

Trial by fire

Postfire development of a tropical dipterocarp forest

Mark G.L. van Nieuwstadt

Cover legend: Sungai Wain forest in different stages before and after burning. From left to right: Unburned forest (9-98), surface fire inside the forest (3-98), burned forest 6 months after fire with a high density of standing dead trees (9-98), burned forest with young *Macaranga* seedlings (12-98), burned forest two years after fire with a dense secondary regrowth dominated by ferns (6-00).

M.G.L. van Nieuwstadt

Trail by fire - Postfire development of a tropical dipterocarp forest

ISBN: 90 – 393 – 3002–6

Keywords: Drought, East Kalimantan, forest fire, Indonesia, large-scale disturbances, lowland dipterocarp forest, plant persistence, succession.

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Printed by:	PrintPartners Ipskam B.V., Enschede
Cover:	Emy Franck
Layout and photos:	Mark van Nieuwstadt

Trial by fire

Postfire development of a tropical dipterocarp forest

De vuurproef

Ontwikkeling van een tropisch dipterocarp bos na brand

(Met een samenvatting in het Nederlands)

Percobaan oleh kebakaran

Pembangunan paska-kebakaran hutan dipterocarp tropis

(Dengan ringkasan dalam Bahasa Indonesia)

Proefschrift

Ter verkrijging van de graad van doctor
aan de Universiteit Utrecht
op gezag van de rector magnificus,
Prof. Dr. W.H. Gispen,
ingevolge het besluit van het College voor promoties
in het openbaar te verdedigen
op maandag 13 Mei 2002
des middags om 16.15 uur
door

Mark Geerten Lambertus van Nieuwstadt

Geboren op 29 juni 1970 te Breda

Promotores: Prof. Dr. M.J.A. Werger
Prof. J.A. Sayer
Verbonden aan de Faculteit Biologie
van de Universiteit Utrecht



Universiteit Utrecht



The studies reported in this thesis were carried out in a collaboration of the Center for International Forestry Research (CIFOR) in Bogor, Indonesia, the International Ministry of Forestry (MOF)-Tropenbos-Kalimantan research institute in Samboja, Indonesia, and the Department of Plant Ecology, Utrecht University, the Netherlands. Financial support was provided through grant 84-408 by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO), and by CIFOR.

Ik trok een streep:
tot hier,
nooit ga ik verder dan tot hier.

I drew a line:
up to here,
never will I go further than up to here.

Toen ik verder ging
trok ik een nieuwe streep
en nog een streep.

When I went further,
I drew a new line,
and yet another line.

De zon scheen en overal zag ik mensen,
haastig en ernstig,
en iedereen trok een streep,
iedereen ging verder.

The sun was shining and I saw people everywhere,
hasty and sincere,
and everyone drew a line,
everyone went further.

Toon Tellegen
Over liefde en over niets anders.
1997, page 12
Querido



Unburned lowland dipterocarp forest. Sungai Wain, September 1998.

Contents

Chapter		Page
1	General introduction	9
2	Separating the effects of severe drought and subsequent fire on tree mortality in a lowland dipterocarp rain forest in East Kalimantan, Indonesia	27
3	Post-fire dynamics of plant functional groups in a lowland dipterocarp rain forest	45
4	Resprouting capacity of tropical saplings after artificial stem breakage, and the storage of non-structural carbohydrates	67
5	Vertical gradient in viable seed density and germination after fire in the seed bank of lowland dipterocarp rain forest	83
6	The ecological consequences of logging in the burned forests of East Kalimantan, Indonesia	95
7	Synthesis: Assessing the consequences of drought and fire in a lowland dipterocarp rain forest	99
	Executive summary	115
	Nederlandse samenvatting	117
	Ringkasan dalam Bahasa Indonesia	124
	References	127
	Acknowledgements	141
	Curriculum vitae	143



The sharp transition between unburned forest (left) and burned forest (right) with a narrow man-made firebreak in between. Sungai Wain forest, January 1999.

1

General introduction

Introduction

For a long time, ecologists used to conceive the tropical rain forest as undisturbed gardens of Eden (MacMahon 1981, Whitmore 1984, Richards 1996). Detailed accounts of the effects of hurricanes, volcanic eruptions and, more recently, large-scale forest fires have altered this perception (Tanner et al. 1991, Bellingham et al. 1994, Whitmore & Burslem 1998, Cochrane et al. 1999). It is now clear that severe disturbances occurring at low frequencies are a natural component of many tropical rain forests. The challenge that ecologists face is to incorporate the effects of such disturbances into the theoretical framework that describes and explains patterns of species composition and species co-existence in the tropical rain forest.

In recent years, probably the most striking example of a large-scale disturbance in tropical rain forest was the occurrence of extensive fires which, in a matter of months, devastated an area of 2.6 million hectares of forest in the Indonesian province of East Kalimantan in 1997-1998 (Hoffmann et al. 1999, Siegert et al. 2001). This region experiences infrequent dry episodes related to the el Niño-Southern Oscillation (ENSO) (Ropelewski & Halpert 1996, Walsh 1996 a, Walsh and Newbery 1999). A single fire does not necessarily destroy the tropical rain forest vegetation completely (Leighton & Wirawan 1986, Woods 1989, Holdsworth & Uhl 1997, Cochrane & Schulze 1999). The damaged area may

still have potential value in terms of nature conservation properties and timber production. These values depend on the ability of a forest to recover after fire, and the speed at which recovery occurs. The processes of recovery need to be understood before we can decide whether it is useful to put effort into the preservation of burned forests.

Many components of the forest are affected by fire and deserve a detailed analysis. Not only does fire cause high tree mortality (Woods 1989, Leighton & Wirawan 1989), but also animal populations are affected, either directly through fire injury, or indirectly through changes in food availability or habitat structure (Azuma 1988, Doi 1988, Suzuki 1988, Yajima 1988, Makihara et al. 2001). Where animals interact with the vegetation in their role as herbivores, seed dispersers or pollinators, they may influence the course of vegetation development. Depending on the fire intensity, the density and composition of the mycorrhizal community may be reduced by the heat produced by a fire, or may change as the result of altered soil characteristics. However, from studies in South Asia and Australia it appears that the mycorrhizal community is damaged only superficially or otherwise recovers quickly after fire (Bellgard et al. 1994, Rashid et al. 1997). Fire may change certain soil characteristics such as pH and availability of nutrients to the vegetation, and may cause a temporal increase in erosion rate (Busch-

bacher et al. 1988, Shimokawa 1988, Holscher et al. 1997, Douglas 1999, Ketterings & Bigham 2000, Ketterings et al. 2000, Kennard & Gholz 2001). As a result of the high plant mortality caused by fire, light penetration to the understorey increases, as does the temperature, whereas the relative humidity decreases (Toma 1999, Toma et al. 2001 a).

Light limitation is frequently identified as one of the most important factors determining plant establishment, growth and survival (Bazzaz 1996, Hubbell 1998). While not denying the possible influence of other factors on post-fire vegetation development, the aim of this study is to improve our understanding of the processes of establishment, growth and persistence that determine vegetation dynamics after drought and fire, including light availability as the variable that is likely to exert the most widely influence on the post-fire development of the vegetation. During a two-year fieldwork that followed directly upon the 1998-fire and the preceding drought, I studied these processes by comparing an unburned core of forest with its burned periphery.

Theoretical framework

Few attempts have been made to place post-fire vegetation dynamics in Borneo within a broader theoretical context. Because of the occurrence of fire-disturbance in an ecosystem which is traditionally studied in a non-fire theoretical context, insight may be gained from analysing the vegetation dynamics within a non-fire (“general”) ecological framework, as well as from a fire-ecological point of view. Due to the specific characteristics of fire-prone ecosystems and fire as a disturbance agent, fire research has developed some distinct approaches from the general ecological literature (Bond & Wilgen 1996).

General non-fire ecology

Patterns of predictable vegetation changes are the subject of succession theory, which has continued to receive much attention throughout the development of

both general ecology and fire-ecology. In its original concept in general ecology, succession (primary succession) was presented as a predictable sequence of vegetation types which started on an initially bare substrate and which ultimately developed towards a climax vegetation (Clements 1904, 1916). It was determined by speed of colonisation and subsequent competition, where species modified the site after their establishment (“reaction”, sensu Clements 1904, 1916), changing the relative abilities of species to germinate and survive. The variety of vegetation dynamics referred to as succession gradually expanded. A distinction was made between primary succession and secondary succession (the first referring to vegetation development on a newly formed or exposed substrate (Glenn-Lewin & van der Maarel 1992)). Principles of succession theory are now used to describe vegetation dynamics over a wide range of spatial scales and intensities of disturbance, varying from colonisation of a sterile volcanic island (Whittaker et al. 1989) to the growth of saplings after tree fall has formed a canopy gap (review by Veblen 1992).

The emphasis of succession theory gradually moved from a holistic view of the ecosystem (Clements 1916) to a process based approach which focuses on life-history characteristics, colonisation and interactions between species (Connell & Slatyer 1977, Horn 1981, Pickett et al. 1987, Tilman 1988, Glenn-Lewin et al. 1992). An important part of modern literature on non-fire succession theory is formed by studies in old-fields, in which differences in colonisation rate, competitive ability, shade tolerance and longevity form the main factors driving the successional sequence (Connell & Slatyer 1977, Huston & Smith 1987, review from a neotropical perspective by Finegan 1996). Following disturbance, species with different competitive abilities dominate a site in a time sequence of replacements (Figure 1.1 a) (Horn 1981, Tilman 1982). In line with this emphasis, the role of a disturbance is primarily determined in terms of its’ ability to “change resources, substrate availability, or the physical

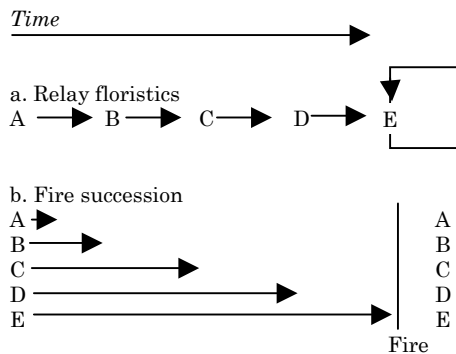


Figure 1.1. Graphic representation of two models of succession, from Bond & van Wilgen (1996). The first model (a) represents traditional non-fire succession in an old field, where a competitive hierarchy of species populations replaces one another. The second model (b) visualises succession in a fire-prone system, where all populations establish immediately after the disturbance, and the vegetation changes are merely an effect of differences in species longevity.

environment” (White & Pickett 1985). While acknowledging that these changes result from a temporarily increased turnover of biomass or an increased mortality, studies which follow this approach rarely investigate disturbance-induced patterns of species-specific mortality, but focus on the post-disturbance colonisation and utilisation of the disposed resources instead (*sensu* Tilman 1988, Bazzaz 1996). Maybe due to the historical emphasis on succession in old fields, vegetative persistence of plants from before the disturbance by whole-plant survival or resprouting is rarely explicitly incorporated into the theory.

Succession appears in the ecological theory of old growth forests in the form of treefall gap dynamics (Bazzaz & Pickett 1980, Brokaw 1985, Veblen 1992). Disturbances in a old growth forest are formed by small canopy gaps caused by the fall of one or a few trees. A gap disturbance usually causes little mortality but for the tree which causes the gap formation. It characterised in terms of increased resource availability (especially light) (Brokaw 1985). An essential difference with the foregoing description of succession in old fields is, that the vegetation in a small

gap is formed in large part by shade tolerant individuals which were present before the disturbance (Uhl et al. 1988 c, Hubbell 1998) and thus, post-disturbance colonisation does play only a limited role. The competitive dominance of the trees growing in the gap is largely determined by their pre-disturbance size distribution, with the tallest trees at the time of gap formation capturing the highest amount of light (Zagt & Werger 1998, Brown et al. 1999). However, the main forces of selection may occur in the absence of disturbance, and are formed by the length of the time period during which light availability is limited (Zagt & Werger 1998, Brown et al. 1999) and the frequency of damage occurring during that period (Canham et al. 1996, Foster 1996, Harms et al. 1997). It has been argued that the strategy of shade tolerant tree species should be to maximise persistence under resource-limited conditions and to accumulate reserves to withstand unpredictable damage, rather than to optimise the acquisition of light and other resources (Iwasa and Kubo 1997, Iwasa 2000).

To facilitate the analysis of processes such as succession in species-rich assemblages, functional groups have been defined, which share certain important life-history characteristics. In tropical forests, this functional grouping is often based on light requirements in the seedling phase, and on longevity (Denslow 1980, Hubbell & Foster 1986). Two groups of trees, including light-demanding tree species and shade tolerant tree species are commonly defined (Whitmore 1984, Swaine & Whitmore 1988) and in the successional sequence, a third group of light-demanding non-woody species can be recognised (Table 1.1). Successional development of a secondary tropical forest is abstracted as the sequence of these functional groups (Finegan 1996). In agreement with the competitive succession model, the successional sequence is predicted as the result of differences in growth rate, longevity, competitive abilities and colonisation rates of the four groups over a temporal gradient in light availability. Following a disturbance, the group of light-demanding non-woody spe

Table 1.1. Characterization of the life-history attributes of the main functional groups in this study.

Life-history attribute	Functional group		
	Approximately ordered from early to late successional		
	Non-woody species	Light-demanding trees	Shade-tolerant trees
Light requirement for germination and survival	high	high	low
Seed size	usually very small	small to very small	large
Seed dispersal distance	long	short to moderate	short
Survival in seed bank	yes	yes	no
Ability to resprout after fire disturbance	often high	unknown	unknown
Time to reach reproductive maturity	± 1 year	> 5 years	usually > 25 years
Life span	Highly variable	> 10-15 years	> 50-100 years
Characteristic species in Borneo	Terrestrial ferns, <i>Imperata cylindrica</i> , <i>Mikania scandens</i>	<i>Macaranga</i> spp., <i>Mallotus</i> spp., <i>Dillenia</i> cf. <i>borneensis</i> , <i>Vernonia arborea</i>	Most tree species in the undisturbed forest

cies dominates the vegetation for a short period of time. At the same time, short-lived and long-lived light-demanding tree species establish from the seed bank and form a closed canopy in a few years time. After one to three decades, the long-lived species overgrow the short-lived trees and start to dominate the canopy. The third and most species-rich group of shade tolerant trees slowly increases in density through colonisation from the seed rain (Gómez-Pompa & Vázquez-Yanes 1981, Finegan 1996). Their competitive superiority enables them to gradually replace the light-demanding species.

Fire-ecology

In the literature on fire ecology, disturbances are most often viewed and analysed in terms of population dynamics. Fire research broadly focuses on two aspects: Interval-dependent effects and event-dependent effects (Bond & Wilgen 1996). Interval-dependent effects refer to the influence of the length of the interval between fires. Event-dependent effects consider the characteristics of a particular fire, which may exert a critical influence on population dynamics, depending on fire intensity, time of year, etceteras.

Following a paper by Hanes (1971) in Californian chaparral, it was increasingly

acknowledged that in fire-prone ecosystems, a fire disturbance does not necessarily start a sequence of successional stages driven by colonisation and competition (Bond & van Wilgen 1996). Instead, Hanes found that all species that were to dominate the later vegetation were already present shortly after the fire, either as resprouts or through establishment from the seed bank. He called this self-replacement “autosuccession”. It is characteristic for vegetations that are adapted to a certain severe disturbance regime. Many species in the community require post-fire conditions for their establishment, and the community may even develop into a “senile” and unproductive phase in the absence of fire (Hanes 1971). The successional pattern that follows after fire is the result of differences in species longevity (Figure 1.1 b). All species are present directly after the disturbance and as time passes, only the longer-lived species remain established in the above-ground vegetation.

Depending on the characteristics of a fire regime, fire can also cause profound changes in the composition of fire-prone ecosystems. For example, in many tropical parts of the world, fire is thought to be responsible for the maintenance of savannahs where otherwise forest would grow (Gillison 1983, Werger 1983). A high fire

Table 1.2. Classification of plant vital attributes after Noble & Slatyer (1980), with the equivalent plant functional group or equivalent plant characteristics in a tropical rain forest. (1) Uhl & Jordan 1984, Stocker 1981, Uhl et al. 1981, Kauffman 1991, Kammesheidt 1998, 1999. (2) Vines 1968, Uhl & Kauffman 1990, Pinard & Huffman 1997.

Plant vital attribute	Description	Equivalent functional group in tropical forest
Establishment requirements		
T Tolerant species	Able to establish at any time, tolerating competition with adults.	Shade-tolerant tree species.
I Intolerant species	Able to establish only immediately after the disturbance.	Light-demanding tree species, many non-woody species.
R Requiring species	Unable to establish directly after the disturbance, but have the ability to establish once mature individuals are present.	Certain shade-tolerant tree species?
Mode of persistence		
D Dispersed species	Long-distance seed dispersal.	Associated with wind-dispersal, i.e. light-demanding trees, lianas, many non-woody
S Soil-stored species	Seeds with long viability in the soil.	Associated with light-demanding trees, lianas, many non-woody species.
G Germinating species	As above, but the seed pool is exhausted after the fire. Individuals must reach maturity before the next fire in order for the population to survive.	Unknown; probably rare or absent.
C Canopy-stored species	Seeds surviving the disturbance in the crown.	Unknown; probably rare or absent.
V Vegetative species	Large part of both juvenile and mature individuals survives the disturbance by resprouting.	Association with functional groups unknown; basal sprouting reported in several slash & burn studies (1).
U Unaffected species	Part of the individuals survives the disturbance unaffected.	Association with functional groups unknown; Importance of bark thickness reported from neotropical studies (2).
W Mature stage unaffected	As in V, but sprouting individuals remain in mature life stage.	As in V
Y Juvenile stage unaffected	As in V, but sprouting individuals are in juvenile (i.e. non reproducing) life stage.	As in V
Time to reach certain life history stage		
<i>m</i> Time to reproductive maturity		Related with shade-tolerance and adult stature.
<i>l</i> Life span of individuals		Related with shade-tolerance and adult stature.
<i>e</i> Time for all propagules to be lost from the community in the absence of disturbance		Unknown; probably rare or absent.

frequency prevents the growth to maturity of trees that persist as resprouting seedlings throughout the grass vegetation (Bond & van Wilgen 1996). The observation that changes in the disturbance regime could lead to changes in the vegetation led to the approach of predicting vegetation development by defin-

ing sets of “plant vital attributes” (Table 1.2) (Noble & Slatyer 1980, Bond & van Wilgen 1996).

Plant vital attributes are key characteristics of species, which define the “regeneration niche” (Grubb, 1977) of species and, characteristic for the fire-oriented approach, also the “persistence niche”

(Bond & van Wilgen 1996, Bond & Midgley 2001) and the timing of critical life-history events. The vital attributes defining the regeneration niche, which determine the ability of a plant to become established at different stages after fire, show considerable overlap with functional groupings commonly used in tropical non-fire research (Table 1.2). The other two classifications, mode of persistence and timing of life-history events, have been only partially considered in tropical non-fire research. The importance of the seed bank is widely acknowledged (i.e. review by Garwood 1989), as is the role of whole-plant persistence of seedlings after a small-scale, low-intensity disturbance such as gap formation (Uhl et al. 1988 c, Zagt 1997, Brown et al. 1999, Brokaw & Busing 2000). In studies on larger and more severe disturbances, whole-plant survival and resprouting are often given little consideration (cf. Finegan 1996), even though some tropical studies show that it can play a significant role after logging (Rijks, Malta & Zagt 1998, Negreiros-Castillo & Hall 2000), hurricanes (Bellingham et al. 1994, Bellingham & Tanner 1995), forest fire (Kauffman 1991), and slashing and burning (Riswan & Kartawinata 1989, Kammesheidt 1998, 1999, Uhl & Jordan 1984). The timing of life-history events does feature in many forest succession models (review in Urban & Shugart 1992, Clark 1996, Pacala et al. 1996, Loehle 2000), but few tropical field studies focus on species characteristics such as age to reproductive maturity and life span (but see Thomas 1996, Davies & Ashton 1999).

