997 and 1998 with +/- 1 standard error and the numbers on the y-axis above the indication of gap size are the number of replicates per plot.

Despite these apparent differences, ammonification and net N-mineralisation were not significantly influenced by gap size and no significant differences were found between any gaps and the forest (Scheffé test, all p's > 0.13), except for N-mineralisation, which was significantly higher in the forest than in the 3200m^2 (Scheffé test, p = 0.0007). Nitrification was significantly higher in the forest compared with the gaps larger than 200m^2 (Scheffé test, all p's < 0.036). On the other hand, ammonification, nitrification and net N-mineralisation rates were significantly higher in the forest compared to all gaps larger than 200m^2 together (ANOVA, p<<0.001: Scheffé test NH_4: p=0.023, NO_3: p= p<<0.001, N-min: p= p<<0.001).

Effect of gap age on N-mineralisation, ammonification and nitrification

The recovery of N-mineralisation rates to the level of the forest occurred in large gaps prior to smaller gaps (Table 8.2). This conclusion was based on the average values of N-mineralisation rates, although no significant differences were present between the experiments in gaps of different size and age (ANOVA p<0.05), with the exception of nitrification and N-mineralisation rates, which was significantly higher in PGE forest and the 2 year old PGE 3200m^2 gap (Scheffé test, p<0.05). The PGE and 2K forests had comparable net N-mineralisation rates: 1.30 and 1.22 mg.kg^{-1}.d^{-1}. In contrast, net N-mineralisation in the forest at FRMH, which was much lower: 0.26 mg.kg^{-1}.d^{-1}. Despite this lower mineralisation rate at 2K, no significant differences were present between ammonification, nitrification or net N-mineralisation rates in the forests of the 3 different locations (Scheffé test, p<0.05). Linear regression analysis of the mineralisation rate in the largest 3200-3400m^2 gaps of 2 and 6 years old suggested that the mineralisation rate could be restored to the level of the forest after 8 years. Linear regression analysis of the 800m^2 2 and 6-year-old gaps suggested the N-mineralisation in those gaps might be equal to that of the forest after 28 years.

Table 8.3 Ammonification, nitrification and net N-mineralisation in forest and gaps of different size and age (mg.kg^{-1}.d^{-1}, value between brackets in kg.ha^{-1}.yr^{-1}). Letters indicate significant differences between gaps of different size and/or age (columns, Scheffé test, p<0.001).

Size	Age	N	NH4		σ	NO3		σ	N-min		σ
Forest	**PGE**	61	0.67	(295)	0.76	0.66[a]	(294)	0.41	1.30[b]	(581)	0.96
Forest	**FRMH**	3	0.09	(46)	0.09	0.16	(79)	0.08	0.26	(125)	0.09
Forest	**2K**	3	0.58	(215)	1.10	0.64	(239)	0.33	1.22	(455)	0.80
200m^2	**1 yr**	6	0.04	(18)	0.34	0.30	(121)	0.23	0.35	(139)	0.45
200m^2	**2 yr**	6	0.11	(46)	0.38	0.46	(184)	0.13	0.57	(230)	0.36
200m^2	**13 yr**	2	-0.20	(-75)	0.13	0.59	(220)	0.19	0.39	(145)	0.06
800m^2	**1 yr**	6	0.07	(34)	0.34	0.32	(152)	0.23	0.39	(186)	0.54
800m^2	**2 yr**	6	-0.13	(-62)	0.21	0.38	(178)	0.28	0.25	(116)	0.45
800m^2	**6 yr**	3	-0.26	(-125)	0.42	0.41	(201)	0.09	0.16	(76)	0.41
800m^2	**13 yr**	3	-0.13	(-50)	0.45	0.65	(241)	0.11	0.51	(190)	0.52
3200m^2	**1 yr**	6	0.24	(103)	0.85	0.32	(137)	0.35	0.56	(240)	1.13
3200m^2	**2 yr**	39	0.13	(55)	0.58	0.10[a]	(45)	0.10	0.23[b]	(100)	0.58
3200m^2	**6 yr**	3	0.30	(147)	0.62	0.66	(321)	0.08	0.96	(468)	0.56

DISCUSSION

Soil moisture as the most important factor affecting N-mineralisation rates

Seasonal variability and soil moisture

In the undisturbed forest, ammonification, nitrification and net N-mineralisation rates were highly variable, both between wet and dry seasons as between spatially closely positioned plots. Ammonification rates were higher in the wet season, seasonal patterns were not found for nitrification rates, but the resulting net N-mineralisation was in general higher in the dry season than in the wet season. The seasonal variability was largely caused by differences in soil moisture and microclimate. A linear correlation between nitrogen transformation and soil moisture has been observed up to a certain level above which it remained constant (Tietema *et al.* 1992). Therefore, it can be argued that the differences between seasons could also be observed between wet and dry days within one season, since high soil moisture content can also occur during the dry season (Chapter 3). The importance of soil moisture was also indicated by the results of the PCA. We expect that the soil moisture content is more important than the season in which it occurs and the seasonal patterns is merely a reflection of the soil moisture condition during the experiment or the weather conditions of the past days prior to the experiment. The higher mineralisation rate in the forest compared to the large gap can therefore be related to, among other factors that are discussed below, the difference in soil moisture content of the top 5cm of soil, which was lower in the gap than in the forest.

Other factors affecting N-mineralisation

Recapitulating, soil N-content and soil moisture conditions were the most important variables that affected N-mineralisation rates within plots with similar environmental conditions, but different N-mineralisation rates between forest and gap are best explained by littermass, living root content, canopy openness and again soil moisture content.

The heterogeneity of the litter layer and the topsoil properties attributed to a large variation in the forest. The factors influencing mineralisation rates were more homogenous in the large gap than in the forest. For example, the litter layer in the gap was almost absent and this bare soil was clearly more homogeneous than a litter layer in a forest. The importance of the litter layer was also stressed by Vitousek and Denslow (1986), who found significantly lower N-mineralisation rates in the root-throw zone due to the removal of the litter layer. It can also be argued that the environmental and edaphic conditions in the gap were more limiting, resulting in a lower mineralisation rate throughout the gap. The differences in N-mineralisation rates between the gap and the forest were clearly regulated by the large differences in mineralisation environments as shown by a smaller littermass, a lower living root content, lower soil moisture content and larger canopy openness in the gap than in the forest.

In our study, soil physical properties were poorly correlated to the mineralisation process. Soil texture had little effect on N-mineralisation, which is in contrast to other studies. In an Australian red earth in New South Wales, clay content had a significant effect on the mineralisation rate (Strong *et al.* 1999a). Cavelier *et al.* (2000) reported an increase in mineralisation rate with a decrease in soil moisture from field capacity (35%) to drier conditions (25%). However, the soil of their study site consisted of sandy clay loam with 24% clay, while the PGE soil has only 10% clay. A high clay content might limit mineralisation rates, since very small pores (< 0.6 μm) can act as a physical boundary against microbial attack (Strong *et al.* 1999b, van Veen and van Elsas 1986). It is therefore not likely that the soil physical properties of the PGE study area hampered mineralisation rates.

Soil N content and acidity are usually correlated to the mineralisation rates (Lamb 1980, Motavalli *et al.* 1995, Paul and Clark 1996), as was also found in our study. N-mineralisation rates in South American tropical rain forest is strongly influenced by soil fertility. The

mineralisation rates were reported in fertile volcanic or alluvial soils of Central America (Vitousek and Matson 1988), while the lowest values were found in seasonally waterlogged forest (Barrios and Herrera 1994) or in highly weathered soils (Cavelier *et al.*2000).

We defined the microclimate of the mineralisation plots by the canopy openness, which has a strong correlation with radiation and air and soil temperature are related to radiation. Canopy openness was strongly negatively correlated with the net N-mineralisation rate. The optimum temperature for nitrification lies in the range from 25 to 35 °C (Prosser & Cox 1982) nitrification or net mineralisation are usually not affected by temperature (Cavelier *et al.* 2000). Although air and soil temperatures over 40°C have been recorded (Chapter 3), the temperature in the soil decreases rapidly, within centimetres, with depth (Brouwer 1996) and most likely did not influence mineralisation rates.

Mineralisation and decomposition
Mineralisation and decomposition (Chapter 7) are closely linked and it is imperative that these processes are discussed together. Mineralisation and decomposition were both gap size independent and both mineralisation and decomposition rates were lower in gaps than in forest. Microclimatic conditions in gaps were clearly drier than in forest and apparently, these drier conditions, which influenced the soil microbial biomass that is responsible for decomposition and mineralisation, can be found in gaps larger than 200m^2. The organic resource that was available for decomposition and mineralisation showed some interesting results. Resource availability is the sum of littermass on the soil and the dead root biomass. Total resource availability in the gap was far more than in the forest, 8.28 t.ha^{-1} versus 2.90 t.ha^{-1}, but consisted mainly of dead roots, 7.96 t.ha^{-1}. However, the littermass in the forest was far more than the littermass in the gap, 1.98 t.ha^{-1} versus 0.32 t.ha^{-1}. Since mineralisation was measured in the top 10 cm of the soil, including dead roots and soil litter, this implies that the littermass is far more important in the mineralisation process than dead roots. This is not so surprising, since root decomposition rate of roots is far lower than that of above ground plant litter, as was demonstrated by our study. High mineralisation rates will favour root growth (Roy & Singh 1995), although it is unlikely that the lower root content in the gap is a result of low mineralisation rate. More likely, the small aboveground biomass compared to the large aboveground biomass of the forest is also found belowground, as living roots.

Effect of gap size and gap age

Gaps that were smaller than 100m^2 had comparable N-mineralisation rates as the undisturbed forest and N-mineralisation rates in gaps larger than 200m^2 was 4 times lower than in forest, but no gap size effect was found. Similar as in this study, no relation was found on the effect of gap size on the N-mineralisation rate in the literature (Jordan 1983, Marss *et al.* 1991, Vitousek and Denslow 1986). Moreover, these authors also did not find significant differences between gaps and undisturbed forest sites. In our study, N-mineralisation rates had the largest increase in time in the largest gap sizes. The lack of differentiation of N-mineralisation rates in different sized gaps coincides well with the absence of difference in decomposition rates between different sized gaps (Chapter 7). Similar conclusions as with decomposition can be drawn:
1) The microclimatic conditions in gaps are equally limiting the mineralisation process. The microclimatic conditions in gaps resulted in drier topsoil (top 5cm) conditions, which reduced mineralisation rates equally. The topsoil moisture conditions of the forest were wetter and thus more favourable for mineralisation.
2) Although patterns of decreasing littermass with increasing distance from the gap edge and thus with increasing gap size exist, the overall effect of large patches of bare soil resulted in N-mineralisation rates, which showed no significant differences between gap sizes.

3) The onset of a recovery of mineralisation rates occurred in large gaps earlier than in smaller gaps, because the regenerating vegetation in the gaps had the largest biomass increase in the largest gaps. The regeneration vegetation in these large gaps consists mainly of pioneer species, which produce easy decomposable leaves after which the mineralisation rate can increase.

A hypothesis on N-mineralisation recovery in different size gaps

Although N-mineralisation was highly variable and only a few significant differences were found, a hypothesis was formulated based on the results of the studies on mineralisation rates in gaps of different size and age. Net N-mineralisation in gaps of different size proceeds through a series of changes in time (Figure 8.3).

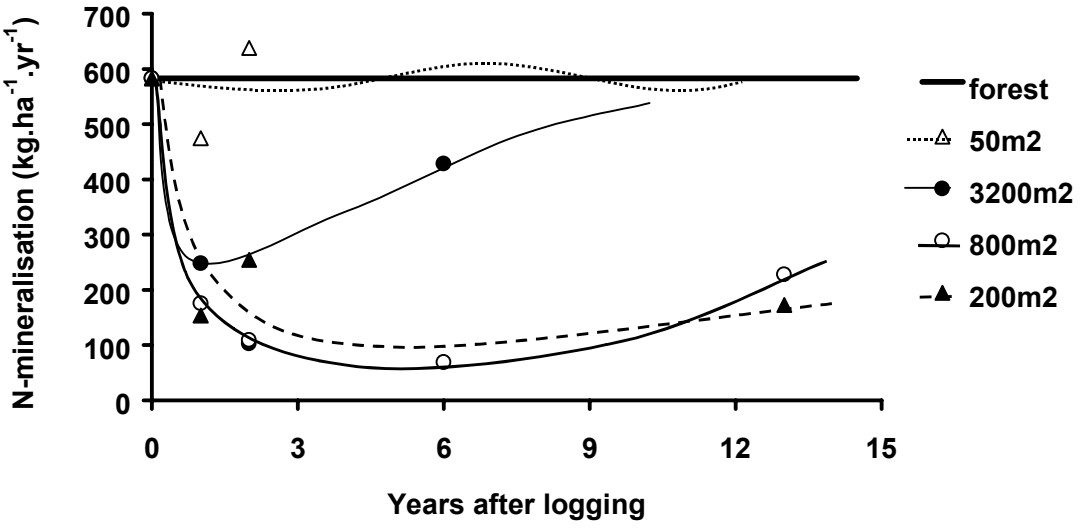

Figure 8.3 Effect of gap size and gap age on nitrogen mineralisation. The top line represents the average mineralisation rate of the undisturbed forest. The hypothetical lines through the data points were fitted manually.

Firstly, N-mineralisation rates in gaps smaller than 100m^2 are not different from forest N-mineralisation rates and do not change in time. The litter layer in these gaps is hardly affected and remains intact due to sufficient input from the forest that surrounds the gap. Microclimatic and edaphic conditions have little effect on the N-mineralisation rate.

Secondly, in the first year after gap creation, N-mineralisation rates in gaps larger than 200m^2 decrease to 30% of the forest level and to 15% in the second year. However, the N-mineralisation rates in the largest gaps (> 3000m^2) show their first signs of recovery in the second year. Microclimatic and edaphic conditions in gaps larger than 200m^2 are strongly affected, resulting mainly in drier conditions that are unfavourable for the microbial biomass involved in mineralisation. Moreover, the litter layer on the soil is in continuous decline due to a reduced input of fresh litter. The first signs of recovery of the litter layer, and thus mineralisation, can be found in the largest gaps, where the regenerating vegetation in the gap have the largest increase in biomass and this vegetation starts to recycle their leaves.

Thirdly, the vegetation in the gaps continues to grow and produce fresh litter. The increase in leaf area of these plants also reduces the effect of solar radiation on the soil, thereby reducing evaporation. Topsoil and litter layer will become less dry, which are more favourable conditions for the microbial community. A gradient of higher vegetation with increasing gap size will develop over time and, likewise, the microclimate and soil moisture factors that influence the

mineralisation process will become more favourable for an optimal mineralisation rate, comparable to the level of the forest.

Finally, net N-mineralisation will attain forest rates in large gaps prior to smaller sized gaps, but net N-mineralisation rate in very small gaps are not reduced.