The vital attribute view assumes that successional patterns can be predicted without considering competitive interactions between individuals. Instead, persistence characteristics determine the community composition shortly after fire, and successional changes in species composition are the result of differences in specific life-history attributes such as growth rate and longevity. Thus, individual species behave in the same way regardless of the species composition that occurs in their surroundings (Bond & van Wilgen 1996).

Hypotheses

Based on the traditional successional approach and the vital attribute approach, we can make two different sets of predictions (Table 1.3). The two main differences are that (1) the vital attribute approach includes species' abilities to survive the drought and fire disturbance, whereas such abilities are not explicitly considered in the non-fire approach, and (2) the non-fire approach predicts that competitive interactions play an important role in structuring the temporal patterns after the disturbance, whereas the vital-attribute approach predicts that, with time passing, light-demanding species will be eliminated not because of their competitive inferiority (i.e. because they are outshaded by shade tolerant species), but simply because of their limited life-span. Likewise, the species composition of the pool of shade tolerant trees is not determined by differences in colonisation rate and competitive dominance, but by the persistence ability of species di

Table 1.3. Hypotheses based on general succession theory and fire succession theory. Functional groups are: Light-demanding (LD) and shade-tolerant (ST).

Community pattern	Non-fire	Fire
1. Vegetation composition directly after fire	Dominated by LD species; Other functional groups virtually absent	All functional groups that are to form the later community are present
2. Density of LD vs. ST species in time	ST species increase because they outcompete LD species	ST increase because of slow growth rate and high longevity. LD species decline because of limited longevity.
3. Species composition of ST species	Determined by colonisation rate and competitive ability	Determined by fire survival rate, growth rate and longevity

rectly after the disturbance, and the species' longevity. The emphasis of this study is on the first and third hypothesis in table 1.3.

Vegetation dynamics after drought and fire

Complex disturbance regimes

Several research studies in Borneo describe the effects of fire on the lowland dipterocarp rain forest, focussing post-fire vegetation development. However, these studies do not provide a satisfying overview of the successional development after fire disturbance, because the disturbance "treatments" were highly variable, and were rarely restricted to a single fire in an "undisturbed" forest (exceptions are studies on tree mortality by Leighton & Wirawan 1986, Woods 1989). In most studies the "treatment" consisted of more complex disturbances which would not occur in the absence of human interference. These complex disturbance regimes included logging and burning (Woods 1989, Nykvist 1996), slashing and burning (Riswan & Kartawinata 1988, 1989) or even more complex sequences of disturbance (Kobayashi et al. 1999, Matius et al. 2001, Mori 2001, Toma et al. 1999, 2001 b). A similar emphasis on complex disturbance regimes exists in tropical studies from other continents. An extensive body of Neotropical literature describes forest development after a single experimental slash and burn treatment (Uhl et al. 1981, Uhl & Jordan 1984, Steiniger 2000), after slashing and burning followed by several years of cultivation (Uhl et al. 1982, Uhl 1987, Uhl et al. 1988, Kammesheidt 1998, Kammesheidt 1999, Peña-Claros 2001), or after a complex regime of fires and other disturbances (Ewel et al. 1981, Cochrane & Schulze 1999, Pinard et al. 1999). Only a few Neotropical studies describe the effects of fire in unlogged forest (Kauffman 1991, Kammesheidt 1999) or the effects of fire in selectively logged forest (Holdsworth & Uhl 1997, Cochrane & Schulze 1999, Pinard et al. 1999).

Our understanding of the impact of fire disturbance may be coloured by the emphasis on experiments with a very severe disturbance treatment. The more severely or frequently disturbed a forest site is, the higher the local mortality and thus the lower the importance of plant persistence. Second, in a small research plot with the undisturbed forest close-by, the input of seeds from shade tolerant species will be relatively high. If few shade tolerant species survive on the site, and if seed input is sufficiently high to ensure a high seedling density, non-fire theories of colonisation and competition may be adequate to describe the successional patterns after slash and burn treatments. However, the importance of species persistence and the timing of life-history characteristics may become of significant importance in the vegetation development after a single, large-scale fire.

The role of drought

In a tropical forest, fire is necessarily preceded by a prolonged drought which causes desiccation of the litter layer. Such an exceptional drought may in itself be an agent of tree mortality. In two studies in perhumid forests, which on average do not experience a monthly rainfall below 100 mm, two-month periods with a total of 50-80 mm precipitation caused a significant increase in tree mortality (Nakagawa et al. 2000, Williamson 2000). A drought in East Kalimantan, which was similar in intensity to the drought that is the subject of this study, caused approximately 25% mortality among canopy trees (Leighton & Wirawan 1986). No studies have analysed species-specific mortality or successional patterns after extreme drought in tropical perhumid forest. Following a dry period of unusual length in the seasonally dry forest of Barro Colorado Island, canopy trees had a higher chance of mortality than smaller individuals (Condit et al. 1995). Patterns of species-specific mortality were not easily explained.

Vegetation dynamics after disturbance by fire

Descriptions of vegetation development after fire are only available for lowland dipterocarp forests which experienced a combination of fire and other disturbances. These studies provide the best available approximation of what can be expected after a single fire in a forest that has not been disturbed otherwise. Together, the studies performed in Borneo suggest that in the first 30-35 years of succession, the vegetation develops through three stages. These stages appear to be predictable and are similar to the successional stages in other tropical rain forests (Finegan 1996).

In the first stage, lasting one to five years after the disturbance, the vegetation is dominated by light-demanding non-woody species. The early vegetation dynamics (up to 1.5 yr.) were studied in detail near Samarinda, where a 0.5 ha plot of primary lowland dipterocarp forest was experimentally slashed and burned (S & B) (Riswan & Kartawinata 1989). After half a year, the cover of non-woody species (notably the grass *Paspalum conjugatum*) reached a maximum cover of nearly 50%. In the following six months the herb cover decreased rapidly, while the cover of tree seedlings increased. The duration of the first phase remains unspecified in a study in Sabah, where ferns dominated the early post-fire vegetation in a burned selectively logged forest (Nykvist 1996). However, it may have lasted longer than in the study by Riswan and Kartawinata since five years after the fire, ferns were still highly abundant.

In the second stage, light-demanding tree species form the dominant component of the vegetation. In the study of Riswan and Kartawinata, this phase started around one year, when the vegetation became dominated by tree seedlings. After 1.5 year the density of tree seedlings was 405 per 100 m², of which 30% were primary forest species. Riswan and Kartawinata were the only researchers to distinguish between woody regrowth originating from resprouts or from seeds. The number of shade tolerant tree

species on 100 m² originating from sprouts was 25, compared to 23 species from seedlings. However, the percentage cover of tree sprouts was only 7%, compared to nearly 70% cover by tree seedlings (shade tolerant and light-demanding species combined).

In the study by Nykvist, light competition between ferns and the developing tree vegetation may have been the reason for the reduction of the former. Eight years after the fire, *Macaranga* spp. formed the dominant component, comprising 45% of the total biomass. Non-woody species added 7%, and shade tolerant tree species 9 to 25% to the total biomass.

Several longer-term studies from the Bukit Soeharto Education Forest (BSEF) provide insight in the tree population dynamics during the second successional phase. The BSEF was selectively logged up to 1976, burned with varying intensity in 1983, was partly logged with different intensities in 1997 and burned again with varying intensity in 1997-1998 (Kobayashi et al. 1999, Matius et al. 2001, Mori 2001, Toma et al. 1999, 2001 b). Toma et al. (2001 b) presented data on the development of a lightly damaged part of the BSEF forest after selective logging and fire in 1982-1983. Their observations on tree cover (>10 cm dbh) started 5 years after the fires, by which time *Mallotus penangensis* had established a stable population of approximately 20 stems ha⁻¹. In the 10-year period that followed, the total density of trees gradually increased from approximately 300 to 340 stems ha⁻¹. Most of this increase was caused by ingrowth into the size class >10 cm dbh of *Macaranga hypoleuca*. Populations of shade tolerant species remained stable at approximately 250 stems ha⁻¹. *Macaranga gigantea* established very abundantly in the more highly disturbed plots (Toma et al. 2001 b, Matius et al. 2001).

Disruption of the closed canopy of light-demanding species interludes the transition to the third stage, in which shade tolerant trees become the most abundant component of the vegetation. In BSEF, the disruption of the uniform canopy of light-demanding species appears to

be determined by the occurrence of drought. When approximately 15 years old, populations of *Macaranga* spp. were decimated as the result of a prolonged drought in 1997 (Toma et al. 2001 b). In the absence of drought, the canopy of light-demanding species probably persists longer.

Riswan and Kartawinata (1988) investigated the result of succession in an abandoned pepper plantation, which was located in a primary forest in East Kalimantan. Thirty to 35 years after abandonment, the vegetation was in the third phase of successional development. With 70% of the stem density (>10 cm dbh), shade tolerant trees dominated the stand. In the plot of 0.8 ha they found 121 species, 85 of which were considered to be shade tolerant species. However, none of the large trees (>50 cm dbh) in the plot were shade tolerant species. The species composition deviated considerably from the primary forest. Especially the near absence of Dipterocarpaceae in the plot was conspicuous. Due to the intensive land use, shade tolerant trees must have

been rare or absent in the plot at the onset of vegetation recovery. Riswan and Kartawinata inferred that the slow ingrowth of shade tolerant trees was caused by a limited influx of seed from the surrounding forest, and a slow growth rate of the shade tolerant species.

Due to the variable disturbance regimes and a lack of information on the persistence mode, the growth, and survival of individuals, these studies are insufficient to test the hypotheses generated from non-fire and fire successional theory in table 1.3. However, the studies suggest that considerations from both approaches have potential explanatory power. For example, competition for light may have played a role in the reduction of non-woody species in the studies of Riswan and Kartawinata (1988) and Nykvist (1996), whereas not competition for light but drought-tolerance seems to have determined the ending of the phase dominated by light-demanding trees in the study of Toma et al. (2001 b).

Ultimately, the performance and fate of shade tolerant populations determines

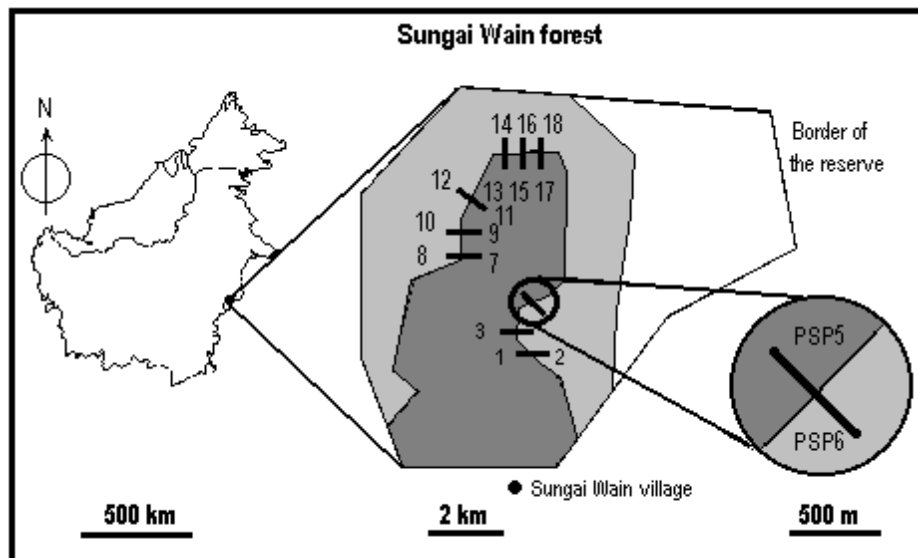


Figure 1.2. Map showing the location of Sungai Wain forest on the island of Borneo. The enlargement shows the Sungai Wain forest indicating the unburned area (dark grey), and the areas which burned once in (1998) (light grey) or twice (1983 and 1998) (white). The location of each pair of permanent sample plots (psp) is shown. The circular inset shows an example of the layout of one pair of psp over the fire edge. Psp 5 is situated in unburned forest and psp 6 in once burned forest.

the recovery of the forest. The diversity of sprouts in the study of Riswan and Kartawinata (1989) and the fact that a substantial density of trees survives the fire (Woods 1989, Leighton & Wirawan 1984, Toma et al. 2001 b) suggest that not only post-fire colonisation by seed dispersal, but also different modes of persistence contribute significantly to the post-fire succession. However, far too little is known of the origin of shade tolerant trees in the recovering forest to understand the relative importance of these processes.

Site description

The main research site is a water catchment reserve of circa 100 km², called Sungai Wain protection forest near to Balikpapan, East Kalimantan (1°16' S and 116°54' E) at 15 km from the Strait of Makasar (Figure 1.2). Three-quarters of the reserve are covered with lowland dipterocarp rain forest. Settlers have cultivated the eastern quarter of the reserve. The reserve borders low-intensity agricultural land (so-called Alang-alang shrub lands) in the South and the East, a mosaic of logged forest and plantations in the North, and a mosaic of logged forest, agricultural fields and mangrove forest in the West. The topography of the reserve consists of gentle to sometimes steep hills, and is intersected by several small rivers. There exists a gentle North-South gradient in altitude, as the result of which the area varies in altitude from 40 to 140 m.a.s.l.

The soil mainly consists of alisols (FAO/Unesco/ISRIC 1988, Bremen et al. 1990, MacKinnon et al. 1996). These are strongly weathered, very deep, infertile soils, which contain a high fraction of loam and clay.

Additional data were collected in the protected Wanariset Wartonokadri research forest (10 km Northeast of the Sungai Wain forest). This is a forest fragment of 50 ha surrounded on three sides by degraded forest and agricultural fields, and on the fourth side it is separated from another forest patch by a nar-

row road. The altitude, soil type and climate are similar to the Sungai Wain forest.

Climate

With an average temperature of 26.5 °C (Berlage 1949), an average yearly rainfall of 2790 mm (Vose et al. 1992) and an average monthly precipitation above 100 mm throughout the year (Figure 1.3), the area has a tropical wet climate (Walsh 1996 b). This classification is somewhat misleading, since dry episodes of several months with extremely low precipitation occur on a supra-annual basis, as an effect of the ENSO phenomenon (Ropelewski & Halpert 1996, Walsh 1996 a, Walsh and Newbery 1999). Based on an inventory made by Leighton (1984, in Mori 2001) we calculated that since 1887, severe droughts occurred with intervals of 18 ± 8 years. During the period 1948-1980, short dry periods (defined as having a monthly rainfall below 100 mm) were frequent (30 x one month, and 3 x two subsequent months), and most frequently occurred between September and November (Vose et al. 1992). Longer droughts were not recorded. Extensive droughts occurred in 1982-1983 and in 1997-1998, which were related to the occurrence of extreme ENSO events.

The drought in 1997-1998, which was the instigator of the fires on which this study is based, consisted of two episodes (Figure 1.3). The first drought lasted for 12-13 weeks. During this period, precipitation was limited to a total of 16 to 48 mm. The following 13-14 weeks were less dry, and experienced a total of 388 to 482 mm rainfall. The wet intermission was interrupted by frequent short droughts: In Balikpapan 33 out of 99 days had a 7-day running average rainfall below 3.3 mm, and in Samarinda 51 out of 91 days. After this wet intermission a second drought of more than 14 weeks followed, with a cumulative precipitation of 3 to 13 mm. The drought ended around 20 April 1998. A more complete analysis of the rainfall data is presented in chapter 2.

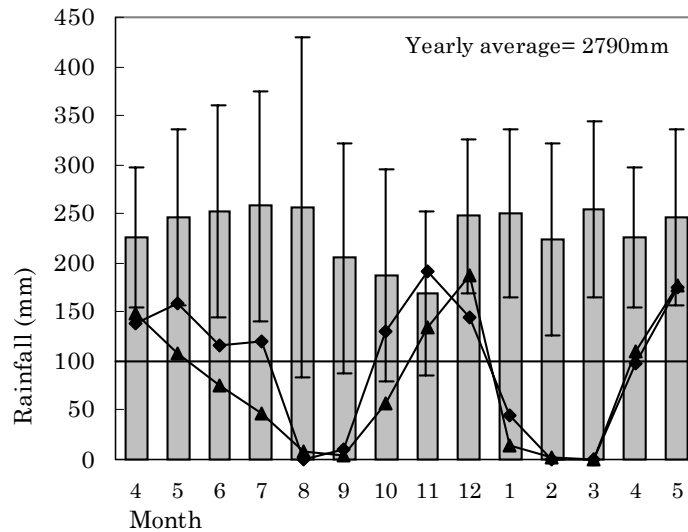


Figure 1.3. Annual pattern of rainfall (bars; average \pm sd) in Balikpapan from April to May over the period 1948-1980 (Vose et al. 1992). The lines represent the monthly rainfall in Samarinda (triangles) and Balikpapan (diamonds) during the 1997-1998 season.

Fire characteristics and historical fire regime

There are records of two fires in the Sungai Wain research forest. One occurred in the eastern part of the forest in the dry episode of 1982-1983, burning one-third of the reserve (Figure 1.2). The second fire occurred during the last part of the exceptional drought in March – April 1998, burning two-thirds of the reserve. A core area of one third of the total area (3 x 8 km) was saved from the fire. The ecological impact of a fire regime depends on many variables, of which fire intensity, fire return interval, extent (or patchiness) and size of the burned area (Whelan 1995) are of particular interest here.

Fire intensity (energy output per meter of fire front, in kW m^{-1}) (Alexander 1982, Whelan 1995) depends on the available fuel load, fuel moisture, wind speed and other variables (Uhl et al. 1988, Whelan 1995). Fires are characterised as crown fires and surface fires. Due to the humid conditions and low wind speed inside a tropical rain forest, fires

are usually confined to the surface and of low intensity (Hopkins 1992, Holdsworth & Uhl 1997). Also in the Sungai Wain forest, the entering wildfires were reduced to a low, slowly advancing “ribbon” of fire. The 1998 fire in the Sungai Wain primary forest was a typical surface fire, burning only the litter layer and the lowest vegetation. The fire had an estimated average flame height of 0.5 m, an estimated depth of 20-30 cm, an estimated speed of 10-15 m h^{-1} (MvN pers. obs., Figure 1.4), and a calculated fire intensity of circa 60 kW m^{-1} (Alexander 1982). A 0.5 m wide firebreak was enough to stop the fire (Figure 1.5), after which permanent control was necessary to prevent its escape.

Even though the fire return interval in tropical forest is presumably very long, charcoal particles that have been found in most of the samples from lowland sites show that fires have occurred in the past in tropical forest in the Amazon basin (Saldarriaga & West 1986) and in Southeast Asia (Goldammer & Seibert 1989, Dam, van der Kaars & Kershaw 2001, Hope 2001, Dam et al. 2001 a & b, Anshari et al. 2001, Suparan et al. 2001). Historical changes in fire return interval



Figure 1.4. A typical surface fire inside dipterocarp rain forest, Wanariset research forest, March 1998.



Figure 1.5. A man-made firebreak, Wanariset research forest, March 1998.

may have been caused by a temporarily drier and more seasonal climate. Such conditions prevailed in a period that began during the Last Glacial Maximum and lasted until the beginning of the Holocene (Dam, van der Kaars & Kershaw 2001, Hope 2001, Dam et al. 2001 a & b, Anshari et al. 2001, Suparan et al. 2001). However, colonising humans may also have changed the fire frequency. Whether the fires were “natural” or have an anthropogenic origin cannot be established, since the sample sequences do not date from before the first human occupation (Dam, van der Kaars & Kershaw 2001).