CONCLUSIONS

In the first two years after gap creation, mineralisation rates in gaps of more than 200m^2 were reduced, but most likely, the nutrient demand in the gaps was also low, since the biomass accumulation of the regenerating vegetation in the gaps was small. Organically bound nutrients were still present in the decomposing litter layer, although nutrient leaching was profound (Brouwer 1996, but see Chapter 9). Two years after gap creation, the vegetation in the largest gaps is in increasing demand for nutrients, while mineralisation rates were still low due to a low supply of organic debris. Potential nutrient stress can occur in these two-year-old gaps and species that can cope with these nutrient starved habitats can have a competitional advantage over less well-adapted species. Although litterfall will gradually increase after a few years, the litter layer, and likewise mineralisation rates, will remain small for the coming 5 years. Mineralisation rates in gaps larger than 100m^2 will not attain forest levels within the coming 10 to 20 years and the regenerating vegetation in these gaps might experience limited growth or increased mortality due to nutrient stress.

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9 LEACHING IN LOGGING GAPS: EFFECT OF GAP SIZE AND GAP AGE ON NUTRIENT LOSS

with Leo Brouwer

Abstract
In gaps, nutrients that are released through decomposition and mineralisation are lost from the ecosystem, because they are not taken up from the soil solution by the roots of plants. A study on leaching was carried out in gaps ranging in size from 40 to 3200m^2 in the first two years after logging and in 7-year-old and 13-year-old gaps.

Leaching of predominantly NO_3, Al, Ca, Mg, Na, Cl and SO_4 increased with increasing gap size in gaps larger than 400m^2 compared to non-logged forest, although small increases in solute transport were also found in 200m^2 gaps. The increase in leaching started a few months after logging and the highest concentrations were found around 10 months after logging, when also the lowest pH of 3.8 was recorded. Concentrations in solute transport increased up to 8 times the concentrations as found in undisturbed forest. A special concern is aluminium, which is toxic for plants, since concentrations of Al in a 3200m^2 gap increased 19 fold to forest concentrations in the first year after logging.

Three years after logging, leaching had returned to the level of the forest, except in the 3200m^2 gaps. Increased solute transport compared to forest was still observed in the 7-years-old 3440m^2 gap, but not in the 7-year-old 740m^2 gap or in the 13-year-old 200 and 800m^2 gaps. We hypothesize that the increased leaching in the 3440m^2 gap was caused by an increase in the amount of organic debris caused by the natural dieback of the regenerating vegetation in a gap as a result of competition for light and nutrients.

INTRODUCTION

Logging and leaching

The strongly weathered soils in central Guyana are almost devoid of nutrients. In forest ecosystems on these soils, nutrients are constantly recycled and the main external source of nutrients is wet and dry deposition, although some symbiotic nitrogen fixation is found as well. The bulk of the nutrients are contained in the vegetation itself; they become available for plant growth after litterfall, litter decomposition, soil organic matter turnover and root turnover. The tight nutrient cycle of these forests is strongly affected by disturbance of the vegetation such as forest fires or logging. Large tracks of the forests of Guyana are being selectively logged, creating gaps in the canopy, which disrupts the nutrient cycle (Brouwer 1996, Chandrashekara and Ramakishnan 1994, Denslow *et al.* 1998, Parker 1985). Nutrients are removed in the boles of the felled trees and less nutrients enter the logging gap through litterfall (Chapter 6). Immediately after gap creation, certain areas in the gap are relatively undisturbed, other areas have large piles of leaves and branches from the crowns of the felled trees, and the in the remaining areas of the gap, bare is soil is found caused by heavy machinery during logging (Brouwer 1996). Due to changes in microclimatic and edaphic conditions in the gaps, decomposition rates (Chapter 7) and mineralisation rates (Chapter 8) are reduced compared to the forest. The remaining vegetation in the gap is still small and few nutrients are extracted from the soil solution. Nutrients not used by the vegetation will percolate to deeper soil layers and eventually leach from the ecosystem, when they percolate below the rooting zone of the

vegetation. Leaching is a natural phenomenon. In an undisturbed forest, nutrients are also lost from the ecosystem through solute transport in percolating water below the rooting zone and in sloping terrain, through surface runoff. However, nutrient loss in percolating water is small, and nutrients like N and P are hardly lost at all (Brouwer 1996). In undisturbed forest, nutrient loss through leaching is of the same magnitude as nutrient input in rainfall.

In logging gaps, the level of disturbance varies between small gaps, where only one or two trees were felled and large gaps, which were formed by felling 5 to 10 trees. In medium to large logging gaps in Guyana, higher concentrations of N, K, Ca, and Mg in leachate water are found than in undisturbed forest (Brouwer and Riezebos 1998). Moreover, due to logging, acidity was higher, which resulted in higher aluminium concentrations in the soil solution. Aluminium is toxic for most plants. Increasing nutrient loss with increasing gap size have been observed (Brouwer and Riezebos 1996, Parker 1985), although it has been suggested that no leaching occurs below a certain gap size (Parker 1985). The presice effects of gap size on nutrient loss is not well documented.

Increased nutrient loss after logging compared to undisturbed forest is caused by: 1) an increase in the amount of percolation water (Jetten 1994a), 2) a decrease in nutrient uptake by the remaining vegetation in the gap and 3) an increase of the amount of decomposable nutrients contained in the crowns of the felled trees (Brouwer and Riezebos 1998, Bruijnzeel 1995, Poels 1987). The fate of cation leaching is strongly linked to the release of nitrogen from organic debris. Organically bound nitrogen is released as NH_4 (ammonification). NH_4 can be taken up by plants, but most NH_4 will be transformed to NO_3 (nitrification). Hereby, two protons are released, which increases the acidity of the soil. In the acid soils of the research area, this results in increased solubility of Al. Exchangeable bases in the soil are displaced by either Al or the protons and together with the nutrients that were released during decomposition are lost from the soil exchange complex. Unlike NH_4, NO_3 is mobile in the soil and will be transported with percolating water to deeper soil layers. NO_3 is accompanied by a cation, which increases the leaching of these bases (Van Breemen *et al.* 1983, Cahn *et al.* 1993, Verstraten *et al.* 1990, but see Brouwer 1996). The intensity of selective logging, expressed as gap size, can therefor have a strong effect on the amount of nutrients that are leached from the gap (Brouwer and Riezebos 1998, Parker 1985).

Gap size and gap age, leaching and acidification

Increasing nutrient loss, increasing concentrations of Al and low soil pH in logging gaps can influence the regeneration potential of the forest in general, and of commercial tree species in particular. As such, leaching and acidification are undesirable features in logging gaps. This study was directed at the amount of nutrient loss in undisturbed forest compared to gaps of different size and age. Besides quantifying the extent of leaching we tried to answer the following questions:

- At what gap size does leaching increase compared to natural leaching in forest?
- How long does the increase in nutrient loss continue?

Soil water was collected at 120cm depth. At this depth hardly any roots are present that extract nutrients from the soil solution, so any chemical that is present there and that percolates to greater depth is assumed to be lost from the forest ecosystem. Total amount of leaching is the product of nutrient concentrations and total amount of percolating water, which was calculated with FORGAP (Chapter 4 & 5). In the first three years after logging, leaching was studied in experimental gaps ranging in size from 40 to 3200m^2. Furthermore, leaching was measured in 7-year-old gaps and 13-year-old gaps.

METHODOLOGY

The research was carried out in three study sites: the study site of the Pibiri Gap Experiment (PGE, van Dam *et al.* 1999), the Forest Reserve Mabura Hill (FRMH) study site and the 2K study site, which are located in the interior of Guyana, 250km South of Georgetown. In the study sites, a mixed tropical rain forest is present, in which *Chlorocardium rodiei* is a dominant tree species. The soils of the study sites are well-drained, sandy to sandy-clay-loam haplic Ferralsols. The climate is characterised by two wet and two dry seasons, with an annual rainfall of 2700mm (Jetten 1994a) (see Chapter 2 for a complete description of the study sites).

Leaching of nutrients below the root zone

Ceramic cup or tension lysimeter samplers

Soil water was extracted from the soil matrix at approximately 120 cm depth with ceramic cup soil moisture samplers (Eykelkamp, Wageningen, NL). The ceramic cup sampler (CCS) or tension-lysimeter consisted of a ceramic cup (diameter of 5 cm, length 7 cm) that was attached to a 150 cm long PVC tube, which was closed with a silicon bung. A tube passes through the bung that is attached to a silicon hose, which is closed with a metal clamp. Prior to installation, the CCS's were thoroughly washed with distilled water. The CCS's were installed in an auger hole of 7 cm in diameter and of approximately 140 cm depth that was drilled under a 60° angle, so the ceramic cup would be positioned at approximately 120 cm depth, supposedly below the bulk of the roots. The auger hole was filled with slurry made of the soil from the deepest part of auger hole and water. The slurry was lowered into the depth of the hole next to the CCS through a small PVC tube. This ensured a good contact between the ceramic cup and the soil after installation. After a settling period of a few weeks, the CCS's could be sampled. The CCS's were put under a 35-kPa vacuum with a vacuum pump with manometer, which ensured that the same tension was applied to each CCS. The effect of the tension on the water chemistry is explained in Appendix 9.1. The vacuum was applied for 2 nights, after which a soil water sample was taken from the CCS. After sampling, the remaining water was removed from the CCS.

Leaching sampling strategies

In July 1996, 24 gaps were felled for the Pibiri Gap Experiment (PGE). From August 1996 to July 1997, in total 30 CCS' were sampled in PGE gaps with sizes of 140, 210, 240, 400, 570, 700, 960, 2680, 2950 and 3200m^2. From August 1997 to August 1999, in total 44 CCS' were sampled in PGE gaps, which were 40, 60, 210, 370, 570, 1280 and 3200m^2 in size. The samples of the 40 and 60m^2 gap were taken together (renamed to 50m^2 gap) In addition, in July 1998, a new 410m^2 gap was made, which was sampled until August 1999. The 370 and 410m^2 are collectively referred to as 400m^2 gap. Paired CCS' were installed in the centre of the gaps and at the western gap edge. The largest gaps (370, 1280 and 3200m^2) had another pair of CCS' located at a few metres from the gap edge in the forest and two CCS' were located in the undisturbed forest. Measurement intensity was approximately 1 sample every 1.5 month in the first 1.5 years after which it was reduced to every 3 months.

In the FRMH gaps, the CCS's of Brouwer and Riezebos (1998) were sampled from June 1997 to August 1999. Nine CCS's were present in a small 740m^2 gap, 14 CCS's were present in a large 3440m^2 gap and 2 CCS's were located in the undisturbed forest. The CCS's were sampled approximately every 3 to 4 months. These collections were an extension of the previous collections of Brouwer and Riezebos (1998), who measured the same CCS from February 1992 to December 1994. In the 2K gaps, nine CCS's were sampled from August 1998 to August 1999. Three CCS's were installed in a 200m^2 gap, three CCS's were positioned in an 800m^2 and 3 CCS's were located in an undisturbed forest plot. The CCS's were sampled approximately every 4 months.

Hydrochemical budgets
The amount of percolating water below the rooting zone in the gaps and forest was calculated with FORGAP (Chapter 4 and 5). Nutrient fluxes were calculated by multiplying the measured concentration of a chemical on a certain date with the sum of the amount of percolated water in the period previous to an earlier sample. No hydrochemical budgets were calculated if there were not sufficient data. The exact edge of each gap and the positions of the CCS's were measured and PCRaster maps and sample locations within these gaps were created. Percolation below 120 cm was calculated from July 1996 to December 1998 for the PGE gaps. The hydrochemical budgets of the FRMH and 2K gaps were calculated for 1998.

General methodology on water sampling and chemical analyses

All water samples were temporarily stored in 50ml plastic tubes, which had been thoroughly rinsed with distilled water. These 50ml tubes were either taken to the Pibiri field camp or to the laboratory in Mabura, where they were processed. The water in the 50ml tube was divided over two 12 ml laboratory tubes and pH and EC were determined on the remaining water with a WTW Multiline P3. To preserve the chemical composition of the water, the contents of a 12 ml tube was acidified with 8 drops (0.6 ml or 5 %) 5% H_2SO_4, while the water of the other 12 ml tube was acidified with 8 drops 25% HNO_3. Prior to this, the 12 ml tubes and their caps had been washed: the HNO_3 tubes were soaked overnight in 25% HNO_3 and then washed in distilled water and the H_2SO_4 tubes were washed in distilled water only. The 12 ml tubes were transported to the laboratory in Utrecht, the Netherlands. The HNO_3 acidified samples were analysed on an Atomic Emission Spectrometer (SpectroFlame ICP-EAS) for concentrations of Al^{3+}, K^{+}, Fe^{2+}, Mn^{+}, Mg^{2+}, SO_4^{2-}, Si^{2+}, and $Ca2^{+}$. The H_2SO_4 acidified samples were analysed colorimetrically (Skalar) for NH_4^{+}, NO_3^{-} and Cl^{-}.

RESULTS

Leaching in different sized gaps

Nutrient concentrations in leachate water
In the PGE gaps, increased leaching compared to forest was found for NO_3, NH_4, K, Ca, Mg and Al in the 570, 1280 and 3200m^2 gaps. Increased concentrations of NO_3 and Al were also found in the 410m^2 gap (Figure 9.1). To account for some of the missing data, the concentrations in Figure 9.1 are 4-monthly averages (Aug-Nov '96, Dec-Mrt '97, Apr-Jul '97, Aug-Nov '97, Dec-Mrt '98, Apr-Jul '98, Aug-Nov '98 and Aug-Nov '99). Significant higher concentrations between the 3200m^2 gap and the forest were found for pH, Al, Ca, K, Mg and NO_3 between 8 and 12 months after gap creation (Scheffé test, $p<0.05$) and in that period, Ca was also significantly higher in the 570m^2 gap compared with the forest. It must be note however, that no samples were made in the 50, 400 and 1280m^2 gap. To compare the peak in leaching for as many different locations as possible, an ANOVA was performed on the solute content between 0.5 and 1 year after gap creation (Table 9.1) Only the 3200m^2 gap had significantly higher concentrations compared to the forest during the largest peak in nutrient loss. Increased concentrations of Mg in the 200m^2 indicate that some nutrient loss also occurred in this smaller gap. Compared to forest levels, increased acidification and leaching of NO_3, K, Ca, Al, Mn (not shown) and Mg occurred in gaps of 570m^2 and larger around April 1997, approximately 10 months after gap creation. Increased concentrations of Mg were found in all gaps, while NH_4 and SO_4 (not shown) had increased concentrations in the first months after gap creation. Concentrations of Fe (not shown), Si (not shown) and Cl in leachate water in gaps were not different from forest concentrations and Na only had increased concentrations in the 3200m^2 gaps.

Concentrations in solute transport increased up to 8 times the concentrations as found in undisturbed forest. The highest concentrations at 120cm depth were found in the 3200m^2 gap for nitrate (80 mg.l^{-1}). The highest electrical conductivity of 180 □S.cm^{-1} was also found around May 1997 in the largest gap and likewise, the lowest pH of 3.8 was also measured around that time in that gap, but not enough samples were measured to exclude an increase of pH and EC in the other gap sizes.