During the last decades, fires have occurred at an unprecedented frequency in the tropical rain forests of Southeast Asia (Leighton & Wirawan 1984, Lennertz and Panzer 1984, Hoffmann et al. 1999) and Latin America (Cochrane & Schulze 1999, Cochrane et al. 1999). The recent catastrophic fires in Borneo were related to extremely dry periods. Much of the burned forests had previously been selectively logged (Hoffmann et al. 1999, Siegert et al. 2001), but following extreme droughts in 1982-1983 and 1997-1998,

also unlogged forests in Borneo caught fire (Leighton & Wirawan 1984, Woods 1989, Hoffmann et al. 1999). The increased fire frequency is caused by a combination of extensive droughts, selective logging and forest fragmentation, and particularly by the intensifying use of fire for land clearing by plantation companies and farmers (Hoffmann et al. 1999).

The size of the burned area and patchiness are important ecological parameters, because they influence scale dependent processes, such as the travel distance of seeds colonising from unburned forest. Covering nearly the entire Southeastern quarter of the province of East Kalimantan (Lennertz & Panzer 1984, Hoffmann et al. 1999, Siegert et al. 2001), the scale of the fires of 1982-1983 and 1997-1998 was larger than any process of biological recovery. Nothing is known about the size of natural fires in East Kalimantan in the past. Given the low spreading rate of a tropical forest fire, the size of the burned forest area will probably have depended mainly on the time lapse between fire ignition and the onset of the rainy season.

Post-facto experimental design

The occurrence of a severe disturbance such as a forest fire is usually highly unpredictable, which makes the study of such a disturbance difficult. In many cases, there may exist little alternative for a *post-facto* experimental research. Three main constraints to *post-facto* studies can be recognised (Wiens & Parker 1995, Turner et al. 1997). First, experimental plots with different treatments cannot be randomly located because the “treatment” has already been applied. Second, a comparison can only be made in space, since by definition comprehensive data from before the disturbance are not available. Thus, an unknown portion of variation between plots in the different treatments is introduced, even if it were possible to locate the plots entirely randomly. Third, pseudoreplication is difficult to avoid, because the disturbance event itself is the only true level of replication (Eberhardt & Thomas 1991, Turner et al. 1997).

In the present study, we aimed at minimising the limitations inherent to these constraints. The particulars of the field situation allowed us to locate research plots with different treatments relatively randomly spread in the landscape: During the drought, the unburned part and burned part of the forest had equal potential to burn. The unburned forest remained unburned because of man-made fire breaks, which did not correspond to any topographical feature in the areas where the research plots were placed. Thus, there is no *a priori* reason to expect differences in the original vegetation of the unburned and the burned plots. To increase insight in the effect of spatial variation in the disturbance regime, we planned sets of replicate research plots over three different sites that were several kilometres apart. To minimise variation in plot characteristics between the two treatments, we designed the *post-facto* experiment in pairs of one unburned and one burned plot, which bordered each other with the firebreak as the only separation. Locating the plots in

pairs minimized pre-fire differences in landscape variation between plots.

The *post-facto* study of a naturally occurring severe disturbance also presents some advantages over the experimental application of disturbance treatments. The area of disturbance in case of a natural event is larger than what is usually feasible to apply experimentally. In the natural situation, the risk of introducing unacknowledged scale-dependent processes in the study is minimised. Also, it may be nearly impossible to mimic the natural disturbance regime accurately. For example, in the present study the fire disturbance was closely linked to a preceding long drought. This drought presented a severe disturbance in its own right, and therefore needed to be analysed in unison with the fire.

By nature, a *post-facto* experimental design concerns a comparison of treatments in space, not in time. Also here, there are advantages as well as disadvantages. Differences in plot characteristics (such as topography, species composition, and vegetation structure) may interfere with a straightforward analysis of the data. On the other hand, processes that have an explicit temporal component may be studied more accurately in a parallel analysis of a disturbed and an undisturbed plot, than by studying pre- and post disturbance at the same location (Wiens & Parker 1995).

Plot description

In the Sungai Wain forest 18 permanent sample plots (psp) of 60 x 300 m (1.8 ha) each were laid out in unburned forest and in forest that burned once in 1998 (Figure 1.2). The set-up of the psp was designed around man-made firebreaks of 0.5 m wide, which were made during the fires. Because the fire-breaks did not correspond to any topographical feature in the places where the psp were positioned, this allowed for a random sampling scheme with paired plots of unburned and burned forest at a short distance from each other. The psp were laid out in nine pairs, each pair of psp adjacent to each other over the firebreak between burned

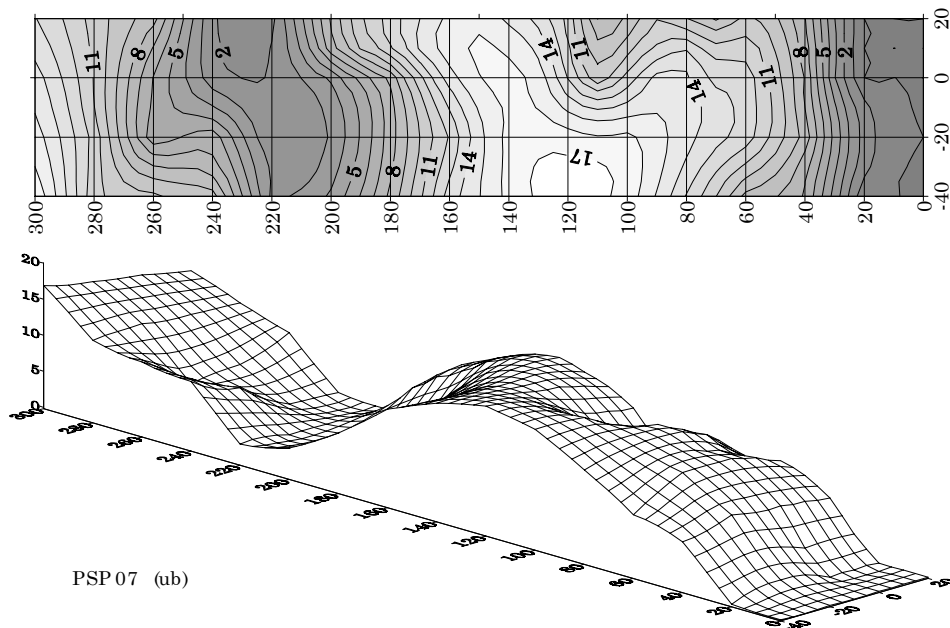


Figure 1.6. Example of the topography of a permanent sample plot. All distances are in meters.

and unburned forest. Thus, each pair of psp forms one contiguous transect of 60 x 600 m half in burned and half in unburned forest. The psp are nested in three groups and spread over a total area of circa 20 km². The distance between two pairs of psp is always more than 500 m.

Areas of different sizes were delineated to allow for a stratified sampling scheme. Each psp consisted of an area of 60 x 300 m (1.8 ha) with a subdivision of 20 x 20 m subplots. Within this area, a smaller plot of 20 x 200 m (0.4 ha) with a subdivision of 10 x 10 m subplots was laid out. The topography was measured at a scale of 20 x 20 m for the 1.8 ha psp and 10 x 10 m for the 0.4 ha plots. Slopes were measured with a Suunto clinometer, after which a map was made of each psp (Figure 1.6).

All psp have a hilly topography. The difference in height between the lowest and the highest point in a 60 x 300 m psp is 24.4 ± 7.2 m (average \pm sd, n= 18). Most of the area (77%) occurs on slopes, whereas roughly equal proportions are occupied by valleys, low flat areas, high flat areas and ridges (varying between 4 and 8% of the total area).

The canopy of the undisturbed dipterocarp forest is irregular and quite open. Some of the poorly-drained valleys and lower parts of the area are infrequently flooded and carry a forest of shorter stature in which Dipterocarpaceae do not dominate. The abundance of tree families in the plots is typical for dipterocarp rain forest (Table 1.4). Above 10 cm dbh, the most common families are Euphorbiaceae, Dipterocarpaceae and Sapotaceae. The relative dominance of Dipterocarpaceae increases substantially in the larger size classes.

No single tree species (stems >10 cm dbh) dominates the vegetation (Table 1.5). Together, the 25 most common species form 40% of the total stem density. The dominance of Dipterocarpaceae in the larger size classes is for a substantial part caused by *Shorea laevis*. Above 50 cm dbh, *Shorea laevis* is by far the most abundant, while *Dipterocarpus confertus*, *Eusideroxylon zwageri*, *Koompassia malaccensis*, *Shorea smithiana*, *Dipterocarpus humeratus* and *Dipterocarpus cornutus* are also fairly abundant. Emergent trees of *Shorea laevis* form nearly monodominant stands on some of the ridges in the reserve. Sungai Wain has many spe-

Table 1.4. Stem density (stems / ha) of most common tree families in the unburned vegetation eight months after the drought (average \pm sd of 9 psp). Data are presented for all trees (excl. Palmae) above a minimum size limit. Percentages indicate the relative contribution of each family to the total stem density.

Family	>9.9 cm dbh			>29.9 cm dbh			>49.9 cm dbh		
	Average	SD	%	Average	SD	%	Average	SD	%
<i>Euporbiaceae</i>	69.2	16.2	14	3.2	1.9	4	0.3	0.5	1
<i>Dipterocarpaceae</i>	57.5	22.8	12	19.1	6.9	26	10.6	5.9	48
<i>Sapotaceae</i>	55.6	23.8	11	3.7	2.0	5	0.2	0.3	1
<i>Myrtaceae</i>	35.6	26.0	7	3.9	1.7	5	0.5	0.6	2
<i>Myristicaceae</i>	27.5	18.1	6	1.5	1.1	2	0.0	0.0	0
<i>Lauraceae</i>	25.0	11.6	5	4.2	4.3	6	1.2	2.0	6
<i>Burseraceae</i>	19.2	8.7	4	2.4	1.3	3	0.6	0.5	3
<i>Ulmaceae</i>	16.9	6.5	3	1.2	1.1	2	0.1	0.2	0
<i>Bombacaceae</i>	15.3	10.9	3	1.3	1.5	2	0.1	0.2	1
<i>Caesalpinioideae</i>	15.0	9.9	3	4.3	1.7	6	1.4	0.9	6
<i>Moraceae</i>	12.5	7.1	3	1.4	1.2	2	0.1	0.4	1
<i>Anacardiaceae</i>	10.6	5.1	2	1.9	1.1	3	0.6	0.6	2
<i>Annonaceae</i>	9.4	6.7	2	0.6	0.5	1	0.1	0.2	1
<i>Melastomataceae</i>	8.6	3.8	2	0.1	0.2	0	0.0	0.0	0
<i>Olacaceae</i>	8.1	5.1	2	0.9	0.9	1	0.0	0.0	0
<i>Fagaceae</i>	7.5	2.5	2	0.7	0.9	1	0.2	0.3	1
<i>Rubiaceae</i>	7.5	5.6	2	0.4	0.5	1	0.1	0.2	0
<i>Ebenaceae</i>	7.2	5.1	1	0.4	0.5	1	0.0	0.0	0
<i>Lecythidaceae</i>	6.7	4.8	1	0.4	0.5	1	0.1	0.2	0
<i>Sterculiaceae</i>	6.4	4.2	1	0.4	0.4	1	0.2	0.3	1
<i>Meliaceae</i>	5.8	4.0	1	0.5	0.3	1	0.1	0.2	1
<i>Guttiferae</i>	5.3	2.3	1	0.4	0.5	1	0.1	0.2	0
<i>Mimosoidae</i>	4.7	3.2	1	1.0	0.8	1	0.2	0.4	1
<i>Polygalaceae</i>	4.7	4.6	1	1.4	1.0	2	0.2	0.3	1
<i>Sapindaceae</i>	4.7	5.2	1	0.2	0.3	0	0.0	0.0	0
Other	42.2	18.0	9	18.6	7.1	25	5.3	5.1	24

cies in common with the research forests Bukit Soeharto (BSEF, Toma et al. 1998) and Wanariset Samboja (Valkenburg 1997), and to a lesser extent with Kutai National park (Miyagi et al. 1988).

In some of the plots small-scale logging activities have taken place at a low density. The main commodity that has been harvested is ironwood (*Eusideroxylon zwageri*) (Fredriksson & de Kam 1999). The cut stumps of this tree, which last for decades, are frequently found. Nevertheless a substantial population of large trees of this species is still present. Other human activities include hunting and the destructive collection of a natural essence from *Aquilaria malaccensis* Lam. (Fredriksson & de Kam 1999). Although also the Wartonokadri forest fragment is inevitably disturbed by small scale harvesting, the existing density of large trees is considered to be natural for the area.

Outline of this thesis

This thesis aims to provide a complete image of the different processes that determine the vegetation dynamics of a lowland dipterocarp rain forest after the occurrence of a severe drought and subsequent fire. Four processes are considered especially important: Tree survival, re-sprouting of trees that were killed above-ground, survival of the pre-fire seedbank combined with the subsequent establishment of seedlings, and the influx of seeds after the fire (the “seed rain”).

Chapter two describes the mortality of trees as the result of drought and fire disturbance. I try to separate the interactive effects of these two mortality agents. Due to their low density, large canopy trees are underrepresented in many studies. The sampling scheme in Sungai Wain aimed at including a representative

Table 1.5. Stem density (trees/ha) of most common species in the unburned vegetation, eight months after the drought (average \pm sd of 9 psp). Data are presented for all trees above a minimal size limit. Percentages indicate the relative contribution of each species to the total stem density. * For *Borassodendron* (Palmae), no dbh was measured. All individuals were <29.9 cm dbh. ** These species were included in the table because they are relatively common in the size class >49.9 cm dbh.

Species	> 9.9 cm dbh			> 29.9 cm dbh			>49.9 cm dbh		
	Aver.	SD	%	Aver.	SD	%	Aver.	SD	%
<i>Madhuca kingiana</i> (Brace) H.J.Lam	27.2	35.6	6	1.2	0.9	2			
<i>Gironniera nervosa</i> Planch	14.7	6.2	3	1.2	1.1	2	0.1	0.2	0
<i>Macaranga lowii</i> King ex Hook.f.	12.2	6.5	3						
<i>Borassodendron cf. borneensis</i> *	11.1	13.0	2						
<i>Shorea laevis</i> Ridl.	10.3	7.6	2	7.7	4.6	13	5.2	3.6	29
<i>Eugenia tawahense</i>	10.3	13.2	2	0.7	0.9	1			
<i>Payena lucida</i> (G.Don) DC.	10.0	9.0	2	1.1	1.5	2			
<i>Koompassia malaccensis</i> Maing. Ex Benth.	9.2	9.3	2	2.3	1.5	4	0.7	0.8	4
<i>Durio acutifolius</i> (Mast.) Kosterm.	8.9	8.0	2	0.1	0.2	0			
<i>Eusideroxylon zwageri</i> Teijsm. & Binn.	7.2	9.4	2	2.7	3.9	4	1.0	2.0	5
<i>Drypetes kikir</i> Airy Shaw	6.9	7.7	1	0.9	0.9	1	0.1	0.2	0
<i>Shorea ovalis</i> (Korth.) Blume	6.4	5.6	1	1.1	0.8	2	0.3	0.4	2
<i>Dipterocarpus confertus</i> Sloot.	5.8	5.7	1	2.3	1.7	4	1.1	0.9	6
<i>Vatica umbonata</i> (Hook.f.) Burck	5.3	4.4	1	0.2	0.4	0			
<i>Gymnacranthera farquhariana</i> (Hook.f. & Thomson) Warb.	4.7	8.5	1	0.2	0.4	0			
<i>Shorea parvifolia</i> Dyer	4.7	3.4	1	0.9	0.9	1	0.2	0.3	1
<i>Dipterocarpus tempehes</i> Slooten	4.7	10.0	1	0.2	0.4	0	0.1	0.2	1
<i>Dacryodes rostrata</i> (Blume) H.J.Lam	4.4	5.1	1						
<i>Chaetocarpus castanocarpus</i> (Roxb.) Thwaites	4.2	6.1	1	1.2	1.0	2	0.2	0.3	1
<i>Dipterocarpus cornutus</i> Dyer	3.9	5.3	1	0.9	1.2	1	0.5	0.7	3
<i>Ochanostachys amentacea</i> Mast.	3.6	2.2	1	0.5	0.5	1			
<i>Diospyros borneensis</i> Hiern	3.6	3.6	1						
<i>Aporosa dioica</i> (Roxb.) Mull.Arg.	3.6	5.9	1						
<i>Barringtonia macrostachya</i> Jack	3.6	4.7	1	0.3	0.4	1			
<i>Madhuca pierrei</i> Van der Assem	3.6	5.3	1	0.4	0.9	1	0.1	0.2	0
<i>Gonystylus affinis</i> Radlk	3.3	5.9	1	0.1	0.2	0			
<i>Shorea smithiana</i> Sym **	2.2	1.5	0	1.0	0.6	2	0.7	0.7	4
<i>Dipterocarpus humeratus</i> Slooten **	0.6	1.1	0	0.8	2.4	1	0.7	2.0	4
Other	278.3	49.7	59	32.0	53	7.3	40		

sample of trees above 30 cm diameter at breast height.

The level of mortality does not only set the density of the remaining seed sources, it also determines the abiotic environment after the fire. Chapter three starts by analysing the light availability after the fire. Subsequently it aims at providing an overview of the dynamics of different post-fire functional groups, and to estimate the relative importance of different vegetation processes that are at work.

Chapter four continues with a more detailed investigation of tree sprouting capacity, which appears to be an important component of the post-fire demo-

graphics of shade tolerant species. The chapter describes the sprouting capacity of saplings after experimental clipping in the unburned forest. It aims at understanding why differences in sprouting capacity between shade tolerant tree species occur. An explanation is sought in the species-specific availability of non-structural carbohydrates.

Chapter five investigates the vertical composition of the soil seed bank, and the effects of fire on the density of seeds. By studying seed germination under experimental conditions, we try to understand the germination sensitivity of seeds to different environmental factors.

Shortly after the fires, the Indonesian government issued a regulation, allowing concessionaires to harvest dead standing trees in their burned concession forests. Chapter six warns for the potentially harmful consequences of this practice, arguing that this so-called salvage felling is detrimental if the aim is to maintain a sustainable forestry concession or indeed any forest cover at all.

In chapter seven I present a synthesis of the preceding chapters, and return to the question what is the value of non-fire and fire succession theories for understanding post-fire vegetation dynamics in a dipterocarp rain forest.

Acknowledgements

I thank M.J.A. Werger and D. Sheil for their critical review of an earlier version of this chapter.



Unburned forest after the severe drought of 1997-1998 which killed one-third of the emergent trees. Sungai Wain, November 1998.

2

Separating the effects of severe drought and subsequent fire on tree survival in a lowland dipterocarp rain forest in East Kalimantan, Indonesia

With Douglas Sheil

Abstract

Over the last decades, extreme droughts and fires damaged extensive areas of forest in Indonesia. Notwithstanding the environmental impact of such large-scale disturbances, their effect on tree mortality has not been investigated in much detail in Southeast Asia. Especially data on the performance of very large trees are generally lacking. This study provides data on the patterns of tree mortality in a lowland rainforest in East Kalimantan after the drought of 1997-1998, which is one of the most extreme droughts that has so far been recorded in tropical ecological literature. Second, it gives a detailed account of the effects of the fire that followed at the end of this drought.