Fourteen months after logging in the 410m^2 gap (created July 1998), concentrations of Al, Mg and NO_3 in leachate water, as well as the electric conductivity and the pH were still higher than in the forest (Table 9.1). In the first four months after logging, the concentrations of Ca, K, Cl, Mn, Na, SO_4 and NH_4 in the leachate water in this 410m^2 gap increased after which the concentration decreased and returned to forest levels after 14 months. The high EC and low pH after 14 months can be explained by the high concentrations of nitrate in the soil water, since concentrations of NO_3 were 10 to 20 times higher than any other element. Apparently, the patterns of leaching that were found in the 800m^2 and larger gaps were also present in the 400m^2 gap.

Table 9.1 Mean electrical conductivity (EC, μS.s^{-1}), acidity (pH units) and chemical concentrations (mg.l^{-1}) in forest and different sized gaps, 0.5 – 1 year after logging (Jan.-Jun. 1997). Letters behind a column indicate significant differences between forest and gaps (Scheffé test, $p<0.05$).

	#	EC	pH	Al	Ca	K		Mg	Na	Si	SO_4	Cl	NH_4	NO_3
forest	20	82.5	9.8	0.2[a]	1.1[a]	0.9	a	0.6[a]	4.0	4.7	1.4	2.8	0.1	12.6[a]
200m^2	12	90.6	5.0	0.1	0.5	0.9		0.8	5.1	4.2	1.0	11.1	8.4	19.1
400m^2	3	73.0	4.2	3.0[b]	0.4[b]	0.4		0.9	0.8	3.2	0.4	1.4	0.1	27.6
800m^2	23	90.1	4.8	0.4	1.9	0.8		0.9	2.8	4.1	0.5	5.5	4.5	22.5
3200m^2	7	112.2	4.5	3.1[b]	2.2[b]	2.4	a	3.5[b]	7.2	5.5	0.3	2.3	0.1	73.4[b]

Note that at 0.5–1year after logging of the PGE gaps, no samples were taken as yet in the 100 and 1600m^2 gaps and that the samples of the 400m^2 gap were taken from a gap that was felled later than the other gaps, so the 0.5–1year sampling period of this gap was from Jan.–Jun. 1998.

Hydrochemical budgets and gap size

The largest flush of chemicals occurred in the first year after gap creation as a result of higher concentrations in solute transport (Figure 9.1) and more percolation water (Table 9.2). The timing of this increase in leaching was different per chemical. The largest flush of Ca, K, Cl and NH_4 was between 0 and 0.5 year after gap creation, while Al, Mg, Na and NO_3 had their peak around 0.5 – 1 year after gap creation. All gaps had increased leaching compared to the forest up to 2 years after gap creation, after which the nutrient loss had attained the level of the forest again. This pattern was not observed in the solute content of the soil water at 120cm depth (Figure 9.1), but which was a result of a larger total percolation loss.

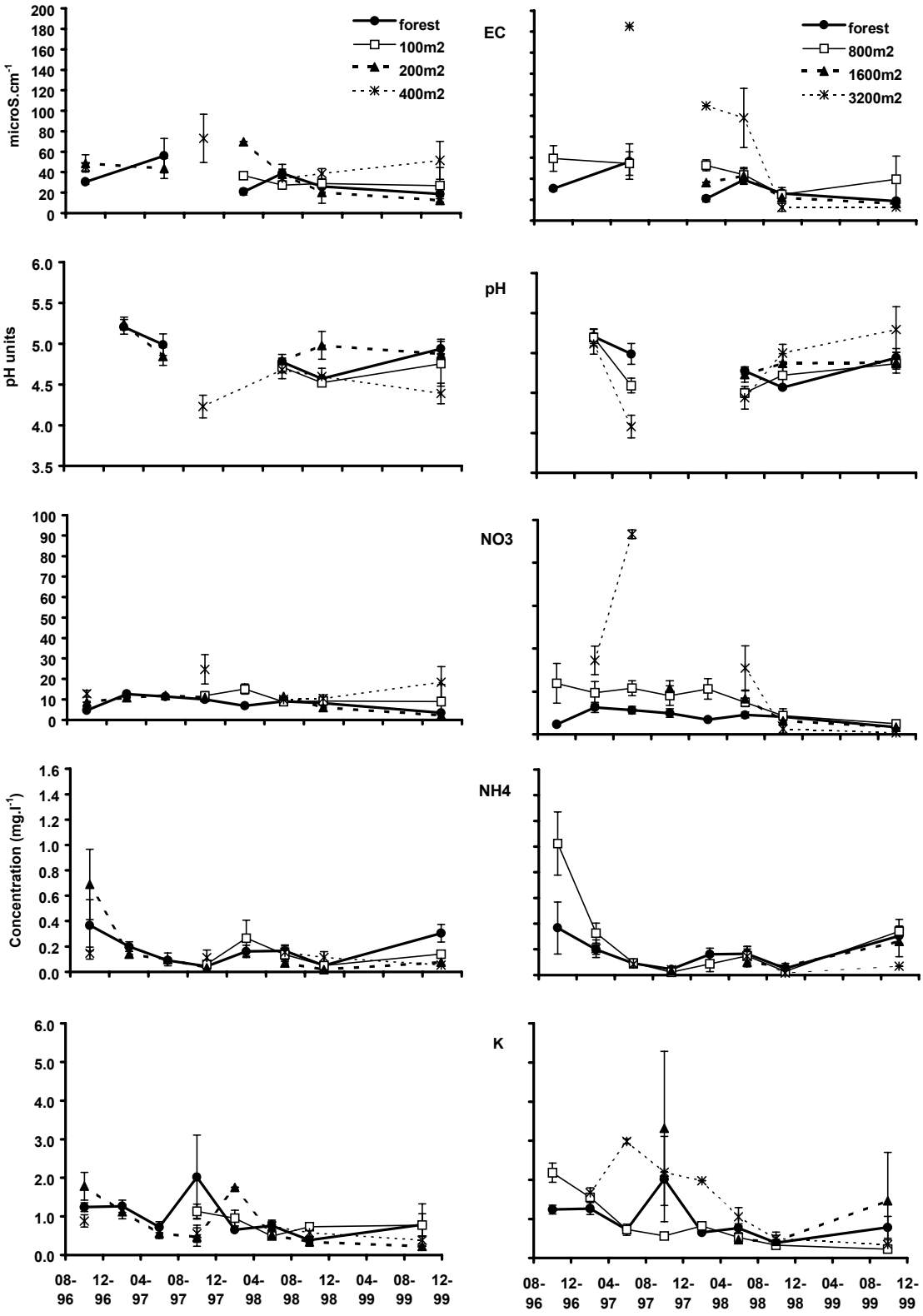
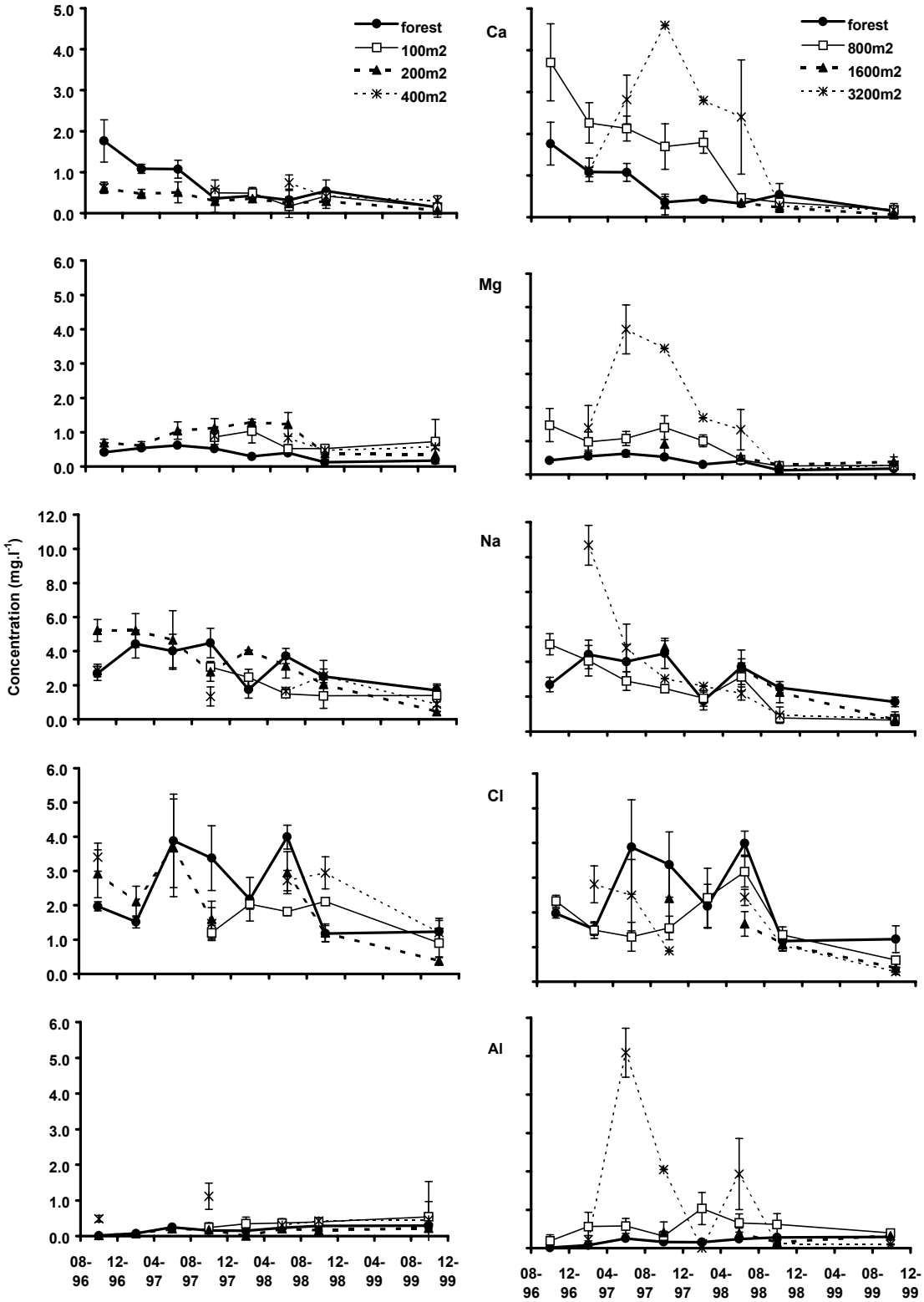


Figure 9.1 Course of 4-monthly-average electric conductivity EC (µS.cm^{-1}), pH (pH units) and concentrations (mg.l^{-1}) of NO_3, NH_4, K – next page – Ca, Mg, Na, Cl and Al in percolation water at 120 cm depth in the Pibiri Gap Experiment 50, 210, 400, 570, 1280 and 3200m^2 gaps and forest from August 1996 to August 1999 (0-3 yr after gap creation). Note that the scale of concentrations is equal per element, but not between elements.



Continuation of Figure 9.1.

Table 9.2 Total leaching of chemical elements below 120 cm in the Pibiri Gap Experiment gaps and forest at different periods after gap creation. Nutrient quantities ($kg.ha^{-1}$) were calculated by multiplying the measured concentration of a sample with the preceding percolation flux (Perc mm) until the previous sample, as calculated with FORGAP. Calculation periods: July'96 – Dec '96 (0-0.5 yr), Jan'97 – June'97 (0.5-1 yr), July'97 – Dec'97 (1-1.5 yr), Jan'98 – June'98 (1.5-2 yr) and July'98 – Dec'98 (2-2.5 yr).

Gap	Year	Perc	Al	Ca	K	Mg	Na	Cl	NH_4	NO_3	N tot
100m²	**1-1.5**	665	2.3	2.6	6.9	6.9	18.7	10.0	0.8	93.9	21.9
	1.5-2	1220	4.0	1.9	4.6	5.4	14.6	17.6	1.1	86.9	20.4
	2-2.5	574	1.9	1.4	2.7	1.9	5.0	9.0	0.1	31.2	7.1
200m²	**0-0.5**	646	0.3	2.6	4.9	3.1	20.5	9.2	1.0	44.3	6.3
	0.5-1	1107	1.2	5.2	7.2	10.5	53.3	36.9	1.1	146.1	33.8
	1-1.5	523	0.4	0.8	3.1	6.8	19.3	13.3	0.3	74.2	17.0
	1.5-2	1157	2.6	2.2	5.8	13.2	35.7	33.2	0.8	123.8	28.6
	2-2.5	545	1.1	1.8	2.4	2.7	14.4	8.7	0.2	40.8	9.3
400m²	**0-0.5** [1]	688	3.2	4.3	6.5	3.9	16.9	21.1	1.1	84.2	19.9
	1.5-2	1282	3.1	9.7	5.8	13.2	17.6	32.7	1.5	108.3	25.6
	2-2.5	660	1.4	1.3	1.7	2.2	6.2	6.0	0.1	28.3	6.5
800m²	**0-0.5**	605	2.9	22.2	15.3	9.7	31.6	12.1	6.7	153.9	35.1
	0.5-1	1167	6.4	20.4	8.9	10.0	29.9	17.9	1.9	227.9	53.0
	1-1.5	666	2.4	8.8	4.2	7.5	19.8	16.2	0.2	133.6	30.4
	1.5-2	1276	10.0	6.0	6.8	5.3	36.4	37.3	1.2	187.8	43.4
	2-2.5	657	4.1	2.1	2.5	1.7	8.2	9.2	0.4	65.0	15.0
1600m²	**1-1.5**	609	0.8	1.7	13.5	4.5	25.9	8.0	0.1	136.4	30.9
	1.5-2	1238	3.4	3.2	4.4	4.4	32.4	17.8	1.2	141.3	32.9
	2-2.5	611	1.0	1.4	2.1	1.0	13.0	5.7	0.3	41.1	9.5
3200m²	**0-0.5**	499	1.4	5.1	10.4	3.0	62.0	20.2	1.7	146.0	34.2
	0.5-1	1105	43.1	36.1	31.3	50.5	76.0	38.7	0.8	990.1	224.2
	1-1.5	593	7.6	21.7	11.4	16.5	15.9	6.2	0.2	413.0	93.4
	1.5-2	1221	19.2	9.7	8.7	7.2	20.7	28.7	1.3	299.2	68.6
	2-2.5	583	1.6	5.2	3.7	2.5	6.6	6.3	0.1	20.9	4.8
Forest	**0-0.5: 96-2**	356	0.1	5.7	6.1	1.7	21.2	8.5	0.8	34.2	1.2
	0.5-1: 97-1	681	1.4	7.4	5.2	4.6	23.9	23.3	0.5	85.3	19.6
	1-1.5: 97-2	339	0.4	0.7	4.2	1.6	14.9	13.2	0.5	38.4	9.0
	1.5-2: 98-1	1007	2.8	2.8	5.9	3.4	31.1	35.7	1.4	72.8	17.5
	2-2.5: 98-2	403	1.4	1.1	1.7	0.9	8.6	10.0	0.4	20.4	4.9
	Avg ½ yr⁻¹	557	1.2	3.5	4.6	2.4	19.9	18.1	0.7	50.2	10.5

Note 1: Based on measurements of chemical composition of leachate water and calculations of percolation with FORGAP in gap 26 ($410m^2$) from July – December 1998.

Note 2: The difference between half-year percolation amount is explained by the amount of rainfall: 96-2 (0-0.5) 987mm, 97-1 (0.5-1) 1525mm, 97-2 (1-1.5) 885mm and 98-1 (1.5-2) 1541mm and 98-2 (2-2.5) 908mm.

Long-term records of leaching in gaps

The 7-year-monitoring of leaching in the FRMH gaps provided an excellent insight into long-term nutrient loss in a medium 740m^2 and large 3440m^2 logging gap (Figure 9.2). The highest concentrations in percolation water at 120cm depth were sampled between 0.5 and 1.5 year after logging in both gaps. The lowest pH values were also found during this period. Concentrations of Al, Ca, Mg, SO_4 and NO_3 were still higher in the large gap at 2.5 year after logging, but had returned to forest levels in the medium gap. Although the effects of logging on leaching clearly had diminished after 7 years, higher concentrations in the large gap compared to the forest were still found for Al, Mg and NO_3. At the end of the '978/'98 El Niño event, a large amount of litter had build-up due to increased litterfall (Chapter 6) and reduced decomposition (Chapter 7). When rainfall was restored in April 1998, an increase in solute transport was found for Al, Mg, Mn, Na, SO_4 NH_4 and NO_3, as can be seen by the peak around April '98 in Figure 9.2. There is no clear explanation for the sudden increase in NH_4 in August 1999, except that NH_4 concentrations were very variable in the past as well.

A difference in leaching between gaps of different size was not found between the 13-year-old 2K gaps, where the concentrations of all chemical elements except NO_3 were not different between gaps and forest (Figure 9.3). This can be partly explained by the fact that, compared to the FRMH gaps, the smallest 2K gap was much smaller and FRMH gaps and the large 2K gap was of similar size as the small FRMH gap. The higher concentrations of NO_3 in the 200m^2 2K gap were found on only 2 consecutive dates and in the same CCS, which could indicate some form of contamination of the CCS. The average concentration of the samples of leachate water in the 200m^2 without these two outliers was 3.17 $mg.l^{-1}$ (σ 2.2, N 7) and the pH in the small gap without these two samples was 4.99 (σ 0.14, N 7). These concentrations of chemicals in these 13-year-old gaps confirmed the results of the 7-year-old gaps that leaching had returned to forest levels in 800m^2 and smaller gaps.

Similar to the PGE gaps, the major loss of nutrients in the FRMH gaps occurred in the first year after gap creation and gap size did not influence the duration of the main peak of nutrient loss, except for aluminium, magnesium and nitrate. Six years after the creation of the FRMH gaps, the 3440m^2 gap had a more than 3 time larger Al, Mg and NO_3 flux than the background level of the undisturbed forest (3200m^2 gap in Table 9.3). This implicates that during those six years, the regenerating vegetation in the gap had to be able to cope with increased levels of mobile Al. The FRMH 740m^2 gap also had a 1.7 times larger aluminium flux than the forest (800m^2 gap in Table 9.3), but these conditions were not present in the 2K 800m^2 gap. The flush of nutrients was not only the result of a large amount of percolating water below 120cm in the gaps compared to the forest, since the lowest percolation flux in the FRMH large gap was calculated in 1998, when there were still high concentrations in soil water.

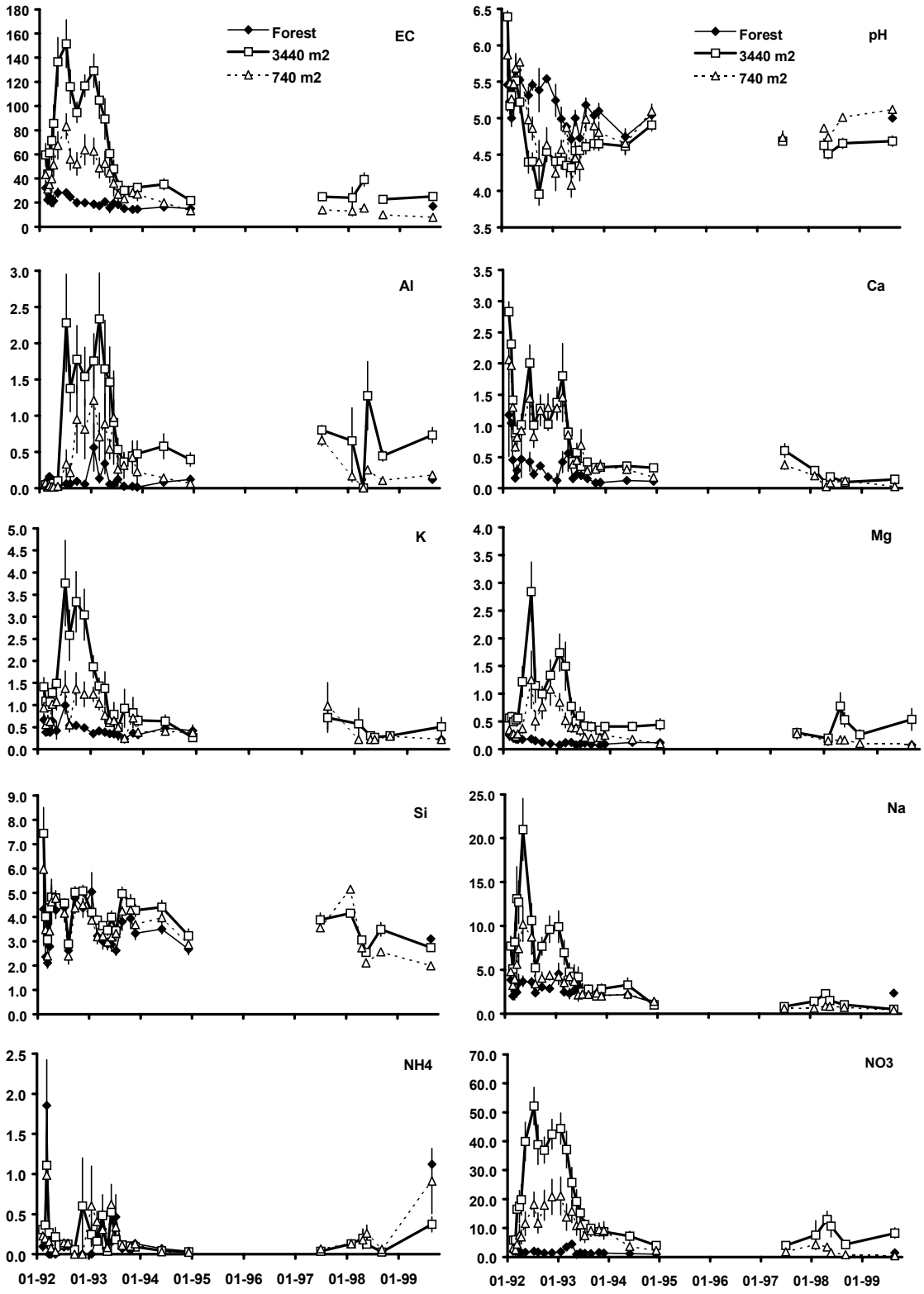


Figure 9.2 Course of the electric conductivity (EC in $\mu S.cm^{-1}$), acidity (in pH units) and concentrations (in $mg.l^{-1}$) of Al, Ca, K, Mg, Na, Si, NH_4 and NO_3 in the Forest Reserve Mabura Hill gaps and forest from February 1992 to August 1999. The error bars indicate 1 standard error, N forest = 4, N small gap = 8 and N large gap = 13 (Note: '92-'94 data from Brouwer and Riezebos 1998).

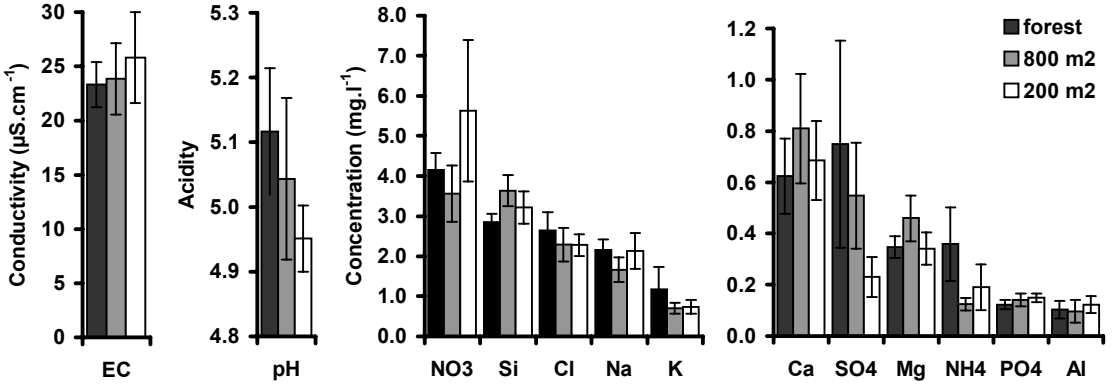


Figure 9.3 Average values (+/- 1 standard error) of EC (in µS), pH (in pH units) and concentrations of NO3, Si, Cl, Na, K, Ca, SO4, Mg, NH4, PO4 and Al (in $mg.l^{-1}$) in soil water at 120 cm depth in the 2K gaps and forest from August 1998 to August 1999.

Table 9.3 Leaching of chemical elements below 120cm in forest and gaps of different size and age (yr) of the Pibiri Gap Experiment (PGE), Forest Reserve Mabura Hill (FRMH) and 2K. Chemical quantities ($kg.ha^{-1}$) were calculated by multiplying the measured concentration of a sample with the preceding percolation flux (Perc in mm) until the previous sample. Percolation was calculated with FORGAP.

Gap	Site	Age (year)	Perc	Al	Ca	K	Mg	Na	Cl	NH_4	NO_3	N-tot
200m²	**PGE**	**1 ('97)**	1753	1.5	7.7	12.2	13.6	73.7	46.1	2.1	190.4	44.6
	PGE	**2 ('98)**	1680	3.0	2.9	8.8	20.0	55.0	46.5	1.1	198.0	45.6
	2K	**13 ('98)**	1492	1.1	14.9	12.2	4.9	36.1	26.2	4.4	98.1	25.6
800m²	**PGE**	**1 ('97)**	1773	9.3	42.6	24.2	19.7	61.5	30.0	8.6	381.7	92.9
	PGE	**2 ('98)**	1942	12.4	14.8	11.0	12.8	56.2	53.5	1.5	321.4	73.7
	FRMH	**7 ('98)**	1513	2.0	1.5	4.0	2.0	11.8	23.9	2.0	20.1	6.1
	2K	**13 ('98)**	1498	0.4	18.2	10.1	6.9	22.7	26.3	3.8	50.4	14.3
3200m²	**PGE**	**1 ('97)**	1604	44.4	41.2	41.8	53.5	138.0	58.9	2.5	1136.1	258.5
	PGE	**2 ('98)**	1814	26.7	31.4	20.1	23.7	36.6	34.9	1.5	712.3	162.0
	FRMH	**7 ('98)**	1429	5.6	1.5	4.3	7.5	0.1	28.8	1.6	120.0	28.3
Forest	**PGE**	**avg 97/98**	1192	2.3	8.3	10.7	5.6	45.5	40.3	1.6	115.3	27.3
	2K	**1998**	1302	0.5	13.7	27.8	5.4	36.5	43.0	2.5	61.8	15.9
	FRMH	**1998**	1175	1.3	3.8	5.2	1.6	0.1	23.9	2.6	20.2	6.6

DISCUSSION

Increasing nutrient loss with increasing gap size

Our study of nutrient loss in percolating water below the root zone suggests that:

1) The solute transport of chemicals below the root zone was increased compared to the forest in the 400, 800 and 3200m² gaps. No increase was found in the 1600m² gap, but this is mainly due to the absence of samples during the main nutrient flush in percolating water, 10 months after gap creation. An increase in leaching compared to undisturbed forest could not be detected in gaps smaller than 400m², although concentrations of NH_4, Na, SO_4 and Mg in

percolation water at 120 cm depth were slightly higher in the 200m^2 gap compared to the forest.

We suggest that the increase in leaching in gaps was a result of a lack of uptake of the diminished vegetation in the gaps. The immediate drop in nutrient uptake by the vegetation in the gaps was best seen at the major flush of NH_4 that occurred immediately after gap creation in gaps over 200m^2. The fate of cation leaching as a result of N release from organic debris and a lowering of the pH was observed in the gaps larger than 400m^2 in the first year after logging. The reduced uptake caused an increase in NO_3 concentrations, which increased the acidity and in turn caused an increase in leaching of K, Ca, Na, Al and Mg, with the peak of leaching around 10 months after gap creation. Such findings have been reported in literature, where at plot level, leaching did not increase in gaps smaller than 200m^2 (Parker 1985, Uhl *et al.* 1988), but larger gaps showed an increase in nutrient loss through leaching (Brouwer and Riezebos 1998).

The results of leaching patterns in gaps were based upon a somewhat incomplete data set for all gaps. In the first two years after logging, data collection of the CCS' was not optimal due to 1) incorrect contact between CCS and soil of some of the CCS' that prohibited an optimal sampling, 2) a change in the set-up in the experimental gaps in July 1997, which made it necessary to reinstall a number of the CCS' at different locations, 3) continuous malfunctioning of the pH and EC meters and 4) the dry weather conditions during the El Niño event (July 1997 to March 1998), which prevented the extraction of soil moisture on numerous occasions (the effects of El Niño are discussed below in more detail). Consequently, the patterns of leaching as displayed in Figure 9.1 and Table 9.2 are probably an underestimation of the actual amount of nutrient loss and increased concentrations of other chemical elements. This is especially the case in the larger gaps (1600 & 3200m^2), where almost no data was collected in the first year after logging.

2) The discriminating factor between gaps of different sizes was the concentration of a chemical in leachate water, since the amount of percolating water did not differ much between gaps of different size. Differences between gaps and forest were a combination of higher concentrations and more percolating water in gaps than in forest.

Although total nutrient loss is a combination of an increase in percolation and an increase in concentrations of chemicals in percolating water, nutrient concentrations were more important than total percolating water in gaps larger than 400m^2. However, the total percolation in gaps smaller than 400m^2 was larger than the forest and consequently, total nutrient loss was also larger in these small gaps, while nutrient concentrations in these small gaps were not different from forest. These conclusions were based upon percolation calculations with FORGAP. Root growth into the gap from the vegetation surrounding the gap is not included in the model, but this could act as an important nutrient conservation mechanism. Possibly, the nutrient losses of the smallest gaps in Table 9.2 are overestimated.

3) Gap size affected the magnitude of leaching, but not the duration of the peak in solute transport, since this duration was approximately 2 years in all gaps larger than 400m^2. However, after 2 years, leaching in gaps larger than 800m^2 remained at a higher level than the forest.