Eighteen permanent sample plots (psp) were established after the drought and fire in nine pairs of one unburned and one burned psp. This layout enabled us to separate the effects of drought and fire, which are entangled in the burned forest. The 1.8 ha size of each psp made accurate estimates of mortality among large trees possible. The psp were monitored twice, 8 months and 21 months after the disturbances.

Tree mortality was high in the first eight months after the drought ($19.1 \pm 4.4\%$ dead trees >10 cm dbh). We observed a high level of retarded mortality, resulting in $28.6 \pm 4.2\%$ dead trees after 21 months. Tree mortality after the drought was positively related to dbh. The burned forest showed an even much higher mortality ($60.6 \pm 10.4\%$ dead trees after eight months, and $74.4 \pm 8.7\%$ after 21 months). By subtracting mortality after drought from mortality after drought x fire in each pair of adjacent psp, we estimated that the fire was responsible for roughly 2/3 of the mortality in the burned psp. Fire mortality was negatively related to dbh: Drought x fire resulted in nearly complete mortality for individuals <10 cm dbh, whereas fire did not cause a significant increase in tree mortality >70 cm dbh. For the community as a whole the relation between dbh and fire mortality could be explained in terms of average bark thickness per dbh class.

For trees >30 cm dbh, mortality after drought and drought x fire ranged widely between species. Trees with a high wood density had a higher drought survival. For the trees in this size class, species-specific bark thickness did not explain the observed patterns in mortality after fire.

We related the intensity of occasional droughts in different everwet tropical forest sites (measured as the cumulative water deficit) with the percentage of drought-induced mortality, and found that below a cwd of 100-200 the increase in mortality is low, whereas it rapidly increases when the cwd becomes larger. We argue that the soil water reserve acts as a buffer which delays the actual onset of water stress for trees after a rainfall deficit has started to develop.

We conclude that the combined effect of drought and fire causes great damage to the forest vegetation, partly because the two disturbances act on different strata of the vegetation. The high level of retarded mortality that we observed underscores the necessity of long-term observations in order to understand the effects of such severe disturbances.

Keywords: Drought, fire, large-scale disturbance, lowland dipterocarp rain forest, Southeast Asia, tree mortality.

Introduction

Extreme droughts and the repeated occurrence of fires have formed an increasing threat to the lowland rain forests of Indonesia over the past decades. On the island of Borneo, dry spells (defined as periods in which the monthly rainfall remains below 100 mm) of three to four months have occurred over the past 50 to 100 years in most locations (Walsh 1996 b, Walsh & Newbery 1999). They are to some extent related to the El Niño-Southern Oscillation (ENSO) phenomenon. During the two extreme ENSO events in 1982–1983 and 1997–1998, these long droughts were accompanied by subsequent widespread forest fires. In the province of East Kalimantan, 2.6 million ha of forests burned during the drought of 1997–1998 (Hoffmann et al. 1999, Siegert et al. 2001). Despite these massive impacts few studies have documented the impact of drought and fire on the forest vegetation.

Increased tree mortality in tropical rain forest caused by an exceptional drought has been observed on several occasions (Leighton & Wirawan 1986, Condit et al. 1995, Nakagawa et al. 2000, Williamson et al. 2000). However, the severity of these “extreme” droughts is highly variable. With three dry months, followed by three wet (but less than average) months and a second dry period of another three months, this study reports the effects of the most severe drought in tropical rain forest modern ecological literature.

Fire can enter a tropical rain forest only after a dry period during which the soil litter layer dries out and becomes flammable (Uhl et al. 1988). Inside a forest with a closed canopy, a burn characteristically takes the form of a ‘surface fire’, which is largely confined to this dry litter layer. The low available fuel load, relatively high fuel humidity and low wind speed inside the forest limit the fire

intensity and the speed at which it spreads (Uhl et al. 1988). Virtually all woody plants that are killed remain standing after the fire (Leighton & Wirawan 1986, Woods 1988). High levels of tree mortality have nonetheless been reported in primary forests after such fire events (Leighton & Wirawan 1986, Woods 1988, Kinnaid & O’Brien 1998).

Since forest fires are confined to long periods of drought, fire induced tree mortality cannot easily be separated from mortality resulting from the preceding drought. The separate effects of drought and fire on tree survival cannot readily be studied on the same location, because the mortality caused by the drought is not yet quantifiable by the time the subsequent fire burns the area. The comparison of a burned forest with a nearby unburned forest is therefore the best available solution. Separating the effect of fire from the effect of drought on tree mortality by making such a comparison between bordering areas is the main objective of this paper.

In the current study we investigated the impact of an extreme drought on the vegetation. We monitored the changes in the overall stand structure of the forest. We analysed the influence of tree size and tree species, on mortality. We expected to find a negative correlation between tree size and mortality rate because larger trees with a deeper root system have more prolonged access to soil water (Wright 1992). Second, we expected that heavy-wooded species would have a lower mortality rate, because wood density is correlated with prevention of xylem implosion during drought stress, especially for wood densities $>0.7 \text{ g cm}^{-3}$ (Hacke et al. 2001). We compared the effect of the drought on tree mortality with other available studies in everwet tropical forest, in order to explore the relationship

Table 2.1. Summary of the rainfall pattern in Balikpapan and Samarinda during the 1997-1998 drought episode, based on the duration of the period during which the consecutive seven-day running average rainfall was below 3.3 mm (which is equivalent to the commonly used limit of 100 mm rain/month, when the dry period is prolonged). Data for 1997-1998 from Balikpapan airport and Samarinda airport, collected by BMG Meteorological Service. * Between brackets is the duration of the wet period (in days).

	First dry period	Wet intermission	Second dry period
Balikpapan			
Date	12-Jul-'97 to 5-Oct-'97	6-Oct-'97 to 12-Jan-'98	13-Jan-'98 to 24-Apr-'98
Number of days with 7 day running average <3.3mm rain	86	33 (99) *	99
Cumm. rain (mm)	48	482	13
Samarinda			
Date	9-Jul-'97 to 5-Oct-'97	6-Oct-'97 to 4-Jan-'98	5-Jan-'98 to 15-Apr-'98
Number of days with 7 day running average <3.3mm rain	89	51 (91) *	101
Cumm. rain (mm)	16	388	3

between the severity of a drought and the resulting increase in tree mortality.

We investigated how fire-induced tree mortality in a primary forest is influenced by tree size and species. Mortality has been correlated with bark insulation properties, and especially bark thickness (Gill & Ashton 1968, Vines 1968, Uhl & Kauffman 1990, Pinard & Huffman 1997). We expected to find a positive correlation between tree size and bark thickness, as well as substantial species-specific differences in bark thickness. As a consequence, we hypothesised tree mortality after fire to be highest amongst small trees and amongst thin-barked species.

Because retarded mortality has been observed after large-scale disturbances (Burslem, Whitmore & Brown 2000, also see Pedersen 1998), we monitored the patterns of mortality over a period of nearly two years following the disturbance. Due to the large proportion of dead trees that remained upright after the drought and the fire we expected an increase in tree fall during this period. The patterns of tree fall in relation to dbh were studied in both unburned and burned forest.

Study sites

The main research site is a water catchment reserve of circa 100 km², called Sungai Wain protection forest near to Balikpapan, East Kalimantan (1°16' S and 116°54' E) at 15 km from the Strait of Makasar (Figure 1.2). The largest part of this area was originally covered with lowland dipterocarp rain forest. A more detailed description of the vegetation is given in chapter 1. Some of the poorly drained valleys and lower parts of the area carry a shorter stature, infrequently flooded forest. The topography of the reserve consists of gentle to sometimes steep hills, and is intersected by several small rivers. The area varies in altitude from 40 to 140 m.a.s.l. Alisols, which are strongly weathered, very deep, infertile soils with a high fraction of loam and clay form the major soil type (FAO/Unesco/ISRIC 1988, van Bremen et al. 1990, MacKinnon et al. 1996).

Additional data on tree mortality were collected in the protected Wanariset Wartonokadri research forest (10 km Northeast of the Sungai Wain forest). This is a forest fragment of 50 ha surrounded on three sides by degraded forest and agricultural fields, and on the fourth

side is separated from another forest patch by a narrow road. The altitude, soil types, topography and rainfall are similar to the Sungai Wain forest. Although also this fragment is inevitably disturbed by small scale harvesting, the existing density of large trees is considered to be natural for the area.

Climate and fire regime

The average yearly rainfall is 2790 mm (Figure 1.3) (Vose et al. 1992). On average, the area does not experience less than 100 mm monthly rainfall. During the period 1948-1980, short dry periods (defined as having a monthly rainfall below 100 mm) were frequent (30 x one month, and 3 x two months), and most frequently occurred between September and November. Longer droughts were not recorded. After 1980, the pattern changed dramatically. Extensive droughts occurred in 1982-1983 and in 1997-1998, which were related to the occurrence of extreme ENSO events.

For a detailed characterisation of the drought in 1997-1998, we calculated the period during which the seven-day running average rainfall remained below 3.3 mm. This is equivalent to the commonly used limit of 100 mm rain per month when the dry period is prolonged. The drought consisted of two periods, which were similar in Balikpapan and Samarinda (Figure 1.3, Table 2.1). The first drought lasted for 12-13 weeks. During this period, precipitation was limited to a total of 16 to 48 mm. The following 13-14 weeks were wetter, and experienced a total of 388 to 482 mm rainfall. The wet intermission was interrupted by frequent short droughts: In Balikpapan 33 out of 99 days had a 7-day running average rainfall below 3.3 mm, and in Samarinda 51 out of 91 days. After this wet intermission a second drought of more than 14 weeks followed, with a cumulative precipitation of 3 to 13 mm. The drought ended around 20 April 1998.

To enable a comparison with other studies, for which only the relatively crude monthly rainfall patterns are available, we also analysed the monthly rain-

fall data. To estimate the intensity of the drought, the cumulative water deficit (cwd) was calculated. We developed the cwd as a refined version of the cumulative rainfall deficit (the sum of the amounts by which the rainfall of each month in a dry month sequence fell below 100 mm) (Walsh & Newbery 1999). In the cwd index, the rainfall deficit is gradually counterbalanced by any surplus precipitation above 100 mm per month, instead of returning to zero instantaneously, once the threshold of 100 mm monthly precipitation is reached.

The 1998 fire in the Sungai Wain primary forest was a typical surface fire, with an estimated average flame height of 0.5 m, an estimated depth of 20-30 cm, an estimated speed of 10-15 m/h (MvN pers. obs.), and a calculated fire intensity of circa 60 kW/m (Alexander 1982). A 0.5 m wide firebreak was enough to stop the fire, after which permanent control was necessary to prevent its escape. One third of the total area in the reserve burned during the 1982-1983 dry episode and burned again in 1997-1998 (Figure 1.2). Another third burned for the first time in March – April 1998, during the last part of the dry period. A core area of one third of the total area (3.5 x 8 km) was saved from the fire. The research was performed in the unburned area and the area that burned once.

Material and methods

In the Sungai Wain forest (SW forest), 18 permanent sample plots (psp) of 60 x 300 m (1.8 ha) each were laid out in unburned forest and in forest that burned once in 1998 (Figure 1.2). The psp were laid out in nine pairs, each pair of psp adjacent to each other over a man-made firebreak between burned and unburned forest. Thus, each pair of psp forms one contiguous transect of 60 x 600 m half in burned and half in unburned forest. The psp are spread over a total area of circa 20 km². In those areas where the psp are located, the firebreak does not correspond to any topographical feature.

Two surveys were done in the two years following the drought and fire. The

Table 2.2. Psp in Sungai Wain and numbers of individuals per dbh category.

Treatment	Number of individuals		Number of individuals	
	Psp	Dbh (cm) < 8	Psp	Dbh (cm) 8 > x > 28
Drought	1, 7, 9, 11, 13, 15, 17	1284	1, 3, 5, 7, 9, 11, 13, 15, 17	2654 1560
Drought x fire	2, 4, 6, 8, 10, 12, 14, 16, 18	3589	2, 4, 6, 8, 10, 12, 14, 16, 18	2214 1497

average date of measurement of the first survey was December 1998 (eight months after the drought and fire). During this survey, all dead and living stems larger than 28 cm dbh (diameter measured at 1.3 m height) were labelled and assessed. In each psp a subplot of 20 x 200 m was established, in which all trees between 8 cm and 28 cm dbh were assessed and labelled (Table 2.2). The lower limits of 8 cm dbh and 28 cm dbh were chosen in order to avoid the omission of trees with a dbh close to respectively 10 cm and 30 cm. In the analyses of the responses of trees, the lower limits of 10 cm and 30 cm dbh are used. *Palmae* above 8 cm dbh were labelled, but not included in the analysis unless specifically mentioned.

For trees which had protruberances at 1.30 m (buttresses or other irregularities), the diameter (D_x) was measured at 30 cm above the protruberances (Sheil 1995). The diameter was measured with a measurement tape up to a height of 2.5 m. Above this height, a ruler attached to a pole was rested against the stem and read from 10 m distance, following the method described in Alder and Synnott (1992).

If the diameters (D_x) collected above 1.30 m height were used as an uncorrected proxy for dbh, stem tapering would introduce a systematic underestimate of stem size in the dataset. To avoid such a systematic error, we estimated the relation between dbh and D_x to correct for stem tapering. For a set of 43 trees between 25 and 82 cm dbh with a straight stem, the diameter at 130 cm (dbh) was measured with a measuring tape, and the diameter (D_x) was estimated with the method described above (Alder & Synnott 1992) at 1.30 m, 2.50 m and 4.00 m height. We then calculated the ratio be-

tween dbh and D_x . We predicted that both the dbh of the tree and the height of measurement would influence the ratio (D_x /dbh). A multiple linear regression revealed that for a fixed height of measuring, the ratio (D_x /dbh) was independent of dbh (multiple regression anova, $n=43$, $F=1.13$, $sign=0.35$). Therefore dbh was not introduced as an independent variable in the equation. Curve estimation showed that the relationship between the ratio (D_x /dbh) and height of measurement was best predicted by a power function with the form $(D_x /dbh)=1.1816 * h^{-0.1168}$ ($R^2=0.40$, $df=123$, $F=80.6$, $p<0.001$). This function was subsequently used to estimate the dbh of stems which had been measured above 1.30 m high. We estimated that, if the correction was not applied, an underestimation of 9% and 16% in basal area would have been made for trees that were measured respectively at 2.0 m height and 4.0 m height.

In 16 unburned and 51 burned subplots of 100 m² each, which were evenly spread over the psp, all (dead and living) seedlings and saplings (stem length >50 cm and dbh <8 cm) were assessed and labelled (Table 2.2). Of these plants, the diameter was measured at 25 cm above ground level with a calliper, this is termed the diameter at ankle height (dah).

The position of each tree in the psp was determined, and the topography of each psp was mapped with a clinometer (Suunto) in steps of 10 m in the 20 x 200 m subplots and 20 m in the 60 x 300 m plots. Individuals with a leafless crown were considered dead in the sense that they had been killed aboveground. This included individuals that were resprouting from the roots or from the base

Table 2.3. Tree species of which living and dead individuals above 28 cm dbh were identified in the unburned and burned plots.

Species	Family	Abbreviation
<i>Artocarpus anisophyllus</i> Miq.	Moraceae	Arto anis
<i>Dipterocarpus confertus</i> Sloot.	Dipterocarpaceae	Dipt conf
<i>Dipterocarpus cornutus</i> Dyer	Dipterocarpaceae	Dipt corn
<i>Drypetes kikir</i> Airy Shaw	Euphorbiaceae	Dryp kiki
<i>Eusideroxylon zwageri</i> Teijsm. & Binn.	Lauraceae	Eusi zwag
<i>Gironniera nervosa</i> Planch.	Ulmaceae	Giro nerv
<i>Koompassia malaccensis</i> Maing. Ex Benth.	Caesalpinioideae	Koom mala
<i>Madhuca kingiana</i> (Brace) H.J.Lam	Sapotaceae	Madh king
<i>Shorea laevis</i> Ridl.	Dipterocarpaceae	Shor laev
<i>Shorea ovalis</i> (Korth.) Blume	Dipterocarpaceae	Shor oval

of the stem. The resprouting of stems that are killed above ground is discussed in chapter 3.

Local experts trained at the herbarium of the nearby Wanariset Sambodja research station identified living trees, as well as dead trees larger than 28 cm dbh belonging to 10 common species (Table 2.3). Dead trees below 28 cm were not identified because the result was expected to be taxonomically difficult and unreliable. Because of this, species-specific mortality is analysed only for trees above 30 cm dbh. Specific wood densities of these species were obtained from the literature (Burgess 1966, Suzuki 1999). Nomenclature follows Sidiyasa et al. 1999.

The average date of measurement of the second survey was January 2000 (21 months after the drought and fire). In this survey, we re-assessed whether trees were living or dead. We did not assess dbh during this survey. We also observed resprouting of trees and tree fall. Tree fall included both uprooting and stem breakage, of which the latter was defined as a stem which lacked primary branches (a snapped stem cannot easily be discerned from a stem that has lost all its primary branches).

In the Wanariset Wartonokadri forest, measurements were taken in five parallel transects of 10 x 200 m spaced at distances of 100 m (Slik et al. 2001). 599 trees above 10 cm dbh were labelled and identified in September 1997, during the early phase of the drought. Tree mortality was re-measured four months after the end of the drought (August 1998) and

again 22 months after the drought (February 2000). To ensure that the Wartonokadri forest and the Sungai Wain forest carried a similar vegetation type prior to the disturbances, which would justify the combined use of some of the data from the two sites, we tested for differences in the overall stand structure between the two sites.

The first survey in Wartonokadri provided us with an estimate of the average percentage of dead trees per transect before the onset of the drought. These results were used to estimate the number of living stems prior to the drought in the Sungai Wain Forest, where plots were established only after the disturbance. We estimated the density of living stems before the drought in Sungai Wain, by subtracting the percentage of dead trees as observed in the earliest survey in the Wanariset forest from the total stem density (i.e. the sum of living and dead stems) in the Sungai Wain forest after the drought.

Fire occurs only in unison with an extended drought, and as a result the tree mortality that is recorded after fire is a combination of drought-induced mortality and truly fire-induced mortality. Our aim is not only to measure tree mortality as the result of the combined effect of drought and fire, but also to partition the effects of these two factors. By subtracting the former from the latter we propose that we can quantify the additional mortality due to the influence of fire on the drought impacted forest stand. Percentages mortality were measured per psp.

The mortality due to fire was calculated by the pairwise subtraction of the mortality rate from burned and unburned forest in each pair of plots at any particular moment in time.

The effect of the drought on tree mortality was compared with data from other studies in everwet tropical rainforest. Census-periods differed between the studies in the comparison, and so did the background mortality (i.e. the annual mortality during a census period in which no major disturbance occurred). We calculated the drought-induced mortality by subtracting the site-specific background mortality from the mortality that was observed over the census period in which a drought occurred. In the case of Wartonokadri and Sungai Wain, the background mortality was estimated as the average background mortality from the other studies. Drought mortality and fire mortality are not presented in annualised rates, because the models used to calculate such rates assume a constant probability of mortality (e.g. Sheil et al. 1995). In the situation where a peak in mortality occurs in time, annualised mortality values are sensitive to small changes in the duration of the observation period and the exact dates of observation relative to the disturbance event.

To test whether the species-specific

thickness of the bark is a good predictor of the mortality of a species after the fire, we sampled the bark from trees of known dbh of 14 species in the unburned forest, using 15 to 34 trees per species (10 for *Macaranga lowii*). Each sample consisted of a single square piece (4 x 4 cm) of bark, which was removed with a chisel at 1.3 m height, avoiding obvious anomalies in the bark caused by buttresses. Bark thickness was measured in the field on four sides of the hole, using a calliper. The best fitting curve to these data was sought, which appeared to be a linear regression on log-log transformed data for all species except *M. lowii*. In order to maintain uniformity in the analysis, the relationship for *M. lowii* was established using the same relationship on log-log transformed data.