The concentrations of most chemicals in leachate water increased after logging and continued to be higher than the forest until 2 years after gap creation, when no distinctions between forest and gaps could be found. After the initial flush of solutes during these 2 years, gaps larger than 800m^2 maintained an increased leaching compared to the forest. Two years after logging, the

uptake of the vegetation in large gaps was still small, while in smaller gaps, root ingrowth from the vegetation that surrounds the gap had started to decrease leaching.

4) The dry weather conditions during the '97/'98 El Niño event and the resulting build-up of the litter layer caused a peak in leaching when rainfall was restored.

Around April 1998, an increase in leaching was found, which was the result of the build-up and sudden release of chemicals in the first month after the '97/'98 El Niño event, when decomposition increased and a large amount of water percolated to deeper layers due to more than 500mm rain in one month. Apparently, an increase in leaching was not only affected by gaps but also by climatic anomalies like an El Niño event. This indicated that the amount of litter on the soil and the decomposition and mineralisation rates of the litter layer were likewise important in affecting nutrient leaching as gap size. It can be argued that the sampling problems during the dry weather conditions, as explained above, also indicated that most likely there was no water transport and therefore no leaching. In addition, certain tropical tree species have been known to withstand dry soil moisture conditions for prolonged periods (ter Steege 1993) or have very deep roots, which most likely indicated that these plants were capable of extracting soil water, including nutrients, at very high soil moisture tensions. This would also result in a decrease in the amount of nutrient loss.

Effect of gap age on nutrient loss

In a 3440m^2 gap, nutrient loss through leaching could still be found, 7-and-a-half years after logging. These results indicate that – in a very large gap like the 3440m^2 – edaphic conditions were created, in which nutrient loss and low pH associated with high concentrations of soluble Al persisted for a prolonged period of time. These conditions may seriously hamper forest regeneration and influence the future species composition of the forest, which were clearly less severe in the medium sized 740m^2 gap than in the 3440m^2 gap. A conclusion that is indirectly supported by the leaching in the 13-year-old gaps at 2K, where no differences were present anymore between an 800 or 200m^2 gap and the forest.

Another possible explanation for the larger amount of nutrient loss in the 7-year-old 3440m^2 gap compared to the forest is related to natural competition of regenerating plants in this gap. It was observed that a lot of the young, approximately 4-5 m tall, saplings in this gap were dying or had died recently, maybe as a result of the El Niño event. Stem density in this gap was large and most of these young plants were pioneer species like *Goupia glabra*. Possibly, the competition for light and nutrients caused this increased dieback of plants. In turn, this caused an increase in litterfall (Chapter 6) and a relatively thick litter layers were present, which increased mineralisation rates (Chapter 8). Finally, the larger nutrient availability and reduced uptake caused an increase in leaching. Whether this is an increase in leaching or whether the amount of leaching had been continuously larger than the forest during those 7 years is unknown.

The results of leaching of most elements in the 800 and 3200m^2 PGE gaps were in line with the results of the 740 and 3440m^2 FRMH gaps, both in timing of the peak in leaching as in duration of the leaching peak. The magnitude of the peak of the concentrations in leachate water, EC and pH were slightly higher in the PGE gaps than in the skidder zone of the FRMH gaps (Brouwer and Riezebos 1998). Differences between the PGE gaps and FRMH gaps are either related to soil conditions and species composition of the forest or are related to the post-logging actions in the gaps. After felling, the logs in the FRMH gaps were pulled-out by a skidder. This created three basic zones in the gaps: a skidder zone where the skidder has been, a crown zone where the crowns of the felled trees are positioned and the remaining undisturbed zone where the remaining vegetation is still present (Brouwer 1996). Skidder activities were prohibited in the

PGE gaps and all logs, tree crowns and the remaining vegetation were either removed by hand or were winched out. Therefore, the main differences between the FRMH gaps and the PGE gaps were a more evenly distributed litter layer in the PGE gaps, no remaining trees in the PGE gaps and consequently more dead roots in the PGE gaps. Especially the damage to the vegetation and consequently reduced uptake can serious influence nutrient loss for prolonged period of time.

Increased leaching in gaps: roots

After gap creation, several processes contributed simultaneously to the increase in leaching. Selective logging not only created a gap in the canopy, but also a root gap. The loss of root biomass in canopy gaps may reduce water and nutrient uptake by plants, leading to increased leaching (Ostertag 1998). The effects of a canopy and root gap can be summarized as follows:

Firstly, the amount of organic debris in the gaps increased as a result of logging. The trees that were killed left behind large amounts of leaves and branches, but also large amounts of dead roots. Denslow *et al.* (1998) argued that gap size effects are due primarily to greater litter densities in gaps. In India, Chandrashekara and Ramakrishnan (1994) reported higher soil nutrients of N, P and Mg in 1-year-old selectively logged gaps due to release from litter and wood in the gap itself and the sparse vegetation in the gap. It can be assumed that in large gaps, more trees were killed and consequently a larger amount of dead organic matter, either above or below ground, was produced. During the first year after logging, the pile of leaves from the crowns of the felled trees and the dead roots in the soil were decomposed and nutrients were released.

Secondly, the removal of the vegetation decreased the demand for water for transpiration, which increased the soil moisture content and thereby increased the percolation flux (Brouwer and Riezebos 1998, Jetten 1994a, Parker 1985, Vitousek and Denslow 1986; but see Chapter 5). The effects of a reduced transpiration were likely to be smaller in small gaps (< 100m^2), where only one or two trees were felled. In these small gaps, Parker (1985) hypothesized that many living roots of the forest around the gap are present that extract water from the gap and thereby decrease the percolation flux. However, differences in soil moisture content between undisturbed forest and gaps have been reported to be far larger than between gaps of different size (Denslow *et al.* 1998). Silver and Vogt (1993) also stressed the important role that ingrowing roots from undisturbed areas into the disturbed area might play in preventing high leaching losses.

Thirdly, there was a reduced uptake of nutrients from the soil solution due to a decrease in demand by the vegetation in the gap. The regenerating vegetation in the gap, which was still small in the first 2 years after logging, needed fewer nutrients than the original forest and consequently, fewer nutrients were extracted from the soil solution. In addition, a close relationship exists between light capture of these young plants and root foraging (Huante *et al.* 1998). Nutrient extraction by the vegetation in the gaps will be restored, when the accumulation of biomass in the gap proceeds, both above and below ground.

Decomposition, mineralisation, leaching and again roots

Between gaps of different size, no differences were found in leaf litter decomposition (Chapter 7) and mineralisation rates (Chapter 8). As a result, there were no differences between gaps of different size in the nutrient release rate from the litter layer. Differences in leaching in gaps of different size must therefore be caused by 1) the total nutrient release from the total amount of organic debris, both above-ground and below-ground, and 2) a reduced extraction of nutrients by the roots of the forest that surrounds the gap and the remaining vegetation in the gap. The

importance of roots, or better the lack of roots, from the surrounding forest in gaps was also stressed by Parker (1985), who suggested that the reduced extraction of nutrients becomes most pronounced in gaps larger that 500m^2. After gap creation, the vegetation that surrounded the gap most likely had an increased root growth into the gap. There was less competition in the gap and there was an increase in water and nutrient availability, due to a reduced extraction of water and nutrients by the remaining vegetation in the gap. Although roots are known to extend over vast distances, it is likely that the density of the roots in the gap, which originate from the trees surrounding the gap, decreased with increasing distance from the gap edge. Therefore, nutrient extraction by the forest also decreased with increasing distance from the gap edge and consequently leaching increased.

The data of solute transport at 120 cm in the PGE gaps provided some evidence of the hypothesis given above. For example at 0.5 year after gap creation, the highest concentrations of NO_3 and Na were found in the centre of the largest gaps (Figure 9.4). Three years after logging, this gap-centre − gap-edge gradient had disappeared. Somewhat similar but less distinct patterns as displayed in Figure 9.4 were also found for Al, Ca and Mg.

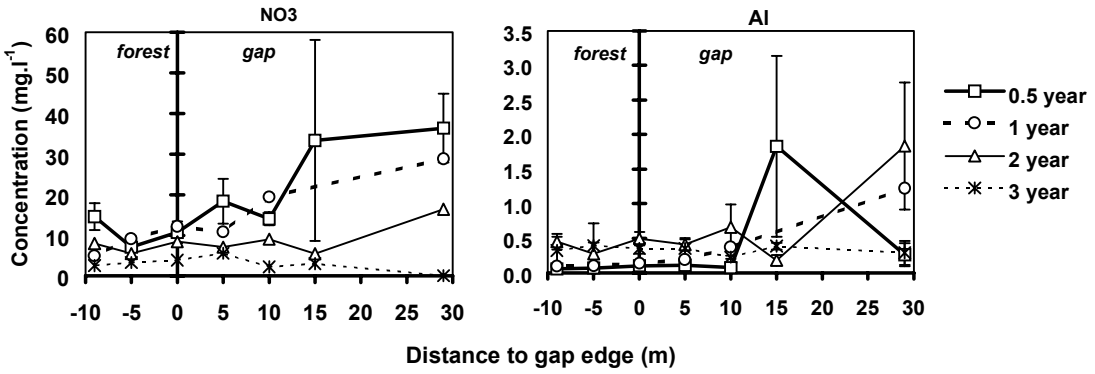


Figure 9.4 Concentrations of NO_3 and Al (+/- 1 standard error) in percolation water at 120 cm depth of all Pibiri Gap Experiment gaps (range 40 to 3200m^2) at 0.5, 1, 2 and 3 years after logging in relation to the distance to the gap edge. (Note: distance of a CCS to the gap edge are grouped, e.g. 10–15m=15m, -5–0m=0m)

The regeneration of the root system will be in line with the regeneration of the above ground biomass, whereby the largest growth rate will occur in the largest gap. After 2.7 years, the average height of the experimental seedlings in the 50 and 3200m^2 gap was 0.8 and 3.2m, respectively (Rose 2000). Consequently, the water and nutrient demand of the regenerating vegetation in the gaps will be larger in largest gaps within a few years. Nutrient loss after logging will increase until either the source of the nutrients − the litter layer and the dead below ground biomass − is depleted or the root mat in the gap is restored.

CONCLUSIONS

Since decomposition and mineralisation rates seem to be relatively unaffected by gap size, although they were lower than the forest, we hypothesize diminished presence of roots is the main reason for nutrient losses in gaps of different size, either by a reduction in nutrient uptake or by a large amount of dead roots that are a potential source of nutrients after decomposition. The density of living roots from the surrounding forest decreases with increasing distance from the gap edge. This results in an increase in leaching with increasing gap size or with increasing distance from the gap edge.

Furthermore, we hypothesize that leaching in gaps can also be increase after a few years due to the natural dieback of the regenerating vegetation in a gap as a result of competition for light and nutrients. The death of these young plants increases the amount of organic debris, but decreases the amount of uptake, thus increases leaching. This is especially the case in large gaps (> 3000m^2), where a strong competition between, predominantly, pioneer species can be found. Since large amounts of leaching and acidification in these large gaps was also found during the first two years after logging, large gaps must be avoided in logging operations.

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Laboratory at the Pibiri Field Station

Appendix 9.1 The effect of vacuum on the water chemistry

Several authors have reported on the effect of tension lysimeters and the chemical composition of the sampled water. Nortcliff and Thornes (1989) stated that the suction that is applied influences the type of pores (pore size) that are emptied and, consequently, the chemical composition of the water. Similar results were obtained in an experiment with tension and zero-tension lysimeters, where the zero-tension lysimeter collected higher concentration of NH_4, K, NO_3, Cl and SO_4 (Haines *et al* 1982). On the other hand, Grossman and Udluft (1991) suggested that tension lysimeters extract water from all pores.

The effect of the vacuum that was applied was tested in a separate experiment. Four 60 cm long CCS's were installed within 2m from each other in the forest near the Pibiri field camp. Each CCS was put under a different tension, which changed every sampling round (N=5). The tensions that were applied were 20, 35, 50 and 65 kPa.

Ceremic cup soil water sampler

Although there was a small trend of decreasing concentrations with increasing tension, except for SO_4 (Figure 9.5), none of the chemicals was significantly different between different tensions (Mann-Whitney test, $p<0.05$, N=5). Despite the fact that there was no statistical difference between different tensions, 35 kPa was chosen as the standard tension because:
1) The average concentrations of K, NO_3, Na and Si were higher at 20 and 35 kPa suction than at 50 or 60 kPa. Since the CCS's were used in a study to determine the amount of leaching, the best estimates would be obtained with the highest concentrations.
2) The number of samples that were taken at 20 kPa tension was considerably smaller that at higher suctions. Apparently, a suction of 20 kPa was sometimes not enough to extract any soil water at all.
3) A tension of 35 kPa or pF 2.5 corresponded best with the overall soil matrix suction at 120 cm depth, which was around field capacity or pF 2.

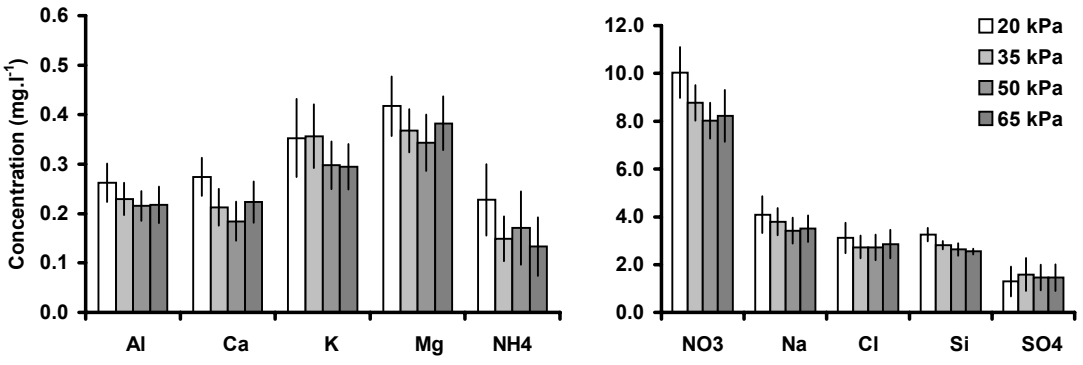

Figure 9.5 Effect of tension in ceramic cup sampler on concentrations in soil water of various chemicals.

Morning light in mixed Greenheart forest

10 SYNTHESIS

THE EFFECTS OF SELECTIVE LOGGING ON MICROCLIMATE, WATER DYNAMICS AND NUTRIENT CYCLING; NOT ONLY A GAP SIZE AFFAIR

NOT ONLY TREES DEFINE A FOREST [1]

This thesis is about gaps; about canopy gaps in the tropical rain forest of Guyana which are created by selective harvesting of trees, and about gaps in our knowledge on how these canopy gaps affect microclimatic and edaphic conditions. Canopy gaps are a natural feature of the forest and important for the regeneration of plant species (Bongers and Popma 1988, Brokaw and Schneider 1989, Whitmore 1989). As such, trees *and* gaps define the forest. However, large parts of the forests in Guyana are logged selectively and as a result, logging gaps are created. The commercial tree species that are felled often have heavy seeds, which have a small dispersal radius so that a clumped distribution of these species is common (ter Steege 1990). Exploitation of these species ultimately results in areas of variable sizes being opened up.

The size of the gap is of particular importance, since research has shown that trees partition gaps of different sizes (Brown and Whitmore 1992, Denslow 1980), caused by differences in microclimatic conditions, soil water availability and nutrient limitations. Extensive knowledge of these abiotic variables is needed to assess the effects of gaps on the regeneration of the forest in general and for tropical rain forest management of commercial tree species in specific. This information is needed to devise a forest management system that is economically beneficial and ecologically sustainable (Chapter 1).

Before reaching the final conclusions of this thesis, let me explain where this study was located and which climatic perturbations occurred in central Guyana during the research period from 1996 to 1999.

Study sites

The study presented in this thesis was carried out in three study areas, which were located near the township of Mabura Hill, approximately 250 km south of the capital of Guyana, Georgetown. In 1996, 25 gaps were created in undisturbed mixed Greenheart forest for the Pibiri Gap Experiment (PGE). Gap size ranged from 40m^2 to 3200m^2 (van Dam *et al.* 1999). A second study area was located in the Forest Reserve Mabura Hill (FRMH), and research activities took place in two 7-year-old experimental gaps of 740 and 3440m^2. A third study area called 2K contained two 13-year-old 200 and 800m^2 gaps (Chapter 2).

[1] "A forest is defined by the presence of trees, which does not imply that only trees define a forest" (proposition of R. Ek, 1997).

Climate and the '97/'98 El Niño event
Guyana has a tropical wet climate, with rainfall throughout the year and no months having less than 60mm. However, from July 1997 to March 1998, the research area was under the influence of a severe drought due to an El Niño event. During the '97/'98 El Niño event, rainfall was on average 27% lower than normal. This reduction in rainfall caused drought effects of the vegetation and even dying of small plants. These extreme climatic conditions provided a unique opportunity to study microclimatic conditions and moisture limitation in gaps and the impact of drought on the nutrient cycle (Chapter 2).

A SYNOPSIS ON MICROCLIMATE, WATER AND NUTRIENT CYCLING IN LOGGING GAPS OF DIFFERENT SIZE AND AGE

Microclimate in gaps: size matters [2]

Microclimatic conditions were strongly affected by gap size and shape. The effect of the gap on the microclimate was noticeable beyond the perpendicular projection of the canopy opening, up to 10m from the gap edge in the largest 3200m^2 gap. Gaps with irregular shaped edges experienced microclimatic conditions that were similar to smaller gaps, which implies that gap size alone was not always a good indicator of the potential impact of a gap on the microclimate (Chapter 3). Microclimate in gaps was regulated by the amount of solar radiation, which increases soil and air temperature and decreases air humidity. The amount of radiation increased with increasing gap size, but air temperature did not increase above a gap size of approximately 600m^2. Due to the regeneration of the vegetation in the gaps, air temperature decreased after two to three years. Soil temperature was more influenced by soil moisture content and especially by soil cover than by gap size.

In conclusion, the increasing radiation, temperature and decreasing humidity with increasing gap size increased the vapour pressure deficit and thus the amount of direct soil evaporation, which reduces the amount of soil moisture in the topsoil. A decreasing amount of soil moisture with increasing gap size can seriously limit seedling establishment and growth in large gaps.

Bridging the gap: soil moisture and roots

It was expected that in gaps the water balance would change due to a reduced uptake by the vegetation and increased direct soil evaporation. Moreover, complex gap edge effects can be expected, since the vegetation at the gap edge receives more solar radiation than the surrounding forest. In general, soil moisture conditions in gaps will be wetter than in the forest which would result in a gradient of wetter soils with increasing gap size (Chapter 3). However, differences between soil moisture content in gap centres, gap edges and forest plots were small. No differences were found between different gap sizes. In gaps, soil moisture was affected by a complex interaction of soil evaporation, transpiration, soil hydrological properties, water uptake by the vegetation at the gap edge and rainfall patterns. The soil moisture distribution in gaps and forest was affected by the presence of roots; either living roots that extract water or dead roots due to logging. Trees that were killed aboveground also created a root-gap belowground.

I suspect that the roots of the regenerating vegetation in a gap and the roots of the trees at the gap edge that try to bridge the gap strongly affected soil moisture conditions. Although the amount of roots from the gap edge will be small in the centre of very large gaps, this is

[2] PhD thesis by S. Rose 2000: "Seeds, seedlings and gaps – size matters."

compensated for by a larger amount of roots of the regenerating vegetation. Gap size becomes irrelevant for the amount of water consumption in gaps, two years after logging.

Modelling microclimate and water dynamics: bold but beautiful [3]

A study of the spatial and temporal patterns of microclimatic conditions, evapotranspiration and soil water dynamics was carried out with the *FORest GAP* model FORGAP (Chapter 4). A selection of the PGE gaps was made, ranging in size from 60 to 3200m^2, for which the radiation and the water balance were calculated. The model was also used to calculate the effect of elongated or circular gaps, gap orientation to the sun and forest fragments in gaps (Chapter 5). Gradients of increasing radiation, evapotranspiration and low soil moisture conditions were found with increasing gap size. The gap edge had drier soil moisture conditions than the undisturbed forest. Along an irregular shaped gap edge, microclimatic and soil moisture conditions can occur that are associated with small gaps and these areas can decrease the total effective gap area substantially. Round gaps clearly had higher evaporation loss and lower soil moisture contents than similar sized but elongated gaps. A similar conclusion was reached for west-east positioned gaps compared with north-south gaps, the latter being the wetter gap.

Evidently, gap shape and orientation are important parameters regulating microclimatic conditions and the water balance in gaps and surrounding areas.

Food for thought: nutrient cycling

Litterfall

The main input of nutrients in gaps is through litterfall. Reduced litter input in gaps could lead to potential nutrient stress for the regenerating vegetation in the gaps. A study into litterfall distribution and nutrient input through litterfall in gaps of different size and age was carried out (Chapter 6). Litterfall in gaps decreased sigmoidally with the distance to the gap edge, which resulted in a reduction in nutrient input of 95% in the centre of a 3200m^2 gap. The recovery of litterfall was faster in larger gaps than in small gaps, because the regeneration of the vegetation, and consequently the litter turnover, is faster in larger gaps than in small gaps.

Potential nutrient stress due to reduced litter input can occur between one and two years after gap creation, when there is still little litter turnover from the vegetation in the gap. This pattern is consistent for all gaps, since in small gaps, litter input from the edge is larger, while in large gaps the vegetation in the gap produces more litter.

Decomposition

Altered decomposition rates in gaps can create potential nutrient stress for the regenerating vegetation in the gap. Decomposition studies were carried out in different sized gaps (Chapter 7). Decomposition rates of leaves, woody plant part and flowers were not different between gaps of different sizes, but decomposition rates of these litter fractions in forest environments were faster. A single layer of leaf litter in the forest decomposed in 4.6 months. The difference in litter weight loss between gaps and forest and the lack of difference between gaps of different size were attributed to 1) the prevailing microclimatic conditions in the gap, which dried out the litter layer, thus limiting microbial attack and 2) damage to the belowground biomass and mycorrhizal infections as a result of logging, which play an important role in the decomposition process.

[3] Owing to V. Jetten (1994b) and his one-dimensional water balance model SOAP, who exclaimed that regarding modelling and TV soap series: “as soon as you think that everything is going smoothly, the next problem presents itself”, which was also confirmed by me, regrettably.

It is not likely that the reduced decomposition rates in gaps are a potential threat for the nutrient availability of the regenerating vegetation. However, minimizing the damage to the vegetation in a logging gap can minimize the effect on the decomposition process, since microclimatic and edaphic conditions are less disturbed.

Mineralisation
The effects of gaps of different size and age on N-mineralisation rates were studied to assess how mineralisation rates are influenced by gap size and for how long (Chapter 8). In gaps larger than 200m^2, mineralisation rates were not significantly different between gaps of different size, but N-mineralisation rates were four times lower in these gaps than in forest. Gaps smaller than 100m^2 had undisturbed mineralisation rates compared to the forest. N-mineralisation rates were mostly affected by soil N-content and soil moisture conditions, but different N-mineralisation rates between forest and gap were best explained by littermass, living root content, canopy openness and again soil moisture content. The recovery of N-mineralisation rates occurred in the largest gaps prior to smaller gaps due to a larger increase in biomass and thus litter production in large gaps.

It is expected that potential nutrient stress can occur in two-year-old gaps, when the vegetation is still low and the remaining litter layer is completely depleted. These conditions are most likely found in gaps larger than 200m^2.

Leaching below the root zone
Nutrient loss and acidification in gaps pose potential problems for the regeneration of the vegetation, which was studied in gaps ranging in size and age, from 40 to 3440m^2 and from 1 to 13-year-old gaps (Chapter 9). Leaching of predominantly NO_3, Al, Ca, Mg, Na, Cl and SO_4 increased with increasing gap size in gaps larger than 400m^2, although small increases in solute transport were also found in 200m^2 gaps. The increase in leaching started a few months after logging and the highest concentrations were found around ten months after logging, when also the highest acidity was recorded. A special concern is for Aluminium, which is toxic for most plants. Al concentrations increased 19-fold in a 3200m^2 gap compared to forest. Three years after logging, leaching had returned to the level of the forest, except in the 1280 and 3200m^2 gaps. In the 7-year-old 3440m^2 gap, the increased solute transport was still observed, but not in the 740m^2 gap, neither was there an increased leaching in the 13-year-old gaps. In gaps larger than 400m^2, the reduced nutrient uptake by the vegetation in the gap caused the increase in leaching, whereas in gaps smaller than 200m^2, root ingrowth from the mature forest that surrounds the gaps prohibited an increase in leaching.

I believe that in gaps smaller than 400m^2, the amount of logging damage was less than in larger gaps and more living roots from trees at the gap edge were still present, hence fewer nutrients were lost. Therefore, nutrient loss and acidification can seriously depress regeneration in gaps larger than 400m^2.

El Niño

Due to the '97/'98 El Niño event in March 1998, air temperature was 1.5°C higher and humidity 8.7% lower than in a normal year. Surprisingly, soil moisture was not completely depleted and only small seedlings and saplings died. Model simulations indicated that only the topsoil had very high pressure heads and trees with roots below 15cm could still find soil moisture. When rainfall restored after 3 weeks without rain, a delayed response of 11 days in percolation at 140cm depth was found. Due to the drought of El Niño, the large trees produced twice as much litter compared to the same period in other years and as a results a relatively thick litter layer had built up, which quickly decomposed when rainfall was restored in April 1998.

Although these climatic anomalies occur irregularly, they most certainly increase the natural dynamics of the forest ecosystem. If larger gaps are created during an El Niño year, the regeneration of the vegetation may be threatened.

A LICENCE TO FELL? [4]

A study on the forest dynamics of the undisturbed forest in the PGE research site showed that 95% of the natural tree fall gaps were smaller than 300m^2 and 55% of the gaps were between 25 and 100m^2. These are important figures, since they indicate that the natural regeneration of the forest occurs within these gap sizes. If it is the objective of a forest management system to preserve the current species composition and biodiversity, any logging operation should not disrupt these figures too much. Preferably, logging gaps should not be larger than 300m^2. By way of illustration, the mean gap size area that is opened up by conventional selective logging of one single tree is 181m^2 and by two trees 355m^2 (van der Hout 1999).

Microclimatic conditions in gaps are regulated by the amount of solar radiation, which is directly related to gap size. The study of Rose (2000) showed that with increasing gap size, pioneer species are likely to thrive better than shade-tolerant species. These latter species are usually commercially interesting trees. Modelling the amount of radiation in gaps showed that elongated gaps, gaps with irregular edges and forest fragments in gaps notably decrease the amount of radiation in gaps. A forest management that aims at providing optimal growth conditions for commercial tree species should be aware that irregular gap edges and forest fragments in logged sites can promote the growth performance of commercial tree species.

No differences in soil moisture conditions were found between gaps of different size. The regular rainfall pattern in the research area prevents the occurrence of prolonged periods of droughts, although perhaps one or two days of unfavvourable dry soil moisture conditions might occur. Most likely, sporadically occuring dry soil moisture conditions in gap up to 3200m^2 are never limiting for regeneration.

Nutrient availability can act as a discriminating factor between species performance in relation to gap size. In gaps smaller than 200m^2, no nutrients were lost due to leaching and little leaching occurred in gaps of 200 to 400m^2. In gaps larger than 400m^2, leaching, acidification and the mobilisation aluminium strongly increased with gap size. Considering these aspects of hydrochemistry, logging gaps should not exceed 400m^2.

In conclusion, my research has pointed out that in logging gaps, the disturbance of the nutrient cycle in gaps larger than 400m^2 generates edaphic conditions that are potentially limiting for all plant species. Gaps created by selective logging should preferably be smaller that this size. In combination with reduced impact logging, a forest management that only has a limited impact on the natural processes of the forest ecosystem is possible. Whether forest exploitation can be sustainable in the long run remains to be seen. A close cooperation between scientists, forest managers and policy makers may prevent a further deterioration of the tropical rain forest. Monitoring forest ecological processes remains a key issue.

[4] In continuation of "Kappen of kappen met kappen" by L. Brouwer, Natuur & Techniek 1997, nr.3.

Natural tree fall

11 SAMENVATTING

DE INVLOED VAN SELECTIEVE HOUTKAP OP HET MICROKLIMAAT, DE WATERDYNAMIEK EN DE NUTRIENTENKRINGLOOP; NIET ALEEN DE GROOTTE VAN DE KRONENDAKOPENING IS VAN BELANG

NIET ALLEEN BOMEN BEPALEN EEN BOS [1]

Dit proefschrift gaat over openingen in het kronendak van het tropisch regenwoud in Guyana die ontstaan als gevolg van het selectief kappen van bomen. Er is een gebrek aan kennis over de invloed van deze openingen in het kronendak op het microklimaat en op edafische factoren. Kronendakopeningen zijn een normaal verschijnsel in het bos en zijn belangrijk voor de regeneratie van planten (Bongers en Popma 1988, Brokaw en Schneider 1989, Whitmore 1989). Als zodanig bepalen zowel bomen *als* openingen het bos. Echter, in grote delen van Guyana wordt selectief gekapt, waardoor kapopeningen ontstaan. De commercieel interessante boomsoorten hebben vaak zware zaden met een geringe verspreiding waardoor deze soorten dicht bij elkaar in het bos voorkomen. Exploitatie van deze soorten heeft tot gevolg dat openingen van verschillende grootte worden gemaakt.

De grootte van de opening is met name van belang, omdat wordt aangenomen dat boomsoorten zich specialiseren in verschillende milieucondities die aanwezig zijn in openingen van verschillende grootte (Brown and Whitmore 1992, Denslow 1980). Deze milieucondities worden gekenmerkt door het microklimaat, de beschikbaarheid van water in de bodem en nutriëntentekort. Om het effect te beoordelen van verschillende kronendakopeningen op de regeneratie van het bos in het algemeen en van commerciële soorten in het bijzonder is diepgaande kennis van deze abiotisch parameters nodig. Deze informatie is van belang voor het opstellen van een bosbouwmanagementsysteem dat zowel economisch rendabel als ecologisch duurzaam is (hoofdstuk 1).