Two approaches were followed to test the effect of bark thickness on species-specific tree survival. Firstly, the populations above 10 cm dbh of 14 species were tested, based on the difference in the density of living trees between unburned and burned forest. A backward stepwise regression was used, which included (1) the values for a and b that described the regression line on the log-log transformed relation between dbh and bark thickness, and (2) the dbh value which is the 95% size limit for each population (95% dbh

Table 2.4. Average percentages of dead trees above 10 cm dbh per permanent sample plot at various censuses in the Wanariset Wartonokadri forest and Sungai Wain research forest.

Treatment	Average date	Time (months)		Cummulative perc. dead trees	
		Since end of drought and fire	Since last observation	Aver.	sd
Wanariset Samboja Wartonokadri forest (5 plots, 599 trees)					
Drought	Sep-97	-	-	2.62	1.7
	Aug-98	4	11	11.4	1.7
	Feb-00	22	19	22.2	2.4
Sungai Wain forest, unburned (9 plots, 3444 trees)					
Drought	Dec-98	8	-	19.1	4.4
	Jan-00	21	13	28.6	4.2
Sungai Wain forest, burned (9 plots, 3104 trees)					
Drought x fire	Dec-98	8	-	60.6	10.4
	Jan-00	21	13	74.4	8.7
Sungai Wain forest (9 paired plots)					
Exclusively fire	Dec-98	8	-	41.5	11.1
	Jan-00	21	13	45.8	8.7

limit). Ninety-five percent of the trees (>10 cm dbh) in a population had a dbh smaller than this value.

The second test, performed on nine populations above 30 cm dbh (of species which could be identified even when they were dead), was different in the respect that it was based on the numbers of living and dead trees in the burned forest.

Results

Stand structure and mortality at the community level

At the first census in the Wartonokadri forest, taken during the beginning of the drought, the average stem density of all trees per plot (living and dead, >10 cm dbh) was 627 ± 105 trees ha^{-1} (mean \pm sd, $n=5$), of which 610 ± 100 trees ha^{-1} were alive (Figure 2.1 a), which can be translated into an average of $2.6\% \pm 1.7$ dead standing trees per plot (Table 2.4). The basal area of all trees (living and dead, >10 cm dbh) was 32.4 ± 7.0 m^2 ha^{-1} (mean \pm sd, $n=5$) and the basal area of all

living trees was 31.5 ± 6.4 m^2 ha^{-1} (Figure 2.1 b). The overall stand structure in Wartonokadri was not significantly different from Sungai Wain (t-test comparison between plots in Wartonokadri forest ($n=5$) and Sungai Wain forest ($n=18$); Tree density of all trees: $F=0.37$, $p=0.86$, $df=21$, and basal area of all trees: $F=2.37$, $p=0.85$, $df=21$), which justified the use of the value of 2.6% as the percentage of standing dead trees present prior to the drought in the plots in Sungai Wain. Four months after the drought the percentage dead trees had increased to $11.4\% \pm 1.7$ in the unburned Wartonokadri plots, which corresponds to a total mortality of 8.8% over this 11 month period (Table 2.4). There was a high level of retarded mortality: The percentage dead stems nearly doubled between August 1998 and February 2000, resulting in $22.2\% \pm 2.4$ dead trees (19.6% mortality) 22 months after the drought.

At the first inventory of the unburned psp in Sungai Wain, eight months after the extreme drought, the stem density of all dead and living trees (>10 cm dbh)

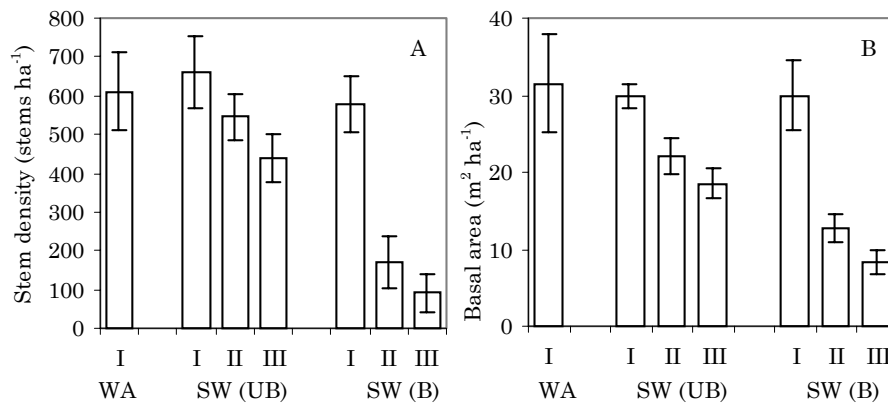


Figure 2.1. Stem density and basal area of the permanent sample plots (I) at the onset of the drought, (II) eight months after the end of the drought and fire and (III) 21 months after the end of the drought and fire. **(a)** Stem density per psp (stems ha^{-1}) of all living trees in Wanariset forest (WA) and Sungai Wain forest (SW). **(b)** Basal area per plot (m^2 ha^{-1}) of all living trees in Wanariset forest and Sungai Wain forest. All bars represent averages \pm sd across psp. The data from Wanariset are based on 5 psp of 0.2 ha each. The data from Sungai Wain are based on 9 psp of 0.4 ha for trees <30 cm dbh and 9 psp of 1.8 ha for trees >30 cm dbh. The stem density and basal area of living trees in Sungai Wain at the onset of the drought are estimates, based on the observation that of all standing trees (both living and dead) at the first census after the drought, an estimated 2.6% was standing dead at the onset of the drought. Two burned psp were excluded from the calculation of the average basal area, because the presence of a few very large trees made them outliers in this respect.

was 683 ± 94 stems ha^{-1} (average \pm sd, $n=9$), of which 545 ± 59 stems ha^{-1} were alive (Figure 2.1 a). Considering that 2.6% of these trees were standing dead prior to the drought, we estimate that the density of living stems at the beginning of the drought was 626 ± 90 stems ha^{-1} . The basal area of all (living and dead) stems was 30.6 ± 1.7 m^2 ha^{-1} (mean \pm sd, $n=9$) per unburned psp, of which the basal area of all living stems was 22.1 ± 2.3 m^2 ha^{-1} (Figure 2.1 b). This translates into an

estimated basal area of living stems of 29.8 ± 1.6 m^2 ha^{-1} at the beginning of the drought.

The stem density per diameter class and basal area per diameter class are presented in figure 2.2 a-d. It appeared that two burned psp (14 and 16) were outliers in terms of their basal area, because of the slightly higher frequency of very large trees. These two psp were excluded from the calculation of total basal area and the basal area per diameter

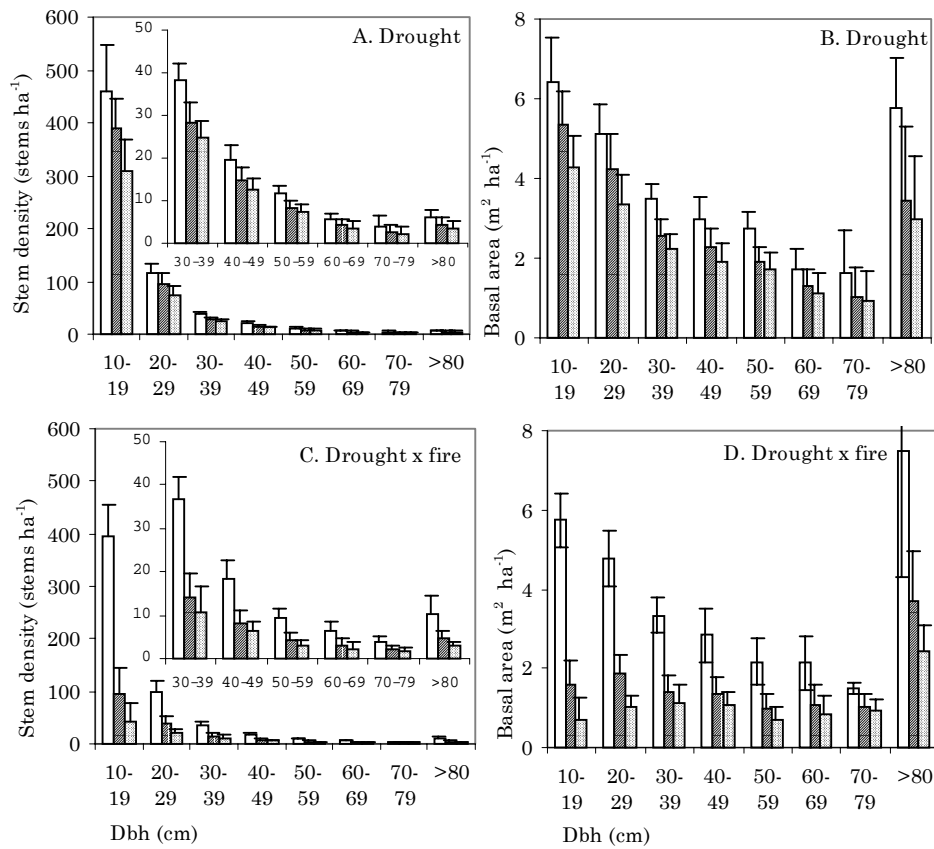


Figure 2.2. Time series of the stand structure of Sungai Wain forest (**a, b**) in the dried out psp and (**c, d**) in the dried out and burned psp. (**a**) and (**c**) show the average density of living stems per dbh class (stems ha^{-1}) (average + sd, $n=9$) per psp, and (**b**) and (**d**) show the basal area per dbh class (m^2 ha^{-1}) (average + sd, $n=9$) per psp. White bars: Stand structure at the onset of the drought, hatched bars: eight months after the end of the drought, and speckled bars: 22 months after the end of the drought. The stem density and basal area of living trees at the onset of the drought are estimates, based on the observation that of all standing trees (both living and dead) at the first census after the drought, an estimated 2.6% was standing dead at the onset of the drought. Two burned psp were excluded from the calculation of the average basal area, because the presence of a few very large trees made them outliers.

class. Tree density rapidly decreases with dbh. After the occurrence of the drought, this pattern is largely maintained, whereas in the burned forest the relation-

ship is greatly flattened. We calculated an average density of living very large trees (>80 cm dbh) prior to the disturbances of respectively 11 ± 3 trees ha^{-1} in the un-

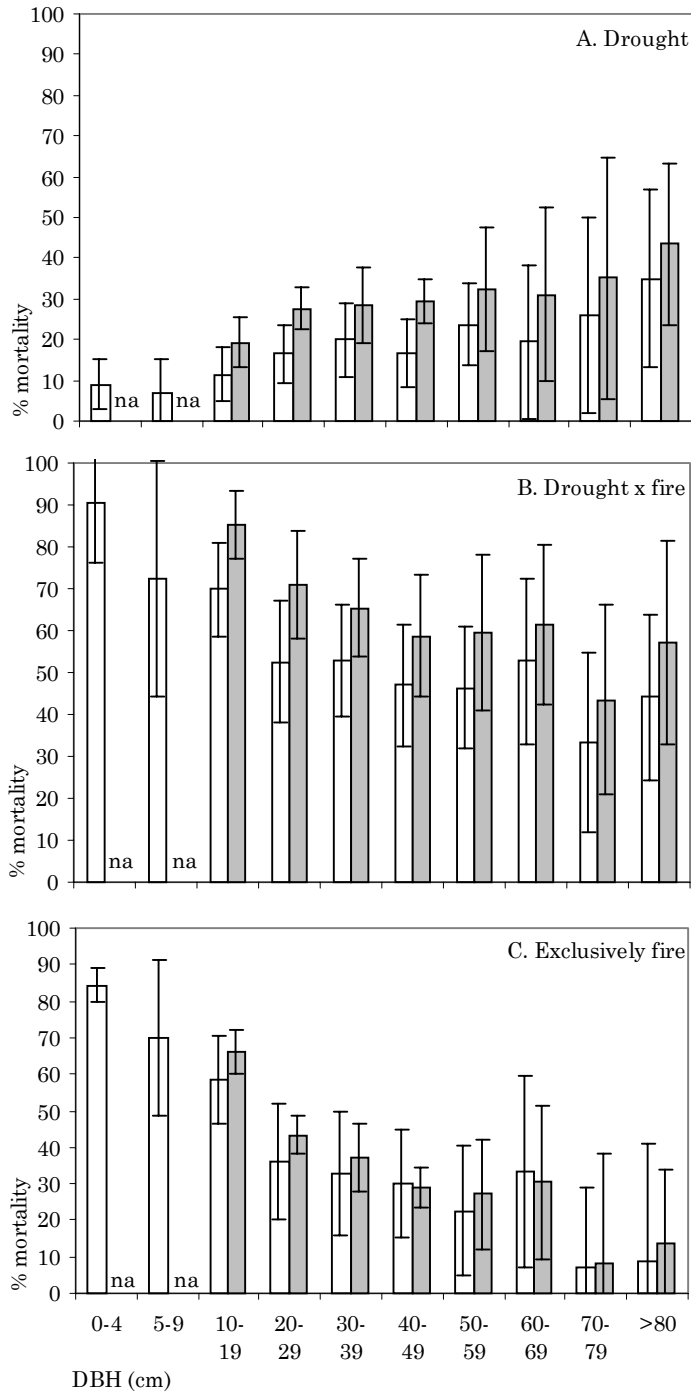


Figure 2.3. Average percentage tree mortality per dbh class per psp (average \pm sd, $n = 9$) in the Sungai Wain forest. **(a)** Unburned psp, **(b)** burned psp, **(c)** exclusive fire mortality. White bars: eight months after the end of the drought. Shaded bars: 21 months after the end of the drought. The exclusive fire mortality is calculated by pairwise subtraction of the drought mortality from the drought x fire mortality for each pair of psp. Stems below 10 cm dbh were monitored only once. Where values were not available “na” is shown.

Table 2.5. Paired samples t-test on the percentage dead trees per dbh-class in nine pairs of unburned and burned psp in Sungai Wain forest 21 months after the end of the drought and fire.

DBH class	df	t	p-value
8-9	8	24.5	< 0.001
10-19	8	24.0	< 0.001
20-29	8	10.7	< 0.001
30-39	8	7.5	< 0.001
40-49	8	5.6	0.001
50-59	8	4.0	0.004
60-69	8	3.6	0.007
70-79	8	0.86	0.417
>80	8	1.3	0.241

burned plots and 8 ± 3 trees ha^{-1} in the burned plots (Figure 2.2 a & c). From the four figures (2.2 a-d) it can be inferred, that these uncommon very large trees contribute largely to the basal area, and that most of the variation in basal area between the psp is caused by the presence or absence of a few of these very large trees.

Eight months after the extreme drought, the mortality rates in the unburned Sungai Wain plots were in the same order of magnitude as the Wartonokadri plots, leaving $19.1\% \pm 4.4\%$ (mean \pm

sd) trees dead per psp (Table 2.4). Also here, mortality remained high during the second year after the drought, resulting in $28.6\% \pm 4.2\%$ dead stems after 21 months.

In the burned psp in Sungai Wain, the percentage of dead stems above 10 cm dbh after eight months was $60.6\% \pm 10.4\%$ per psp, and increased to $74.4\% \pm 8.7\%$ after 21 months. This was equivalent to a mortality rate of $39 \pm 8.1\%$ among the trees that were alive at the first inventory. The exclusive fire induced mortality was $41.5\% \pm 11.1\%$ at the first census and $45.8\% \pm 8.7\%$ at the second census.

In both the unburned forest and the burned forest, mortality is related to dbh (Figure 2.3 a & b). However, while the percentage dead trees in the unburned forest increases with increasing dbh, the opposite is true in the burned forest. Below 10 cm dbh, mortality in the burned forest is above 85%. Above 40 cm dbh, where drought induced mortality becomes increasingly important, the percentage of dead trees in the burned forest remains approximately constant. For trees with a dbh above 70 cm, we found no significant difference between the percentages of

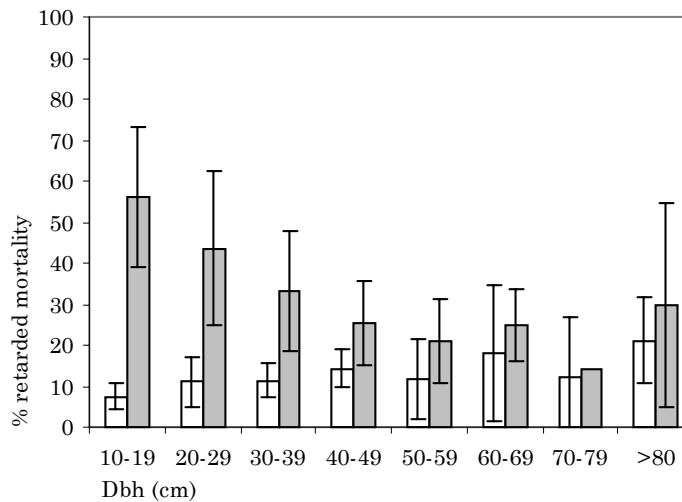


Figure 2.4. Percentage retarded mortality (average \pm sd, $n=9$) in Sungai Wain forest in the period between eight and 21 months after the end of the drought and fire in the unburned forest (white bars) and burned forest (shaded bars).

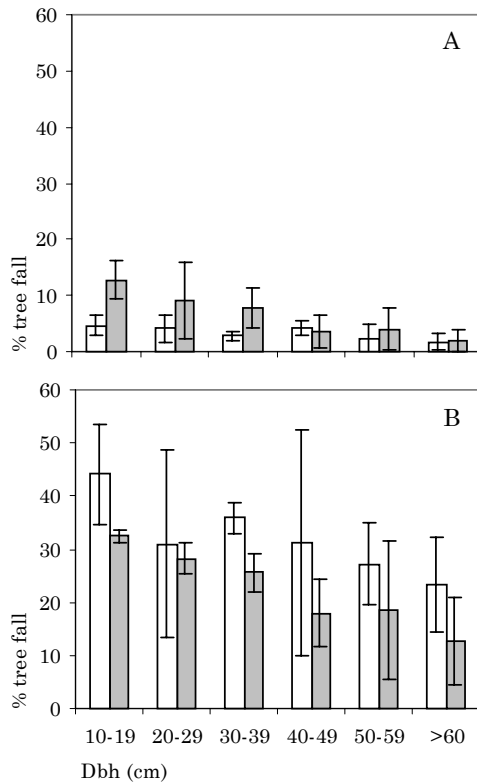


Figure 2.5. Percentage tree fall (average \pm sd, $n=9$) in Sungai Wain forest in the period between eight and 21 months after the end of the drought and fire of (a) trees living at the start of the census period and (b) trees that were dead at the start of the census period. White bars: Unburned forest. Shaded bars: Burned forest.

dead trees in the unburned and burned plots after 21 months (Table 2.5).

The retarded mortality showed a similar pattern in relation to dbh class as the mortality during the first observation period. In the unburned forest, retarded mortality between 8 and 21 months was fairly constant over all dbh classes, whereas in the burned forest the retarded mortality was negatively related to dbh (Figure 2.4). The frequency of tree fall was high in the burned forest: 28% of the standing dead trees and 7.5% of the living trees fell during the second year after the fire (Figure 2.5 a & b). Living trees had nearly twice as much chance to fall in the burned forest as compared to the unburned forest (4.0%), a difference which

was mainly due to the high rate of small trees falling in the burned forest (Figure 2.5 a). Tree fall of living and dead trees decreased with increasing dbh in both the unburned and the burned forest.

Species-specific mortality

Twenty-one months after the drought, the percentage of dead trees above 30 cm dbh ranged from 5% to 30%, while *Koompassia malaccensis* was an outlier with a mortality rate of 69% (Table 2.6). We assume that the high mortality of *Koompassia* was caused by another factor than the drought. Species-specific drought mortality of trees >30 cm dbh was negatively correlated to wood density (Figure 2.6, Pearson $\text{corr.} = -0.84$, $p = 0.005$, $n=9$). Especially *Eusideroxylon zwageri* appeared to be highly drought resistant.

In the burned forest, the percentage dead trees per species varied from 11% to 91%. For half the species, the exclusive fire mortality among trees above 30 cm dbh roughly equalled the drought mortality. In some species (*Dipterocarpus confertus*, *Shorea ovalis*) the trees above 30 cm dbh were unaffected altogether by the fire, while for most species the exclusive fire mortality was around 25%, with an extreme 75% mortality for *Artocarpus anisophyllus*. It should be noted that, obviously, the measured impact of the fire would have been manifold higher, had it been possible to include species-specific mortality amongst smaller size classes in the census. The percentage of dead Palms above 10 cm dbh (mainly *Borassodendron* sp. and *Oncosperma* sp.) was $3\% \pm 4\%$ after the drought and $10\% \pm 11\%$ after the fire (not shown in table).

Fire mortality and bark thickness

Curve estimation revealed that for all species combined, the relation between dbh and bark thickness was best described by a linear regression on log-log transformed data (Figure 2.7 a). The percentage mortality per dbh class that was caused exclusively by fire (i.e. corrected for drought mortality) is linearly related to the average bark thickness of trees in

Table 2.6. Species-specific mortality after drought and fire of trees above 30 cm dbh in Sungai Wain forest 21 months after the end of the fire and drought. The percentage dead trees after “drought” and “drought + fire” are given as the average percentage dead trees per psp (n= 6). To calculate the mortality exclusively caused by fire, the mortality after drought per psp is subtracted pairwise from the mortality after “fire + drought” for each pair of adjacent psp.

Species	Wood density (g cm ⁻³)	Percentage dead trees					
		Drought		Drought		Fire	
		Drought	sd	x fire	sd	Fire	sd
<i>Arto anis</i>	0.718	20	27	92	17	67	24
<i>Dipt conf</i>	0.803	15	18	8	10	-14	19
<i>Dipt corn</i>	0.843	14	13	29	6	15	18
<i>Dryp kiki</i>	0.999	13	14	31	30	27	18
<i>Eusi zwag</i>	1.066	5	6	39	5	30	10
<i>Giro nerv</i>	0.603	30	23	59	39	29	39
<i>Koom mala</i>	0.934	64	24	92	12	29	24
<i>Madh king</i>	0.79	17	19	59	38	42	38
<i>Shor laev</i>	0.933	23	18	44	14	29	21
<i>Shor oval</i>	0.537	28	22	20	27	-5	33

that class (Figure 2.7 b). The same linear regression based on log-log transformed values provided the best predictive relationship for the 14 individual species (Figure 2.8).

To test the influence of bark thickness on species-specific tree survival, populations above 30 cm dbh of nine species (which could be identified even when they were dead) were tested based on the numbers of living and dead trees in the burned forest.

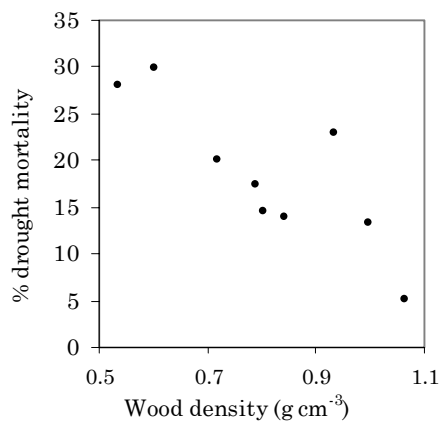


Figure 2.6. Species-specific mortality of trees >28 cm dbh versus specific wood density. *Koompassia malaccensis* was an outlier and has been excluded from the figure (for further explanation see text).

A backward stepwise regression revealed that for trees above 10 cm dbh, differences in population density in the unburned and the burned forest could not be explained by either the values a or b from the log-log transformed relation between dbh and bark, nor by the 95% dbh limit (n= 14, for all fitted models $F < 2.52$, $p > 0.13$).

Likewise, a backward stepwise regression on the percentage fire mortality of nine species above 30 cm dbh showed that neither the 95% dbh limit, nor the values a and b, explained a significant part of the variation of the species-specific fire mortality (n= 9, for all fitted models $F < 0.52$, $p > 0.57$). In other words, in neither case was bark thickness a good predictor of species-specific fire sensitivity.

Discussion

Drought mortality

The current paper gives an account of tree mortality as a result of large-scale disturbance caused by an extreme drought and fire in the tropical lowland rainforest of East Kalimantan. Notwithstanding the severity of the drought event, similar droughts have been natural to tropical rain forest ecosystems in South East Asia and Latin America (Walsh &

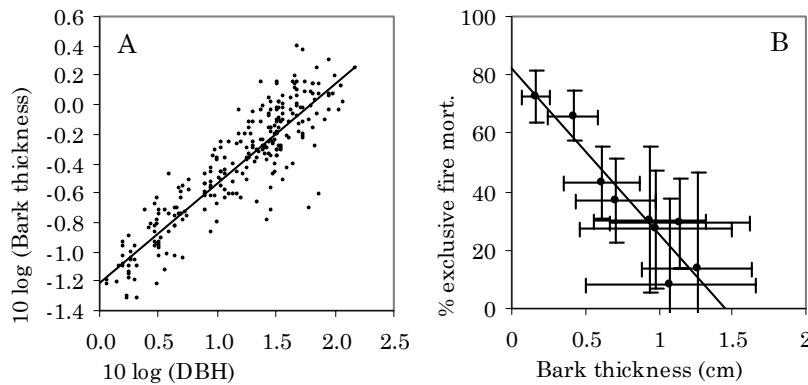


Figure 2.7. The relationship between dbh, bark thickness and exclusive fire mortality. **(a)** The relationship between log dbh and log bark thickness for 16 species combined. Regression line: $y = 0.669x - 1.21$ ($R^2 = 0.788$). **(b)** Average bark thickness (\pm sd) per 10 cm dbh class (of 16 species combined, as in figure 8a and the percentage mortality per dbh class (mean \pm sd) caused exclusively by fire. Regression line: $y = -56.3x + 82.1$ ($R^2 = 0.892$).

Newbery 1999). This study shows to what extent an extreme drought may affect forest structure and species composition. Mortality soared to 20-26% amongst trees >10 cm dbh two years after the drought, and species-specific mortality amongst trees >30 cm dbh varied ten-fold. Thus, differences in species-specific mortality may cause significant changes in local species composition.

In several researches it has been observed that in mixed tropical rain forest, mortality rate is not related to dbh for trees above a certain minimum size limit (Gentry & Terborgh 1990, Lieberman & Lieberman 1987, Manokaran & Kochumen 1987), or shows a slightly decrease with dbh (Rankin-de-Merona et al. 1990, Clark & Clark 1996). The marked size-dependent increase in mortality that was found in our study strongly deviates from this general pattern. A similar, if less pronounced, pattern of dbh-dependent mortality was found after unusual drought in the Neotropics (Hubbell & Foster 1990). It was expected that large trees would be least affected by drought due to their deep root system (Condit et al. 1995). However, the large trees in the present study appeared most vulnerable to drought, as was found in various other

studies (Leighton & Wirawan 1986, Hubbell & Foster 1995, Condit et al. 1995).

Xylem cavitation is the most frequent cause of death (Walsh & Newbery 1999). It seems that during a drought larger trees build up a water deficit more rapidly than smaller trees do. Probably, a smaller tree, which is more likely to grow in the shade, has a lower water evaporation rate per unit leaf area and thus depletes the available water in its root zone more slowly. The hypothesis that small individuals have an insufficient access to water supplies during drought may only apply to seedlings and saplings (Cavender-Bares & Bazzaz 2000), which were observed in some neotropical forests to suffer from high mortality during excessive drought (Hartshorn 1990), although this was not observed in the present study, nor in some other neotropical sites (Hubbell & Foster 1990, Condit et al. 1995). Differences in soil characteristics such as depth and drainage are probably responsible for this.

Species mortality after drought was negatively related with wood density. In a tropical dry forest, hardwood species grew on the driest sites, and could withstand a strongly negative xylem pressure (Borchert 1994). Hacke et al. (2001) argued that high wood density is primarily the

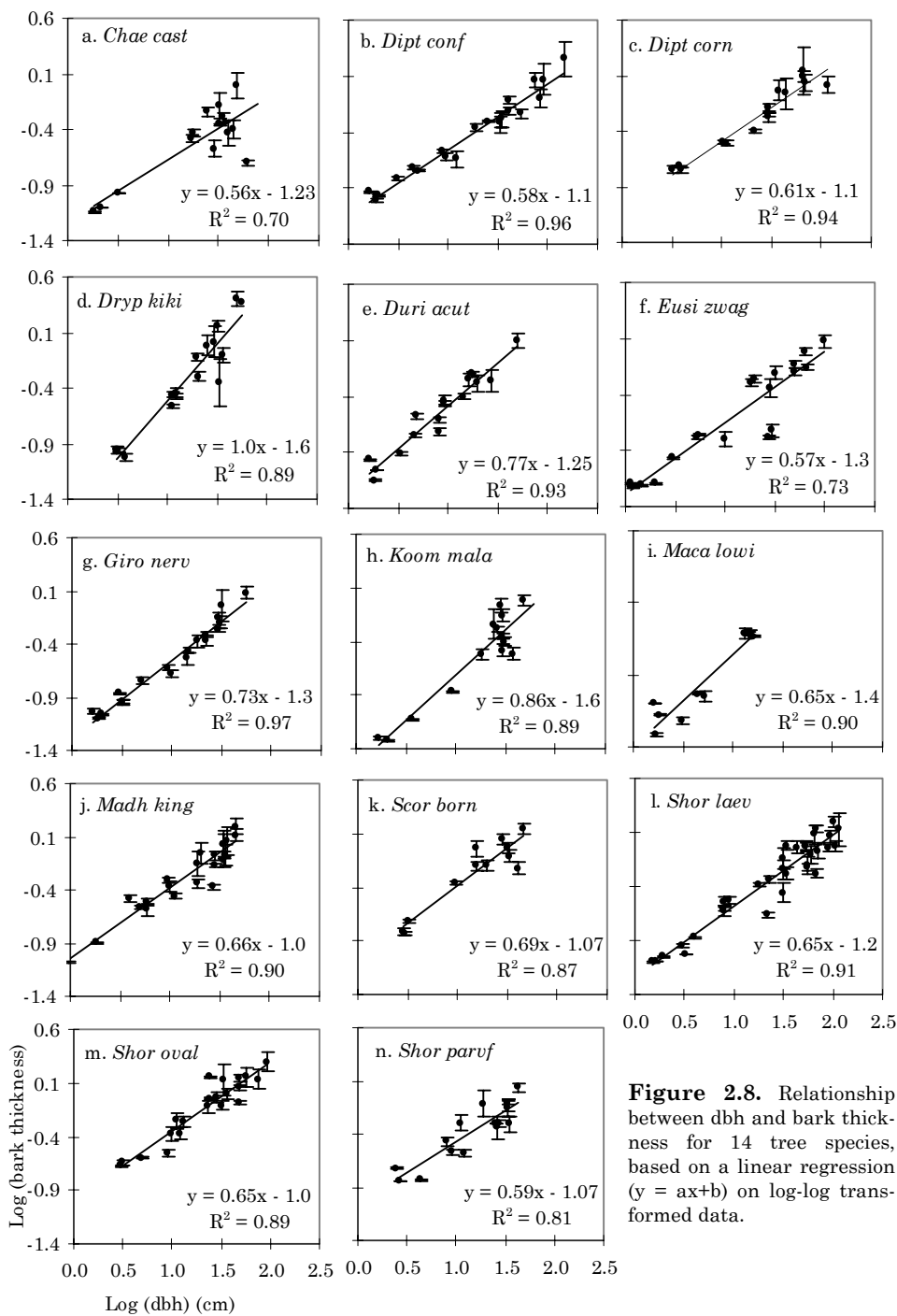


Figure 2.8. Relationship between dbh and bark thickness for 14 tree species, based on a linear regression ($y = ax + b$) on log-log transformed data.

consequence of thick walls of xylem vessels, which prevent their implosion under high negative xylem pressure. The observed pattern of drought mortality sug-

gests that the hypothesis of Hacke forms a highly meaningful alternative to the common view that high wood density is

Table 2.7. Mortality of trees above 10 cm dbh resulting from drought events in tropical rain forests in Asia and Latin America. None of the selected sites does experience an average monthly rainfall below 100 mm. # Balikpapan weather station: Two dry spells, intervened by a three months wet period with a total 482 mm rainfall. ## Mentoko weather station: Two dry spells, intervened by a three months wet period with a total 460 mm rainfall. * Annual background mortality calculated from data from from 1976 to 1982 in 6.5 ha psp's in virgin forest in the ITCI concession, East Kalimantan (Eijk-Bos & de Kock 1996). ** The measure for the drought induced mortality decreases because in the second year after the drought the post-mortality is below the average mortality before the drought. \$ The percentage drought induced mortality is calculated as the observed mortality minus the expected background mortality during the observation period.

Site	Sarawak, Lambir (core and periphery)	Central Amazon, Manaus (site 1501)	Central Amazon, Manaus (site 1301)	East Kalimantan, Wartono- kadri	East Kaliman- tan, Sungai Wain
Average					
Yearly rainfall (mm)	2700	>2000	>2000	2790	2790
Number of dry months	0	0	0	0	0
Drought event (<100 mm rain per month)					
Year	1997-1998	1997	1997	1997-1998	1997-1998
Duration rainfall deficit (months)	3	4	4	2 + 4 #	2 + 4 #
Total rain fall (mm)	139	195	195	10 + 142 (152)	10 + 142 (152)
Duration cwd (months)	3	5	5	3 + 5	3 + 5
Total rain fall during cwd period (mm)	139	295	295	140 + 316 (456)	140 + 316 (456)
cwd	162	205	205	190 + 258	190 + 258
Severe drought event (<50 mm rain per month)					
Duration (months)	1 + 1	2	2	2 + 3	2 + 3
Total rain fall (mm)	37 + 49 (86)	55	55	10 + 45 (55)	10 + 45 (55)
Tree mortality					
Background annual mortality (% per year)	0.89	0.94	1.19	1.69 *	1.69 *
Time between observations (months)	12	19 - 13	14 - 13	11 - 19	15 - 13
% mortality since pre- drought observation and [time since end of drought]	6.4 [4] - 4.3 [4]	3.0 [8] - 4.8 [21]	2.2 [7] - 3.4 [20]	8.8 [4] - 19.6 [22]	16.5 [8] - 26.0 [21]
% drought induced mortality \$	5.5 - 3.4	1.5 - 2.2	0.85 - 0.75 **	7.3 - 15.4	14.4 - 22.1
Reference	Nakagawa et al. 2000	Williamson et al. 2000		This study	

produced to avoid damage by external forces (Niklas 1992).

The substantial level of retarded mortality found in this study indicates that a single measurement in time will in general not suffice to estimate the mortality caused by an extreme drought. Ideally, measurements should be repeated every year until the yearly mortality has returned to the annualised mortality rate

prior to the disturbance event. The repeated measures on tree mortality in the study by Williamson et al. (2000) and in this study (Table 2.7) show that total retarded mortality increases as the drought event becomes more extreme.

In comparison with the other available studies on drought events in everwet tropical rain forest (Table 2.7), the drought in Sungai Wain caused a very

high mortality. Whereas the cumulative water deficit in Sungai Wain was two to three times larger than in the other studies, the resulting tree mortality was on average six times higher. The relationship between the percentage drought induced mortality after 20-22 months and the cwd (Table 2.7) is described adequately by an exponential relationship ($y = 0.023e^{0.016x}$ ($R^2 = 0.92$)) as well as by a linear relationship ($y = 0.048x - 4.32$ ($R^2 = 0.80$)). It is currently not possible to define the exact relationship between cwd and tree mortality. However, both models predict a negligible effect of drought as long as the cwd remains below 100 (linear model) to 200 (exponential model). Above that value the mortality rapidly increases with cwd. This pattern probably results from the fact that trees experience a delay in their actual water shortage after the onset of a rainfall deficit, resulting from the water reserve that is buffered in the soil (Poorter & Hayashida-Oliver 2000, van Dam 2001).

Fire mortality and its interaction with drought

The current paper presents the first study in a Southeast Asian rain forest comprising of a comparison between burned and unburned forest complete with replicates and a large set of trees >10 cm dbh as well as >30 cm dbh. For trees larger than 10 cm dbh the mortality in Sungai Wain was 74% 21 months after the fire, compared with 57% mortality 22 months after fire in Sabah (Woods 1988), 36% after four months in Kutai National Park, East Kalimantan (Leighton & Wirawan 1986) and 25% after six months in south-west Sumatra (Kinnaird & O'Brien 1998). Partly these differences result from methodology: the actual mortality in the study of Woods (1988) may have been higher, because trees that had fallen by the time of observation were not taken into consideration. The other two surveys were done shortly after the fire, and therefore have missed retarded mortality. Still, part of the variation is likely to be explained by differences in the intensity of the droughts preceding the fires. The

comparison of unburned and burned plots in our study elucidated the additive effect of drought and fire on tree mortality. Out of the total mortality among trees >10 cm dbh 21 months after the fire, almost 40% was caused by the drought.

Like in the unburned forest, a substantial level of retarded mortality was observed in the burned forest. The retarded mortality in the burned forest was two-fold higher than in the unburned forest, and was caused by a much higher mortality rate amongst trees of 10-40 cm dbh. Tree fall among trees in these size classes that were still alive at the first census was much higher in the burned forest. This can partly be explained by the high density of falling dead trees in the burned forest (even if the frequency of dead trees falling was not increased), which took living trees with them in their fall. Because the open canopy in the burned forest forms little obstacle for gusts of wind, wind throw of living trees was higher as well.

Tree specific fire mortality rate

Several studies have aimed at predicting the species-specific and dbh-specific chance of mortality of tropical rain forest trees after fire by assessing bark insulation properties and experimentally heating the bark of living trees (Gill & Ashton 1968, Vines 1968, Uhl & Kauffman 1990, Pinard & Huffman 1997). In these studies bark insulation turned out to be mainly determined by bark thickness. Few studies looked at the actual species-specific mortality of tropical rain forest trees after fire to validate the predictions made by the above mentioned experiments.

We found that, over the entire range of dbh classes, mortality caused by fire was negatively related to dbh and to bark thickness. Above 70 cm dbh, we did not observe a significant effect of fire on tree mortality. Leighton & Wirawan (1986) found the same pattern of dbh-related mortality. However, bark thickness did not explain the species-specific survival rates of trees >30 cm dbh. This may be due to the rather small differences in bark thickness between species of that

size, but it may also indicate that other factors than merely bark thickness have a large influence on tree mortality, such as an increased risk of fire mortality for size classes and species which frequently have a damaged stem base (Yeaton 1988). At any rate, the results suggest that in order to predict the fire sensitivity of a species, it is more effective to assess the dbh structure of the population than the species-specific bark characteristics. Attaining a large dbh appears one effective means to increase the chance of fire survival.

Conclusion

Our study shows that fire as well as drought may cause high levels of tree mortality. The effect of both disturbances is for a large part on different strata of the vegetation: Drought causes high mortality among trees in the canopy, whereas fire destroys most of the understorey and midstorey. Since fires only occur in unison with extended drought, their effect is disastrous to the forest vegetation. The most vulnerable tree species seem to be those which are confined to the understorey and midstorey. Species that grow to a large stature are likely to survive as a population, although interspecific differences in sensitivity are considerable, and not well understood.