Voordat de eindconclusies van dit onderzoek worden toegelicht, wil ik de lezer een korte toelichting geven op het studiegebied en de klimaatsomstandigheden tijdens het onderzoek in centraal Guyana van 1996 tot 1999.

Studiegebieden
Het onderzoek werd uitgevoerd in drie studiegebieden, gelegen nabij het dorp Mabura Hill, ongeveer 250 km ten zuiden van Georgetown, de hoofdstad van Guyana. In juli 1996 werden 25 kronendakopeningen gemaakt in ongestoord gemengd Groenhartbos voor het 'Pibiri Gap Experiment' (PGE). De grootte van de openingen varieerde van 40 tot 3200m^2 (Van Dam et al. 1999). Een tweede studiegebied bevond zich in het 'Forest Reserve Mabura Hill' (FRMH). De onderzoeksactiviteiten in dit gebied vonden plaats in twee 7 jaar oude kronendakopeningen van

[1] "Een bos wordt gedefinieerd door de aanwezigheid van bomen, dat wil echter nog niet zeggen dat alleen bomen het bos definiëren" (stelling van R.Ek, 1997).

740 en 3440m^2. In een derde studiegebied, 2K genaamd, waren twee 13 jaar oude kronendakopeningen aanwezig van 200 en 800m^2 (Hoofdstuk 2).

Klimaat en het '97/'98 El Niño–fenomeen
Guyana heeft een nat tropisch klimaat met het gehele jaar door neerslag en geen maand met minder dan 60mm neerslag. Van juli 1997 tot maart 1998 kreeg het studiegebied echter te maken met extreme droogte als gevolg van het klimaatfenomeen El Niño, waardoor de neerslag gemiddeld 27% minder was dan normaal. Alle bomen en planten hadden een gebrek aan vocht en sommige jonge planten verdroogden. Deze extreme klimaatscondities verschaften een unieke gelegenheid om microklimaat en vochtlimitatie in kronendakopeningen te bestuderen, alsmede het effect van extreme droogte op de nutriëntenkringloop (Hoofdstuk 2).

EEN OVERZICHT VAN MICROKLIMAAT, WATER- EN NUTRIENTENCYCLI IN KRONENDAKOPENINGEN VAN VERSCHILLENDE GROOTTE EN LEEFDTIJD

Microklimaat in kronendakopeningen: de grootte is van belang [2]

Het microklimaat in kronendakopeningen wordt sterk beïnvloed door de grootte en de vorm van de opening. De invloed van de opening op het microklimaat was merkbaar buiten de loodrechte projectie van het gat in het kronendak. Het microklimaat werd beïnvloed tot 10m het bos in bij een opening van 3200m^2. Openingen met een onregelmatig gevormde rand hebben microklimaatcondities die vergelijkbaar zijn met kleinere openingen. Dit impliceert dat alleen de grootte van de opening niet altijd een goede indicator was voor de potentiële invloed van de opening op het microklimaat (Hoofdstuk 3). Het microklimaat in openingen werd gereguleerd door de hoeveelheid zonnestraling, waardoor de bodem- en de luchttemperatuur toenamen en de luchtvochtigheid afnam. De hoeveelheid zonnestraling bleef toenemen bij een groter wordende opening, maar de luchttemperatuur nam niet meer toe bij een openingsgrootte van 600m^2. Door de regeneratie van de vegetatie onder de opening nam de temperatuur in de opening na twee tot drie jaar af. De bodemtemperatuur werd meer beïnvloed door bodemvocht en bodembedekking dan door de grootte van de opening.

Concluderend, bij een toenemende grootte van de kronendakopening neemt de hoeveelheid straling en temperatuur toe en neemt de luchtvochtigheid af, waardoor de verzadigings-dampdruk toeneemt. Daardoor neemt de directe bodemverdamping toe en neemt de hoeveelheid vocht in de bovenste laag van de bodem af. Bij een toenemende grootte van de kronendakopening wordt, door de afnemende hoeveelheid vocht in de bovenste laag van de bodem, de vestigings- en overlevingskans van zaailingen direct na kap wordt sterk gereduceerd.

Bodemvocht, wortels en wortelgroei

Aangenomen werd dat in de opening, door een verminderde opname van water door de vegetatie en een toegenomen bodemverdamping, de waterbalans zou veranderen. Bovendien werden complexe randeffecten verwacht, omdat de vegetatie aan de rand van de opening meer straling ontvangt en daardoor meer water verbruikt dan het omliggende bos. Over het algemeen zal het bos een drogere bodem hebben dan de opening en een gradiënt van nattere bodems bij toenemende openingsgrootte werd verwacht (Hoofdstuk 3). Uit het onderzoek bleek echter dat de verschillen in bodemvocht tussen de centra van openingen, de randen van openingen of het bos klein waren. Ook waren er geen verschillen tussen openingen van verschillende grootte. De

[2] Academisch proefschrift van S. Rose 2000: "Seeds, seedlings and gaps – size matters."

bodemvochtcondities in openingen werden beïnvloed door een complexe interactie van bodemverdamping, transpiratie, bodemhydrologische eigenschappen, bodemvochtonttrekking van de bomen aan de rand van de opening en het neerslagpatroon. De bodemvochtverdeling in openingen en bos werd beïnvloed door de aanwezigheid van wortels, zowel wateronttrekkende levende wortels van bomen aan de rand en van de regenerende vegetatie als dode wortels als gevolg van houtkap. Door de bovengrondse extractie van biomassa ontstond er ondergronds een wortel-opening.

Ik vermoed dat de bodemvochtcondities in de opening sterk worden beïnvloed door de wortels van de regenererende vegetatie in de opening en de wortels van de bomen in de openingsrand, die proberen de opening in te groeien, op zoek naar water en nutriënten. De hoeveelheid wortels van de bomen in de openingsrand zal afnemen in het centrum van de opening naarmate de opening groter is, maar deze wordt gecompenseerd door de grotere hoeveelheid wortels van de sterk teruggroeiende vegetatie in de opening zelf. Twee jaar na kap wordt hierdoor de grootte van de opening van ondergeschikt belang bij de waterconsumptie.

Modelleren van microklimaat en waterdynamiek: 'bold but beautiful' [3]

De ruimtelijke en temporele patronen van microklimaatcondities, evapotranspiratie en bodemwaterdynamiek werden bestudeerd met het *Bos – Opening* model *FORGAP* (Hoofdstuk 4). Een selectie van PGE-openingen werd gemaakt, in grootte uiteenlopend van 40 tot 3200m^2, waarvoor de hoeveelheid zonnestraling en de waterbalans werd berekend. Daarnaast werd het model gebruikt om de effecten te berekenen van langgerekte versus ronde openingen, de oriëntatie van de opening ten opzichte van de zon en het effect van bosfragmenten in een opening (Hoofdstuk 5). Bij een toenemende grootte van de opening werden gradiënten van toenemende zonnestraling, evapotranspiratie en afnemende hoeveelheid bodemvocht aangetroffen. De rand van de opening was droger dan het ongestoorde bos. Langs een onregelmatig gevormde openingsrand werden microklimaat- en bodemvochtcondities aangetroffen die vergelijkbaar waren met kleine openingen. Hierdoor verminderde de grootte van de opening aanmerkelijk. Ronde openingen hadden een beduidend hoger verdampingsverlies dan uitgestrekte openingen van gelijke grootte. Een gelijkluidende conclusie kon worden getrokken tussen openingen die in westelijke naar oostelijke richting waren gepositioneerd ten opzichte van openingen in een noordelijke naar zuidelijke richting, waarbij de laatst genoemde het natst waren.

De vorm en oriëntatie van de opening waren overduidelijk belangrijke parameters die het microklimaat en de waterbalans beïnvloedden, zowel in de opening als in de openingsrand.

Nutriëntenkringloop

Bladval
De belangrijkste aanvoer van nutriënten in een opening is via bladval. Een verminderde bladval in openingen kan leiden tot een potentieel nutriëntentekort voor de regenererende vegetatie in de opening. De ruimtelijke verdeling van bladval en nutriëntenaanvoer in bladval in kronendakopeningen werd bestudeerd in openingen van verschillende grootte en leeftijd. (Hoofdstuk 6). De bladval in openingen nam af volgens een sigmoïdale functie in relatie tot de afstand tot de rand van de opening. Hierdoor daalde de nutriëntenaanvoer in het centrum van een opening van 3200m^2 met 95%. Het herstel van bladval ging sneller in grotere openingen dan in kleinere. De vegetatie in een grotere opening groeide namelijk sneller, waardoor de bladval

[3] In navolging van V. Jetten (1994) en zijn één-dimensionaal waterbalansmodel SOAP, die verzuchtte dat het bij modelleren is als bij TV soap series: " Zodra je denkt dat alles soepel verloopt, kondigt het volgende probleem zich aan". Dit moet ik helaas bevestigen.

en bladaanmaak van de vegetatie – de bladomzet – in grote openingen sneller plaatsvond dan in kleine openingen.

Potentiële nutriëntenstress als gevolg van een afgenomen bladval kan ontstaan tussen één en twee jaar na het maken van de opening, als de bladomzet van de vegetatie in de opening nog gering is. Deze situatie doet zich voor in alle openingen, aangezien in kleine openingen de bladval van de openingsrand groter is en in grotere openingen de bladval van de vegetatie in de opening groter is.

Decompositie
Veranderingen in de decompositiesnelheid in kronendakopeningen kunnen een nutriëntentekort veroorzaken voor de regenererende vegetatie. Daarom werden decompositiestudies uitgevoerd (Hoofdstuk 7). Tussen openingen van verschillende grootte waren er geen verschillen in decompositiesnelheden van bladeren, houtige plantdelen en bloemen, maar de decompositiesnelheden van deze plantdelen waren in ongestoord bos wel hoger dan in openingen. Eén strooisellaag in het bos werd afgebroken in 4.6 maanden. Het verschil in gewichtsverlies van het strooisel tussen openingen en bos en het ontbreken van een verschil tussen openingen onderling kan worden verklaard door 1) de overheersende microklimaatcondities in de opening, waardoor de strooisellaag uitdroogt en waardoor de microbiële activiteit wordt geremd en 2) de schade aan de ondergrondse biomassa en schimmelinfecties als gevolg van houtkap, die een belangrijke rol spelen in de afbraak van plantaardig materiaal.

Het is niet aannemelijk dat de afgenomen decompositiesnelheid in kronendakopeningen een potentiële dreiging vormt voor de nutriëntenbeschikbaarheid voor de regenererende vegetatie. Het is echter wel zo dat een vermindering van de aantasting van de resterende vegetatie in de opening na kap verminderd de veranderingen in decompositie, omdat microklimaat en edafische factoren minder zijn verstoord.

Mineralisatie
Het effect van kronendakopeningen van verschillende grootte en leeftijd op de N-mineralisatiesnelheden zijn bestudeerd om te achterhalen hoe de mineralisatiesnelheid wordt beïnvloed door de openingsgrootte en hoe lang de invloed van de opening merkbaar is (Hoofdstuk 8). Tussen openingen van verschillende grootte, maar groter dan 200m^2, was er geen significant verschil in N-mineralisatiesnelheid, maar de mineralisatiesnelheid in deze openingen was vier keer langzamer dan in het ongestoorde bos. Kronendakopeningen kleiner dan 100m^2 hadden een mineralisatiesnelheid vergelijkbaar met het bos. De N-mineralisatiesnelheid werd het meest beïnvloed door de hoeveelheid stikstof in de bodem en de bodemvochtcondities, maar verschillen in de N-mineralisatiesnelheid tussen bos en opening worden het best verklaard door de hoeveelheid strooisel, de hoeveelheid levende wortels, de kronendakbedekking en wederom het bodemvocht. De mineralisatie herstelde zich eerder in grote openingen dan in kleine openingen: in grote openingen verliep de biomassaproductie sneller dan in kleine, waardoor de hoeveelheid bladval toenam, wat het basismateriaal voor mineralisatie is.

Een potentieel nutriëntentekort kan ontstaan in twee jaar oude openingen, als er nog relatief weinig vegetatie is en de oude strooisellaag bijna volledig is uitgeput. Deze condities kunnen vooral worden aangetroffen in openingen van 200m^2 en groter.

Uitspoeling onder de wortelzone
Uitspoeling van nutriënten en verzuring in kronendakopeningen zijn potentiële bedreigingen voor de regeneratie van vegetatie. Uitspoeling van nutriënten werd gemeten in een serie openingen van verschillende grootte en leeftijd, van 40 tot 3200m^2 en van 1 tot 13 jaar

(Hoofdstuk 9). In openingen groter dan 400m^2 nam de uitspoeling toe van voornamelijk NO_3, Al, Ca, Mg, Na, Cl en SO_4. Het nutriëntenverlies nam toe met een toenemende grootte van de kronendakopening. Ook in openingen van 200m^2 werd een geringe toename opgeloste stoffen in percolatiewater aangetroffen. De toename in uitspoeling begon enkele maanden na kap en de hoogste concentratie werd ongeveer 10 maanden na kap aangetroffen, gelijktijdig met de hoogst gemeten zuurgraad. De hoge concentraties aluminium zijn van belang, omdat Al toxisch is voor de meeste planten. Al-concentraties in een 3200m^2-openingen waren 19 keer hoger dan in het bos. Drie jaar na kap was de uitspoeling weer op gelijk niveau met het bos, behalve in de 1280 en 3200m^2-openingen. Een verhoogde uitspoeling werd nog steeds aangetroffen in de 7 jaar oude 3440m^2-opening, maar niet meer in de 7 jaar oude 740m^2-openingen en de 13 jaar oude openingen. Uitspoeling werd veroorzaakt door een verminderde opname door de vegetatie in kronendakopeningen groter dan 400m^2, terwijl in openingen kleiner dan 200m^2 uitspoeling werd voorkomen door de opname via de wortels van de vegetatie aan de rand van de opening.

Ik denk dat in openingen kleiner dan 400m^2 de schade door kap kleiner is dan in grotere openingen. In deze openingen zijn meer levende wortels van bomen van de openingsrand aanwezig zijn, waardoor er minder nutriënten verloren gaan. In openingen groter dan 400m^2 kan uitspoeling en verzuring doorom de regeneratie nadelig beïnvloeden.

El Niño

Als gevolg van de droogte tijdens de '97/'98 El Niño in maart 1998 was de luchttemperatuur 1.5°C hoger en de luchtvochtigheid 8.7% lager dan in een normaal jaar. Het was echter opmerkelijk dat het bodemvocht niet volledig was uitgeput en dat alleen jonge kleine zaailingen overleden. Modelsimulatie gaf aan dat alleen de bovenste laag van de bodem zeer hoge zuigspanningen had en dat de vegetatie vocht kon onttrekken onder de bovenste 15cm bodem. Op het moment dat de neerslag zich, na drie weken zonder regen, herstelde, was een vertraagde reactie van 11 dagen merkbaar in percolatie op 140cm diepte. Als gevolg van El Niño produceerden de bomen twee keer zoveel bladval, waardoor een relatief dikke strooisellaag werd opgebouwd, die vervolgens snel werd afgebroken toen de neerslag zich herstelde in april 1998.