Because of the high levels of retarded mortality, the full extent of the damage resulting from drought and fire can only

be determined if a forest is monitored for a considerable period of time after the disturbance. It seems likely that even our inventory 21 months after the event did not record the entire mortality caused by the disturbance events.

Acknowledgements

This research was performed at the International-Ministry of Forestry (MOF)-Tropenbos-Kalimantan research station, East Kalimantan. We are grateful for the support we received from the many staff members working there, especially M. de Kam and A. Susilo. K. Sidiyasa, Ambriansyah, Z. Arifin and Adriansyah from the Wanariset Herbarium were responsible for the tree identifications, and the staff from the Wanariset forest economy and monitoring unit established the permanent sample plots in Sungai Wain. Furthermore the fieldwork benefited greatly from the dedication of J. Helleman, N. Syah, F. Udin, and S. Laysa Putra. J.W.F. Slik kindly provided data from the Wartonokadri plots. We are grateful to J.A. Sayer, M. van Noordwijk, D.W. Dijkman, and G.M. Fredriksson for their support and fruitful discussions. M.J.A. Werger and F.J. Sterck made valuable comments on earlier versions of this manuscript. The research was supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) with grant 84-408 to M.v.N.

3

Post-fire dynamics of plant functional groups in a lowland dipterocarp rain forest

With Kade Sidiyasa and Heinjo During

Abstract

Following widespread fires, we studied the vegetation dynamics of a lowland dipterocarp rain forest in East Kalimantan, Indonesia. We used a *post-facto* experimental set-up of nine burned plots and nine unburned plots, the latter being protected by man-made firebreaks.

Three main functional groups of plants were distinguished *a priori*, and a fourth group *a posteriori*, on the basis of life-history attributes. These functional groups were shade tolerant tree species, light-demanding tree species, non-woody plants (including grasses, herbs, vines and ferns) and litter-gap demanding species. The virtual absence of non-woody species and light-demanding tree species in the unburned forest made a comparison for these functional groups between the two treatments redundant.

Unburned patches formed only 4% to 7% of the area that was not protected by a firebreak and were unevenly distributed over the nine burned plots. Apart from these patches, the burned area was fairly homogeneously affected. The canopy openness in the unburned forest was 5% and differed sharply from the 24% canopy openness in the burned forest. Canopy openness was significantly related to the percentage dead trees in the burned forest.

In the burned forest the species diversity of surviving stems (>10 cm dbh) per 0.4 ha was only 30% of the pre-disturbance diversity. The number of species per number of stems was nearly identical between the unburned forest and the burned forest. The relative abundance of families remained largely unchanged.

Contrary to our expectation, the percentage tree mortality explained little of the variation in the post-fire vegetation, apart from the percentage cover of *Pteridium caudatum*. Fern cover was negatively related to sapling density, while there was no such relation with sprout density. The patterns of individual species did often divert considerably from the patterns of these broad functional groups.

Establishment from the seed bank and post-fire seed dispersal determined the demography of light-demanding non-woody species and light-demanding tree species. These species formed an abundant element of the post-fire vegetation, even though mature trees of the same species were rare in the unburned forest.

Together with survival of trees >10 cm dbh, resprouting played an important role in the post-fire dynamics of the functional group of shade tolerant tree species, whereas seed rain appeared to be much less important than expected. The average density of sprouts was 22 per 100 m². The majority of the sprouts originated from (just) below ground parts of the stem (64%). Small parent stems contributed enormously to the density of sprouts, mainly because of their high pre-fire density, relative to larger stems. A single shrub species (*Fordia splendidissima* (Blume ex Miq.) Buijssen) with an estimated 100% sprouting frequency dominated the sprout community. Nevertheless, the sprout diversity (species per number of stems) was comparable to the diversity of stems >10 cm dbh in the unburned forest.

Species-specific sprouting frequency of shade tolerant tree species was negatively related to wood density, and so was the average stem length growth of sprouts in the second year. Sprout survival in the second year was 83% or higher and was not related to wood density. These patterns are discussed in terms of life-history trade-offs. They are important for predicting the successional

development of the post-fire vegetation. The capacity of stems to resprout allows for a relatively rapid recovery of the functional group of shade tolerant species. However, we predict that repeated disturbances will diminish this recovery potential by rapidly reducing the densities of resprouts.

Keywords: East Kalimantan, ferns, forest fire, forest succession, functional groups, Indonesia, large-scale disturbance, light availability, lowland dipterocarp forest, pioneer trees, plant-functional attributes, resprouting, secondary succession, seed bank, shade tolerant trees, tree mortality, vegetation recovery

Introduction

Over the past decades, extensive wildfires have become a recurring phenomenon in the evergreen dipterocarp forests of Borneo and Sumatra (Leighton & Wirawan 1986, Woods 1989, Nykvist 1996, Hoffmann et al. 1999, Siegert et al. 2001). The most devastating episodes of forest fires, during which large tracks of forest were severely damaged, occurred during periods of extreme drought that were related to supra-annual El Niño-Southern Oscillation (ENSO) events. Knowledge about the post-fire development of the tropical rain forest is very scattered. The major vegetation transitions following fire in Kalimantan have been studied (Riswan & Kartawinata 1988, 1989, Nykvist 1996, Kobayashi et al. 1999, Matius et al. 2001, Mori 2001, Toma et al. 1999, 2001 b) and for other tropical sites, successional transitions following large-scale disturbance have been summarised in comprehensive schemes (Hopkins 1981, Whitmore 1984, Whittaker et al. 1989, Richards 1996, Cochrane & Schulze 1999). However, these approaches provide only a sketchy understanding of the processes that determine the successional development.

Functional groups of plants can be defined on the basis of life-history attributes (Noble & Slatyer 1980, Bond & van Wilgen 1996). In fire-prone ecosystems, life-history attributes are an important tool in predicting post-fire vegetation dynamics. In the tropical rain forest, fire is an extremely infrequent disturbance (Sanford et al. 1985, Goldammer & Seibert 1989) and it is unlikely that plant species in a tropical rain forest developed adaptations to fire disturbance. Nevertheless, it can be useful to divide tropical rain forest plant species into broad groups, which

share common life-history attributes that determine their population dynamics and that may influence the vegetation development after fire. A study in which these functional groups are studied in unison will enhance our understanding of their relative importance in structuring the post-fire forest vegetation. We used an *a priori* deductive classification (Gitay et al. 1999) that was based on light requirements in the seedling phase and on plant growth form. We defined three functional groups of plants: shade tolerant woody species, light-demanding woody species and light-demanding non-woody species (Whitmore 1984, Swaine & Whitmore 1988, Finegan 1996). The research focuses on four main processes that are closely linked with certain life-history attributes, e.g. tree survival, resprouting, germination from the pre-fire seed bank and seed arrival through the post-fire seed rain.

Different light requirements form the most important discriminating factor in the characterisation of the different functional groups, since these are expected to exert a large influence on population development following fire. We expect that spatial variation in the vegetation matrix creates a spatially variable light climate at ground level, which likely determines the local development of the vegetation.

Our objectives are (1) to determine the changes in the abiotic environment, and more specifically the light availability, caused by fire, (2) to assess the relative importance of different regenerative processes in each functional group for the development of the vegetation structure and species composition of the post-fire vegetation, and (3) to characterise the

spatial heterogeneity of the vegetation after the fire. This research serves as a framework for the following chapters in this thesis, which probe into the details of the different processes of post-fire vegetation dynamics.

Non-woody species

All herbs, grasses and ferns were lumped into a single functional group, which was determined by maximum height of the species (<3 m) and the absence of woody stem tissue. For our purpose it was not necessary to define the functional group more narrowly, but it should be noted that we only included species that share a larger set of characteristics. Because the selected species were absent in the unburned forest and established widely after the fire, they must share characteristics of long-distance seed dispersal, high survival in the seed bank and a high light requirement for establishment and growth. The group of non-woody species included three terrestrial ferns (Pteridophytae), *Imperata cylindrica* [L.] Beauv. (Gramineae) and the vine species *Mikania scandens* Willd. (Compositae). We hypothesise that the local population densities of these species depend on variation in canopy openness. The presence of these species is important, because they can form dense stands. Such stands have been observed to inhibit the establishment, survival and growth of tree seedlings and resprouts in different forest types, including forests in Europe (den Ouden 2000) and Australia (Adam 1992), and tropical rain forest in Southeast Asia (Whitmore 1984, Richards 1996).

Light-demanding tree species

The functional group of light-demanding tree species is defined as those tree species which need relatively high light availability for successful seedling growth and establishment (Swaine & Whitmore 1988). Research in the Neotropics (review by Garwood 1989) and in Southeast Asia (Saulei & Swaine 1988, Metcalfe & Grubb 1995) has shown that populations of typical light-demanding

tree species are maintained in the undisturbed forest through the presence of long-lived seeds in the soil seed bank. In the soil, these seeds await the formation of a canopy gap, in which the increased light availability triggers them to germinate (review by Pons 2000). The gap-like environmental circumstances after fire may provide the appropriate circumstances for the germination and establishment of these species. We expect light availability to be the main determinant for the density of light-demanding tree seedlings and saplings in the burned forest.

Shade tolerant tree species

We defined the functional group of shade tolerant tree species as all tree species that are able to survive in the deep shade of the forest canopy (Swaine & Whitmore 1988). Accordingly, the species in this functional group were present as both juveniles and adults in the unburned forest. Population dynamics of shade tolerant tree species are influenced by whole-plant survival, resprouting, and post-fire seed dispersal. Here, we focus on stem survival and resprouting. Post-fire seed dispersal was not explicitly measured in the current study, because very few tree species fruited in the first two years after the fire in the unburned as well as the burned forest (G. Fredriksson, unpubl. data). Obviously the local density and diversity of surviving stems is one of the main factors determining the post-fire development of the vegetation. The patterns of community-wide mortality have been described in chapter 2. In the current chapter, we analyse the consequences of this mortality for the local species diversity.

Resprouting of stems remains a relatively understudied aspect of rain forest ecology, although its importance has been recognised repeatedly (Clark & Clark 1991, Kauffman 1991, Bellingham et al. 1994, Guariguata 1998, Bellingham 2000, Bond & Midgley 2001). Species-specific sprouting capacity includes the sprouting frequency (the percentage of stems that produces sprouts), as well as the survival rate and growth rate of resprouting

plants. In studies on resprouting after natural disturbances such as hurricanes (Putz & Brokaw 1989, Bellingham et al. 1994), and in experimental studies where saplings were severely damaged (Guariguata 1998, Chapter 4), species-specific and size-dependent variation in sprouting capacity has been observed. Such variation may be influenced by the amount of stored energy and nutrients in the plant (Bell et al. 1996, Chapin et al. 1990, Canham et al. 1999, Chapter 4), or by morphological constraints such as the density of dormant buds (Jobidon 1997).

Especially after fire, the capability of plants to sprout from well-insulated parts at or below ground-level may influence the size-dependent pattern of resprouting. If resprouting is limited to above ground stem parts, sprouting frequency is expected to be related to stem dbh and specific bark thickness, because with the increasing level of heat insulation provided by thick bark, tissue that has the capacity to resprout will have a higher chance of survival. If sprouting occurs from below ground parts, with the soil acting as an insulator, the frequency of sprouting may be independent of bark thickness.

We aim at explaining species-specific differences in sprouting capacity through a comparison with sapling ecology. Inter-specific differences in the performance of saplings have been characterised as a life-history trade-off between growth rate in high light environments and survival rate in understorey shade (Hubbell 1995, 1998). Since high maximum growth rates of species are associated with low wood density (Suzuki 1999, ter Steege & Hammond 2001), one may expect that (1) at sites with high light availability there is a negative correlation between wood density and growth rate, and (2) when light availability is low, there is a positive correlation between wood density and survival rate. Given the high light availability in the burned forest, we predict that the rgr of sprouts will be negatively related to wood density, whereas sprout survival will be independent of wood density.

Interactions between functional groups

The different functional groups in the post-fire vegetation may inhibit the establishment, growth and survival of other groups. In this respect, *Pteridium caudatum* is known to inhibit establishment and survival of other species in many forest types worldwide (Fletcher & Kirkwood 1979, den Ouden 2000), and *Imperata cylindrica* is a notoriously persistent species in many parts of Southeast Asia. Light may become quickly limited close to the ground in places where a dense undergrowth develops. In such cases, fast-growing species are expected to reduce the growth and survival of slower-growing species. We predict that the presence of each functional group is negatively correlated with the density of other functional groups. Since ferns and light-demanding tree species obtained roughly equal height during the first year after the fires (MvN pers. obs.), it is not possible to make a general prediction which of these two functional groups would reduce the performance of the other group. Due to their much slower growth rate, we predict that the sprouts of shade tolerant trees are negatively affected by the presence of the other two functional groups.

Material & methods

Site description

The study was conducted from 1998 to 2000 in the Sungai Wain protection forest (1°16' S and 116°54' E; altitude 40 to 140 m.a.s.l.) near Balikpapan in East Kalimantan, Indonesia. The local climate is tropical perhumid with an average yearly rainfall of 2790 mm. The average temperature at mid-day is 30°C (Toma et al. 2001 a). More detailed accounts of the drought episodes that occur in the region and of the local soil characteristics are given in chapter 1 and 2.

In 1997-1998 an exceptional drought occurred, during which a large part of the 100 km² Sungai Wain reserve burned. Only an area of approximately 3.5 x 8 km in the core of the reserve was prevented from burning by a network of man-made

firebreaks of 0.5 m wide. This core area supports a primary lowland dipterocarp forest. A 70 km² area of burned forest surrounds the core on three sides. As a result of the fires this surrounding forest was heavily damaged. After the fire, the standing dead and living trees formed a spatially variable matrix (Chapter 2). Eight months and 21 months after the fire, the density of surviving trees (>10 cm dbh) was respectively $218 \pm 80 \text{ ha}^{-1}$ and $128 \pm 65 \text{ ha}^{-1}$ (average \pm sd, $n=9$). This is approximately one third and one fifth of the total stem density (dead + living stems) of $594 \pm 76 \text{ ha}^{-1}$ that was found in the adjacent unburned plots. The decrease in living basal area was similar, with a decrease of 56% and 70% relative to the original $33.1 \pm 6.1 \text{ m}^2 \text{ ha}^{-1}$. Nearly all dead individuals from seedlings to emergent trees remained upright after the fire. Therefore the area supported nearly the original density of stems.

Plot design

Permanent sample plots (psp) were set up at both sides of the man-made firebreaks. Because the fire-breaks did not correspond to any topographical feature in the places where the psp were positioned, this allowed for a random sampling scheme with paired plots of unburned and burned forest. The set-up of the study consisted of 18 permanent sample plots (psp) which were distributed in nine pairs of one unburned and one burned psp over an area of circa 20 km². A man-made firebreak separated the two adjacent psp in each pair of plots.

Within the psp, areas of different sizes were delineated to allow for a stratified sampling scheme. Each psp consisted of an area of 60 x 300 m (1.8 ha) with a subdivision of 20 x 20 m. Within the psp, a smaller plot of 20 x 200 m (0.4 ha) with a subdivision of 10 x 10 m was located. The topography was measured at a scale of 20 x 20 m for the 1.8 ha psp and 10 x 10 m for the 0.4 ha plots. Slopes were measured with a Suunto clinometer, after which a map was made of each psp. Chapter 1 provides more details on plot topography.

Light availability

We estimated the light climate in the unburned and burned forest in January 1999, 10 months after the fire. In the centre of six 10 x 10 m subplots per psp, hemispherical photographs were taken at 1 m above ground level ($n=54$ in unburned forest and $n=54$ in burned forest). On the basis of these photographs, canopy openness was estimated using Winphot 5.0 (ter Steege 1996). With a general factorial anova we tested the hypothesis that, in the burned forest, canopy openness increased with the percentage of dead basal area and decreased with total basal area (living + dead) in 54 burned subplots of 100 m².

Sampling scheme

To measure the dynamics of the vegetation, observations were made in the burned forest at two times after the fire, in December 1998, eight months after the fire, and in January 2000, 21 months after the fire. Each observation consisted of a stratified scheme of measurements on different components of the vegetation. For the field inventory, dead, living and resprouting trees were divided in three size classes: >30 cm dbh; >10 cm dbh; and >50 cm high and <10 cm dbh. Other components of the vegetation that were studied included tree saplings and non-woody species. Ferns and light-demanding saplings were studied only in the burned forest, since they were virtually absent from the unburned forest. Resprouting stems were also studied in the burned forest, and for six common species the densities of small stems were also studied in the unburned forest. Nomenclature follows Sidiyasa et al. (1999) and Slik (2001).

The term "dead" was used for trees of which the above ground parts had died. Dead trees did not possess green leaves in the crown or along the stem (both indications that the cambium had survived in at least some section of the stem). However, the root system of such trees may have been alive: Trees that resprouted from their basal parts, either below ground or just above-ground, but which did otherwise not possess green leaves, were con-

Table 3.1. Different points of origin of resprouts.

Abbrev.	Location	Description
as > 2m	along stem above 2 m	sprout originating along the stem, from a point at least 2 m above the soil surface
as < 2m	along stem below 2 m	sprout originating along the stem, from a point >0.3 m and <2 m above the soil surface
bag	base above ground	at the base, sprout originating from above the soil surface
bbg	base below ground	at the base, sprout originating from below the soil surface
rag	roots above ground	from the roots, sprout originating from above the soil surface
rbg	roots below ground	from the roots, sprout originating from below the soil surface

sidered dead. Such cases were recorded in a separate category.

Stem survival above 10 cm dbh

At the first observation period, all dead and living trees >28 cm dbh in each 1.8 ha psp were labelled, mapped and their diameter at 1.30 m above ground level (diameter at breast height, dbh) measured using a measuring tape to the nearest millimetre. In the 0.4 ha plots, all dead and living trees >8 cm dbh were labelled, their position recorded and their dbh measured. The lower limits of 28 cm and 8 cm dbh were chosen in order to avoid the exclusion of individuals with a dbh close to the lower limits of respectively 30 cm and 10 cm dbh. Where appropriate, individuals between 28-30 cm dbh and between 8-10 cm dbh were later excluded from the analyses. Living individuals were taxonomically identified. Numbers of resprouts were recorded, and the length and diameter at 25 cm above the point of attachment of the tallest sprout were measured when the point of attachment was below 2 m on the parent stem. In the second inventory, all trees above 8 cm dbh were re-inventoried. We recorded whether they were living or dead and when present, the diameter and length of the tallest sprout was measured.

For trees which had protruberances at 1.30 m (buttresses or other irregularities), the diameter (Dx) was measured at 30 cm above the protruberances (Sheil 1995). Using a subset of regular stems, we measured the degree of stem tapering. The resulting curve estimation allowed us to calculate the dbh for trees of which the diameter had been measured above 1.30 m (Chapter 2).

Stems below 10 cm dbh, post-fire saplings and non-woody species

In six burned psp (2, 4, 6, 8, 10, 12) we selected 10 subplots of 10 x 10 m (total n= 60 subplots) spread over the entire length of the psp. In these subplots, all living and dead small trees (defined as stems over 50 cm high but <10 cm dbh) were labelled and mapped. Living trees were identified taxonomically. Stem diameter was measured either at 1.30 m (dbh) or, for individuals <1.30 m high, at 30 cm above ground level (diameter at ankle height, abbreviated as dah). We observed a linear relationship between dbh and dah, based on measurements of both characteristics on a large number of individuals ($Dah = 0.527 + 1.021 * dbh$, n= 286, $R^2 = 0.90$, $p < 0.001$). Where needed, this relationship was used to allocate individuals to their appropriate size category.