Ook al komen deze klimaatsanomalia slechts sporadisch voor, ze verhogen zeer zeker de natuurlijke dynamiek van het bos. Als grote openingen worden gemaakt tijdens een El Niño jaar, dan kan de regeneratie van het bos worden aangetast.

EEN VERGUNNING TOT KAPPEN? [4]

Een studie naar de bosdynamiek in het onderzoeksgebied toonde aan dat 95% van alle natuurlijke openingen kleiner zijn dan 300m^2 en dat 55% van de openingen tussen 25 en 100m^2 zijn. Dit zijn belangrijke getallen, omdat ze aangeven dat de natuurlijke regeneratie van het bos opereert binnen deze openingsgrootte. Als het de doelstelling is van een bosbouwmanagement-systeem om de huidige soortensamenstelling en biodiversiteit te handhaven, moeten houtkapoperatie zich niet te ver buiten deze getallen begeven. Bij voorkeur moeten kronendakopeningen niet groter zijn dan 300m^2. Ter illustratie: de gemiddelde openingsgrootte van een enkele boom bij conventionele kap is 181m^2 en van twee bomen 355m^2 (Van der Hout 1999).

[4] In navolging van "Kappen of kappen met kappen" door L. Brouwer, *Natuur & Techniek* 1997, nr.3.

Microklimaatcondities in kronendakopeningen worden gereguleerd door de hoeveelheid zonnestraling, die direct gerelateerd is aan de grootte van de kronendakopening. De studie van Rose (2000) toont aan dat bij een toenemende grootte van de opening, pioniersoorten harder groeiden dan schaduwtolerante soorten. Deze laatste soorten zijn echter veelal de commercieel interessante boomsoorten. Het modelleren van straling in openingen toonde aan dat uitgerekte kronendakopeningen, onregelmatig gevormde openingen en openingen met bosfragmenten de hoeveelheid straling in de openingen aanmerkelijk verminderde. In een bosbouwsysteem dat gericht is op het creëren van optimale condities voor de regeneratie van commerciële soorten zou rekening moeten worden gehouden met de effecten van dit soort openingen op de groeimogelijkheden van commerciële soorten.

Er zijn geen verschillen aangetroffen in bodemvochtcondities tussen openingen van verschillende grootte. Het regelmatige neerslagpatroon in het onderzoeksgebied voorkwam dat er lange periodes van droogte voorkwamen, alhoewel kortdurende drogere periodes van één à twee dagen wel voorkwamen. Sporadisch voorkomende droge bodemvochtcondities in kronendakopeningen tot 3200m^2 zijn hoogstwaarschijnlijk nooit limiterend voor de groei.

De nutriëntenbeschikbaarheid kan een discriminerende rol spelen in de mate waarin soorten regenereren in relatie tot de grootte van de kronendakopening. Nutriëntenverlies kwam niet voor in openingen kleiner dan 200m^2 en slechts weinig uitspoeling werd aangetroffen in openingen tussen 200 en 400m^2. Uitspoeling, verzuring en de mobilisatie van Al namen sterk toe in openingen groter dan 400m^2. Uitgaande van deze aspecten van de hydrochemie, zouden kronendakopeningen niet groter moeten zijn dan 400m^2.

Tot slot, mijn onderzoek toont aan dat, kronendakopeningen groter dan 400m^2 een verstoorde nutriëntenkringloop hebben die edafische condities genereert die potentieel limiterend zijn voor alle plantsoorten. Openingen gemaakt door kap zouden bij voorkeur niet groter moeten zijn dan 400m^2. Een bosbouwsysteem dat slechts een geringe invloed heeft op de natuurlijke processen in het bos is mogelijk in combinatie met schadebeperkende houtoogstmethoden. Of de exploitatie van het bos ook op de lange termijn duurzaam is valt nog te bezien. Een nauwe samenwerking tussen onderzoekers, bosbouwmanagers en beleidsmakers kan een verdergaande afbraak van het tropisch regenwoud voorkomen. Monitoring van bosecologische processen vormt hierin een sleutelrol.

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How many trees do you need for a thesis?

Making tropical 'soil-soup'

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The Pibiri Gap Experiment was a *co-production* with Simmoné Rose, Nico Houter and David Hammond, without whom the gaps would never have seen the light. Simmoné, thanks for the continuous management of my part of the project during my absence. Our discussions provided me with indispensible knowledge on seeds, seedlings and their demography. David, thanks for the financial helping hand for this movie and our antless discussions on ecology, evolution, forestry, fly-fishing and how to barbecue steaks.

The other *co-stars* of the Tropenbos-Guyana team include Raquel Thomas (thanks for the introduction to catching litter and life in Guyana outside work), Kristel Perreijn (thanks for the many nights you dragged me from behind my computer for a beer at Sandra's or soca at Hector's), Yvez Basset, Peter van der Hout, Eric Arets and Bert van Ulft, without whom life in Mabura would have been a rather boring one.

Filming a documentary in the tropics is almost impossible without an excellent *local crew*, who lit(t)eraly sorted out half the forest, enlighted me with their knowledge of the local plants and animals and showed me 'the ways of Guyana'. My stay in the Georgtown Guesthouse was always a pleasant one, due to the good care of Joan Watson and Sybil Stewart. Harry and Anthony La Cruz assisted with felling the trees and cleaning the gaps, which were made by the best feller of Guyana, Wilfred Jarvis. Linsey Nathan and Maureen Daniels always supprised me with their Guyanese breakfast of fried corned-beef with lots of onions and garlic, but made my day with chicken-curry with roti! Although driving on dirt-roads in a landrover is every boy's dream, it was always a pleasure to sit beside Terry Lieu-Ken-Pen, Linden Cummings or Kissoon, the Tropenbos drivers, after a long day of hard work in the forest. And then there were my field assistants, without whom this movie would never have seen the theatres: Quincy Smart, George Roberts and later Norland Bovell. 'Bounty' was my silent force in gathering data (see photo). Thank you guys for your patience in sorting litter and roots, the weighing of an uncountable amount of samples and sharing the fun when playing with mud to install equipment.

This production would not have been possible without the help and *support* of Demerara Timber Ltd., who provided us with a skidder and personel to clean the gaps and who helped us with stranded landrovers on more than one occasion.

Geen hit-film zonder spectaculaire *stunts*. Ik deed al mijn stunts zelf en daardoor werd deze documentaire bijna een 'Mission Impossible'. Skidder-salto's, landrover-slides, kajak-floods, cutlass-chops, crossmotor-crashes en uiteindelijk een tower-dive, welke ik wonderbaarlijk genoeg overleefde. Er moeten toch heel veel engeltjes of andere bovennatuurlijke wezens met me meegeleefd hebben op die onfortuinlijke dag in oktober '96.

My sincere gratitude goes to all those people who took care of a swift and safe return from the forest to the Netherlands: the Pibiri-crew for the adequate first-aid and especially Quincy Smart, who witnessed my 'flight', Yvonne van Rosmalen for the first medical assistance in Mabura, Hans ter Steege, Celina Harewood and George Walcott at the Tropenbos-Guyana Office in Georgetown for the arrangement of the air-bridge from Mabura to Georgetown, transportation from Ogall airport and the (almost) open telephone line with the Netherlands (insurance, family, doctors), the staff at St. Mercy Hospital, the flying doctors Robert de Jong and Jan Haeck for organising the trip to the Netherlands and their good company during this flight, the staff of the Academic Medical Centre in Utrecht, the medical-mechanic prof. dr. van de Werken and of course all family, friends and colleagues who supported and visited me in the hospital or at home during my recovery. A big KISS to you all.

Vele tropen-*acteurs* hebben Mabura Hill, Pibiri, Hector's, Field Station, Sandra's en Waraputa bezocht en hebben me geholpen bij de verzameling van alle blaadjes, worteltjes, buisjes zand, bodemwater en zonlicht. Zoals in een goede SOAP (bestaan die?) wisselde de samenstelling: in 1996 werden de hoofdrollen gespeeld door Jiske Burema en Reinier Romein gevolgd door Raymond Niemijer en Martijn Mekkink en in 1998 werden deze rollen vertolkt door Raymond Sluiter en Niels Smit en tenslotte Saskia Visser en Jakolien Leenders. Als cast waren jullie onmisbaar, want niet alleen hebben jullie me onschatbaar geholpen met het, gedeeltelijk, herverplaatsen van het bos, maar ook waren jullie fijn gezelschap, slechte darters en goede koks tijdens de avonduurtjes.

Zoals in elke moderne film kon ook deze productie niet zonder *special effects*. De electronics-wizzards van het fysische laboratorium, Bas van Dam en Marcel van Maarsenveen hebben keer op keer de prachtigste apparaten voor me in elkaar gezet en schimmel uit dataloggers verwijderd. Dankzij jullie vernuft bleef het Pibiri Climate Station operationeel. Henk Markies en Theo Tiemessen, bedankt voor jullie hulp met de meteotoren. Jullie zijn waarschijnlijk de enigen die ooit gas hebben aangeboord op 1m diepte met een grondanker in komklei. De *chemical-stunts* zijn verzorgd door Cees Klawer, Ton van Warmerhoven en Marieke van Duin. Gelukkig waren jullie altijd bereid om mijn watermonsters weer een keer over te doen, als ik dacht dat het nog nauwkeuriger kon. Het is dan ook niet eenvoudig om concentraties te moeten meten in water waar niets in zit.

Mijn *correctors* ben ik zeer erkentelijk voor het bijschaven van de Engelse (Astrid) en Nederlandse (Ingeborg) samenvattingen. Taal was al nooit mijn sterkste kant en na 5 jaar in het Guyaans schrijven was er van mijn Nederlands weinig meer over. Als er iemand een betere vertaling weet voor 'gap size' dan 'kronendakopeningsgrootte' laat het me dan weten. MS-Word weet er ook geen raad mee en maakt er 'kronendagopening' van.....

Mijn verblijf in Guyana werd ingekleurd en verfraaid door een fijn team van *grimeurs*, waarmee ik menig dagje Waraputa, avondje Hector's, emmertje fruit-punch en decibelletje Byron Lee heb gedeeld. Miranda, Jessica, Eustas, Paddy, Bas, Charlie, Peter, Niels and Bernard, many thanks for the necessary distraction of the work! Het thuisfront, alle vrienden en familie, VAGgers, Geo's, Snipkippen & haantjes en collega's, bedankt voor de niet aflatende stroom brieven, faxen (vorige eeuw) en e-mails (deze eeuw) waarmee jullie mij op de hoogte hielden van het wel en wee in kikkerland. Deze keer geen ellenlange verhalen over nijlpaarden, maar kaaimannen en weer die landrover.

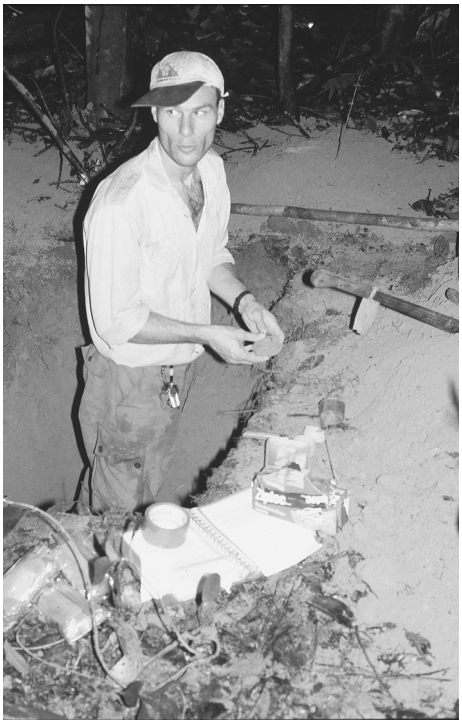
Tussen de shoots-op-locatie werd mijn *cinematography* opgeluisterd door mijn collega's van de Zonneveldvleugel*gang* Anja, Simone, Marcel, Nico en kamergenoot Leo opgevolgd door mijn oplichtende kamergenoot Jakob, het PCRaster*team* Derkjan, Kor en Cees, de hydro-*FAQ's* Rens, Thom en Theo, de Alpenzon van Karin en de *Stat-Man* Edzer. Zonder al jullie koffiezorgen, tafelroffels, looplunches, muizenjachten, neuriejamsessies, koffiebonnetjes, de vrijdagmiddagborrels in de Uithof-Inn (waarom, waarom, moest die strandtent weg???) en de James Bond trailer zou het een hele eenzame productie zijn geweest in kamer 007.

En tenslotte mijn *personal-assistants*: ouders, zus, Alida, Wim en Astrid. Bedankt voor jullie niet aflatende interesse (en af en toe bezorgdheid) over al mijn verblijven in zowel Afrika en Guyana, de afgelopen 9 jaar. En Astrid; zonder jouw vele e-mails (Guyana) en luisterend oor (Nederland), steun als er weer van alles mis en/of kapot ging en hulp (verpleging, worteltjes sorteren; 'wat een lol') was het niet gelukt! En uiteraard was 1 december 2000 een absoluut hoogtepunt, waaruit ik het laatste restje energie putte voor de eindsprint naar de deadline! En nou is mijn debuut af; weer een reden voor een feest!

Oscar van Dam

Maart 2001.

CURRICULUM VITAE



Oscar van Dam werd geboren op 5 december 1967 te Groesbeek. Hij groeide op in Enschede alwaar hij in 1987 het Atheneum-B eindexamen behaalde op het Kottenpark College. Datzelfde jaar begon hij in Utrecht aan de studie Fysische Geografie met als specialisaties landevaluatie en landdegradatie. Als afstudeer-onderzoek werd in 1991 een eco-hydrologische inventarisatie gemaakt van het natuurlijk laaglandveen nabij de rivier de Biebrza in Polen. Na dit onderzoek volgden twee stages in Afrika. In Burkina Faso, bij het Antenne-Sahélième van de Landbouwuniversiteit Wageningen, werd in 1992 een landdegradatie onderzoek uitgevoerd met behulp van satellietbeeld interpretatie. In 1993 werd bij het Luangwa Integrated Resource Development Project te Zambia een bodemkundig onderzoek en landevaluatie verricht. Na deze studie werkte hij als gewetensbezwaarde bij DLO-Staring centrum op een tweetal projecten: model studie naar bosverdroging in Nederland en een schattingmethode voor beschikbaar vocht met behulp van de Europese bodemkaart.

In november 1995 begon hij als assistent in opleiding aan de vakgroep fysische geografie van de Universiteit Utrecht en bij het Tropenbos-Guyana Programme. Het onderzoek richtte zich op de effecten van kronendakopeningen als gevolg van selectieve bosexploitatie op het microklimaat, de waterhuishouding en de voedselkringloop, waarvan dit proefschrift het resultaat is.

Kurupukari-main: just before Akaiwan bridge