In this chapter, the terms “seedling” and “sapling” refer to individuals that were present in the post-fire vegetation either as the result of whole-plant survival, or when they established from seed after the fire. Plants were identified as resprouts when they consisted of one or more post-fire shoots which originated from a parent stem which had been killed by the fire.

Parent stems of resprouts were usually still standing upright, even for the smallest individuals. The diameter of the parent stem was measured at dah for individuals <1.30 m high, and at dbh for individuals >1.30 m high. To distinguish between sprouts originating from below ground and seedlings, sprouting points were excavated. Based on the location of

origin, resprouts were classified into five classes (Table 3.1). All resprouts were labelled, and identified taxonomically. We measured the length of the tallest sprout and its diameter at 30 cm above the point of origin. In the second inventory the size and survival of the resprouts was assessed. In this inventory, we also recorded the Dawkins light class for each sprout at its highest stem point (Dawkins & Field 1978). Because taking herbarium samples from resprouts would have affected their growth, resprouts were taxonomically identified in the field, which explains the sometimes restricted level of identification.

In each of these six burned psp, we selected three subplots of 10 x 10 m (n=18) in which we measured the density of all dead stems >50 cm high. This allowed an estimate of the sprout frequency for the community as a whole (e.g. independent of species). To allow for a species-specific estimate of the sprout frequency, the density of individuals >50 cm high of six common species (Table 3.11) was estimated in 60 unburned subplots of 10 x 10 m evenly spread over three psp. Here, the ratio of the density of resprouts in the burned forest and the number of individuals in the unburned forest gives an estimate of the species-specific sprouting ratio. Wood densities of these species were obtained from the literature (Burgess 1966, Soerianegara & Lemmens 1993, Suzuki 1999).

The density of saplings (>1.30 m high) establishing from the post-fire seed bank was measured in the second inventory. We limited our observations to a few characteristic taxa (Table 3.7). In the same area a full inventory of seedling density and seedling diversity was made by other researchers (Priadjati 1999, Eichhorn unpubl. data). The dbh of all saplings >1.30 m high of *Macaranga gigantea*, *Dillenia cf. borneensis* and *Vernonia arborea* were measured.

In the first inventory, ferns and other non-woody species were scarce, and not recorded. In the second inventory, the percentage ground cover of the three most common fern species, *Imperata cylindrica* and *Mikania scandens* was estimated.

Percentage ground cover was defined as the percentage of the total area which was covered by a specific species when projecting its canopy on the ground. We estimated the number of square meters covered by a species surveying each 10 x 10 m subplot from an elevated position.

Data analysis

A correspondence analysis (ca) was used to explore variation in vegetation composition between the subplots, and to explore the correlation between vegetation composition and environmental variables. Independent variables were included as factors (Site with two classes, Topography with 5 classes and slope with 3 classes) or as co-variables (the other independent variables). The two classes for "Site" were the two locations ("East" and "West") where three pairs of plots were located (Figure 1.2). Topographic classes are identified in table 3.5. The three slope classes were flat to gentle (slope <10°), moderate (slope 10-20°) and steep (slope >20°).

With multivariate anovas, we tested the effect of various environmental factors and components of the vegetation on the density of several taxa. Initially, multivariate anovas were performed in which all two-way interactions between independent variables were included. Where these interactions were not significant, they were excluded from the final analysis. The densities of other elements of the vegetation were only included as independent variables when these elements were expected to influence the establishment of the dependent taxa. Data on stem densities were square-root transformed, data based on percentages were arcsin transformed, and the total ba per subplot was log transformed (Sokal & Rohlf 1981).

Results

Unburned patches

The area that was not protected by the firebreak had burned for the largest part. Unburned patches were rare and were unevenly distributed over the

Table 3.2. Distribution of topographical units and their fire history in the burned psp.
* The “unburned” category includes plots that naturally escaped the fire completely or partly.

Fire history	Topographical unit							Total
	Valley	Low flat	Lower slope	Mid slope	Upper slope	High flat	Ridge	
<i>10 x 10 m subplots</i>								
Burned	14	17	20	170	75	25	12	333
Unburned*	2	10	0	5	1	1	0	19
Total	16	27	20	175	76	26	12	352
<i>20 x 20 m subplots</i>								
Burned	9	13	27	120	60	25	13	267
Unburned*	3	5	5	11	3	3	0	30
Total	12	18	32	131	63	28	13	297

burned forest. They added up to $7.5 \pm 12.7\%$ (average \pm sd, $n= 9$) of the area in the 0.4 ha plots, and to $4.4 \pm 8.5\%$ in the 1.8 ha plots. Unburned patches occurred in 4 out of the 9 permanent sample plots of 1.8 ha. The unburned area in one of the sample plots made up for half the total area that naturally escaped the fire.

Unburned patches and partly unburned patches were significantly associated with certain topographical units in the landscape, mainly occurring in valleys, low slopes and low flat areas (Chi² test on 10 x 10 m subplots: Chi²-value= 59.2, $p < 0.001$, $n= 356$; Chi² test on 20 x 20 m subplots: Chi²-value= 26.9, $p= 0.008$, $n= 297$). However, even these areas had a high chance to burn (Table 3.2).

Canopy openness and its relation with local damage to the vegetation

Canopy openness increased sharply after the fire. In the unburned forest, canopy openness was $5.3 \pm 2.9\%$ (average \pm sd, $n= 54$) and in the burned forest it was $24.1 \pm 7.1\%$. Canopy openness in the burned forest was significantly related

Table 3.3. Relation between canopy openness and stand characteristics per 100 m² subplot, analysed in a multiple regression anova. $N= 24$. Percentage dead trees and percentage dead ba were arcsin transformed, and total ba was log transformed.

Source	df	F	Sig.
Corrected Model	3	8.99	0.001
% dead trees	1	14.66	0.001
% dead ba	1	2.74	0.114
Total ba	1	0.21	0.652
Error	20		

with the percentage dead trees per 100 m² plot (Table 3.3). The linear regression between canopy openness and percentage dead trees (not transformed) was $y= 2.4 x + 19.7$ ($df= 22$, $R^2= 0.41$, $p < 0.001$). Total ba and percentage dead ba did not add significantly to the explained variance. In the following analyses, the percentage dead trees has been used as a proxy for light availability.

Diversity of surviving shade tolerant trees

At 0.4 ha plot level, the number of species in the unburned forest (>10 cm dbh, excluding *Palmae*) decreased from 70.1 ± 5.3 (average \pm sd, $n= 9$) in the first census to 62.8 ± 7.8 in the second census. In contrast, the number of species in the burned forest at the second census was only 20.8 ± 10.6 per 0.4 ha. The species-area curve for the area (Figure 3.1 a) shows that up to an area of at least 3.6 ha, the species number in both the unburned and the burned forest continued to rise. Even on a logarithmic area scale, the slope of the curve continued to increase with area. Over all the scales of measurement the species number in the burned forest was at least a factor two lower than in the unburned forest. In contrast, the number of species per number of stems was nearly identical between the unburned forest and the burned forest (Figure 3.1 b). The difference in species number per area must therefore be caused by the drastically reduced stem density in the burned forest.

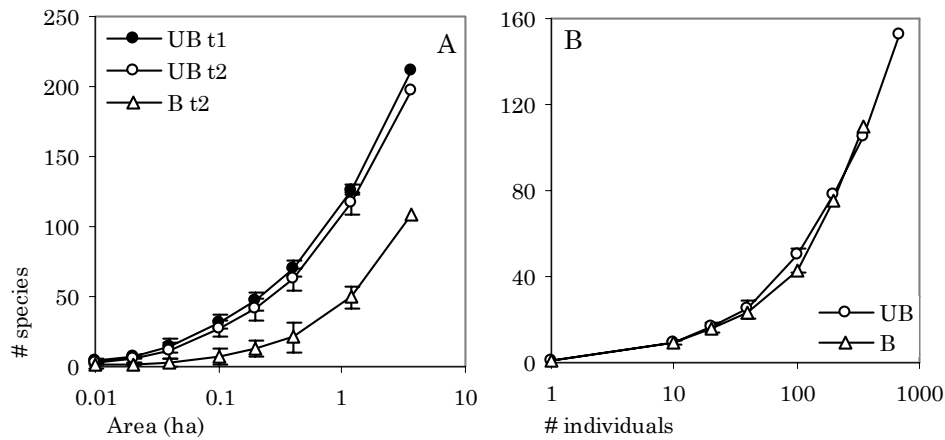


Figure 3.1. (a) Species-area curve of stems >10 cm dbh in the unburned and the burned forest at two time steps after the disturbances. (b) Species diversity per number of stems after 21 months.

The pattern of reduced diversity in the burned forest was similar at the genus level and family level. Eight months after the drought the number of tree genera was 54.3 ± 4.2 per 0.4 ha (average \pm sd, $n=9$) in the unburned forest, and 21 months after the drought it was further reduced to 49.6 ± 5.3 per 0.4 ha. At that second inventory the number of genera was 18.2 ± 8.5 per 0.4 ha in the burned forest plots. The number of tree families per area was also greatly reduced by the fire. In the unburned forest we counted 30.9 ± 2.5 families 0.4 ha^{-1} (average \pm sd, $n=9$) eight months after the drought, and 29.4 ± 2.6 families 0.4 ha^{-1} 21 months af-

ter the drought. In contrast, the burned forest contained only 13.3 ± 5.3 families 0.4 ha^{-1} 21 months after the fire. The relative abundance of families remained largely unchanged (Table 3.4). Changes in the populations of individual species have been analysed in chapter two.

General patterns of post-fire functional groups

The relative abundance of the three different functional groups in this study was drastically different between the unburned and the burned forest. The three species of terrestrial ferns were not observed in the unburned forest, while they formed the most prominent element of the post-fire vegetation. Ferns occurred with an average ground cover of $61\% \pm 26\%$ (average \pm sd, $n=59$) in the burned forest at the second inventory. In none of the 100 m^2 sample plots did their total ground cover fall below 12%. Also saplings of tree species such as *Macaranga* spp., *Mallotus* spp., *Vernonia arborea* and *Dillenia cf. borneensis* were encountered only sporadically in the unburned forest, while in the burned forest the average saplings density (>1.30 m high) was 17.6 ± 9.6 per 100 m^2 for these species combined. In contrast, the density of small stems (<10 cm dbh) of shade tolerant trees in the understorey had decreased by 83%. In the burned forest, resprouts were

Table 3.4. Rank-change graph showing the family composition of surviving trees (>10 cm dbh) in the unburned plots (left) and burned plots (right), based on 9 psp of 0.4 ha each.

Unburned plots		Burned plots	
Family	Aver	Family	Aver
Euph	26.3	Dipt	5.8
Sapo	21.7	Euph	4.6
Dipt	21.0	Sapo	3.3
Myrt	13.3	Myrt	2.3
Myri	10.6	Myri	2.0
Laur	9.6	Laur	1.8
Burs	7.1	Burs	1.2
Ulma	6.3	Eben	1.1
Caes	5.9	Bomb	1.0
Bomb	5.4	Anac	0.9
Other		Other	

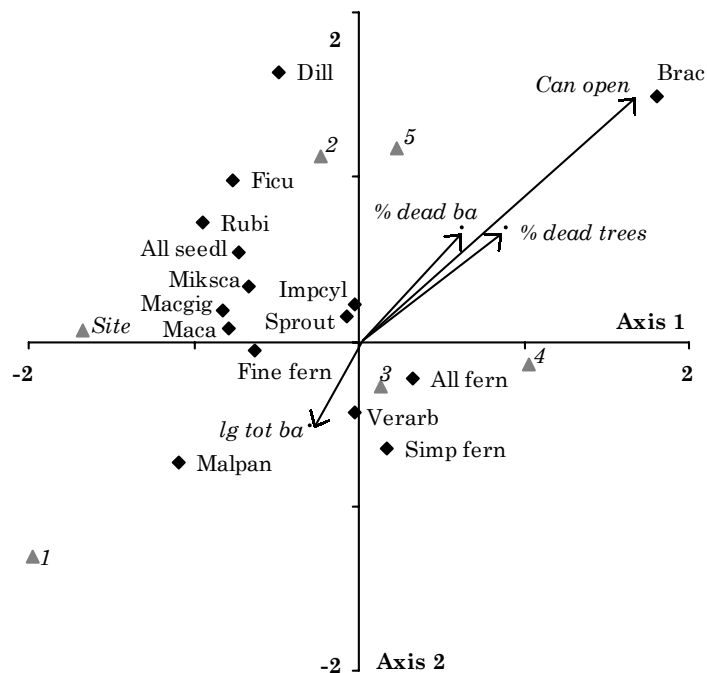


Figure 3.2. Representation of 15 taxa 21 months after fire based on a correspondence analysis on 59 burned subplots of 100 m² in Sungai Wain forest. The sum of all eigenvalues is 0.53. Axis 1 has an eigenvalue of 0.18 and explains 34 % of all variance. Axis 2 has an eigenvalue of 0.11 and explains 20.5 % of all variance. Environmental variables are depicted as centroids (topographic class, site) or as biplot scores (other variables). The position of canopy openness was calculated in spss in order to account for missing values, and its absolute position cannot be readily compared with the other environmental variables.

Legenda: Species data points represent: Brac= *Pteridium caudatum*, Fine fern= *Microlepia spelunca*, Simp fern= *Blechnum orientale*, All fern= three fern species combined, All seedl= sum of all recorded seedlings, Dill= *Dillenia* sp., Ficu= *Ficus* spp., Impcyl= *Imperata cylindrica*, Maca= all *Macaranga* spp., Macgig= *Macaranga gigantea*, Malpan= *Mallotus paniculatus*, Miksca= *Mikania scandens*, Rubi= Rubiaceae, Sprout= sum of all resprouts, Verarb= *Vernonia arborea*. Environmental variable datapoints represent: Can open= canopy openness, % dead ba= percentage dead basal area, % dead trees= percentage dead trees, lg tot ba= logarithm of total basal area (living + dead), Site= location of the plot (see text), 1-5 are topographical units (see table 5). Correlations between axes and environmental variables are given in table 5.

present at a density of 22 ± 9.6 per 100 m², compared with a density of stems <10 cm dbh before the fire of 129 ± 38 per 100 m². The fact that the main post-fire functional groups, ferns and light-demanding saplings, were all but absent from the unburned forest makes an in-depth comparison between the unburned and burned vegetation redundant. The following analyses principally concern vegetation patterns in the burned forest.

A correspondence analysis was employed as an exploratory analysis of the vegetation composition in the burned for-

est (Figure 3.2). The first axis was strongest related to the percentage ground cover of *Pteridium caudatum*. The stem density of *Dillenia* cf. *borneensis* was most strongly related with the second axis. Especially on the first axis, saplings tended to be far removed from *Pteridium caudatum*. The environmental variables correlating best with the first axis were site and canopy openness (Table 3.5). The second axis was marginally correlated with canopy openness and the percentage dead trees. Topographic units tended to be ordered in a sequence along the first

Environmental factor	n	Axis 1	Axis 2
Site	59	0.51 **	0.08
Canopy Openness	24	0.42 *	0.36 (*)
% dead trees	59	0.223 (*)	0.24 (*)
% dead BA	59	.30 *	0.21
log BA	59	-0.08	-0.13
1. low flat / valley	9	-0.24 (*)	-0.20
2. Low slope	8	-0.07	0.13
3. Mid slope	23	0.03	-0.10
4. High slope	11	0.21	0.01
5. High flat / ridge	8	0.04	0.20

Table 3.5. Pearson's coefficients of correlation of environmental variables with the 1st and 2nd axis of the correspondence analysis. Significant correlations are flagged: (*) : p < 0.10, * : p < 0.05, ** : p < 0.01.

axis, but unit 5 (ridges and high flat areas) did not fit this pattern. Based on the correspondence analysis, we decided to include *Pteridium caudatum*, where appropriate, as an independent variable in the multivariate analyses below.

The multivariate analyses were employed to test for (1) the influence of the level of fire-damage to the vegetation, (2) possible inhibiting effects between functional groups, and (3) effects of location and topography on the density of three post-fire functional groups. The tests provided significant levels of explanation for the density of ferns and sprouts, and a nearly significant level of explanation for the density of all saplings (Table 3.6). As expected, we found a negative relation between fern cover and the density of saplings (Figure 3.3). There was no such relation with sprout density. Contrary to expectation, the percentage dead trees

was not related to the density of any of the three groups. Total fern cover was best explained by the density of saplings and partly by slope class. Sapling density was partly explained by slope class and fern cover. The density of pre-fire stems with a dbh < 10 cm largely explained the density of sprouts. The patterns of individual species did often divert considerably from the patterns of these broad functional groups.

Non-woody species

Three fern species were highly abundant (Figure 3.4). Especially *Blechnum orientale* L. was extremely common in the burned forest. Spatial variation in the density of these three species depended on different factors (Table 3.6). *Pteridium caudatum* (L.) Maxon. was associated with high percentages of dead trees, especially in the west-site (Figure

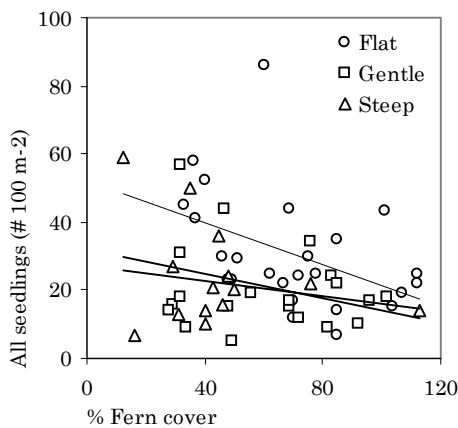


Figure 3.3. Percentage ground cover of ferns versus the density of seedlings in the burned forest. Different symbols indicate slope classes. n = 59.

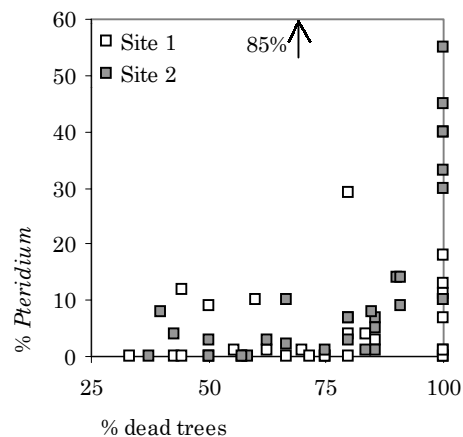


Figure 3.5. Percentage ground cover of *Pteridium caudatum* versus the percentage dead trees in the burned forest. n = 59.

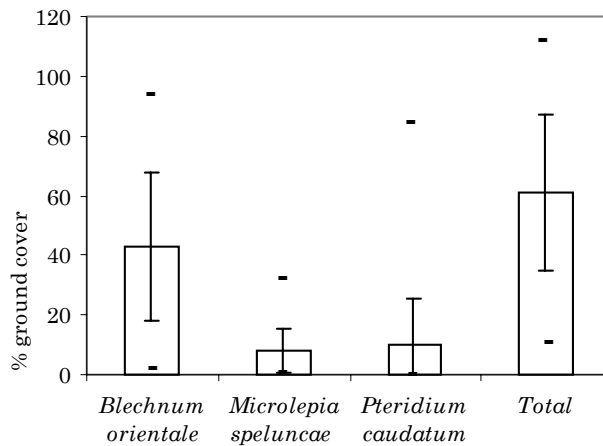


Figure 3.4. Percentage ground cover of the three most common fern species in the burned forest, 21 months after the fire. Given are the average \pm sd. The short bold markings indicate maximum and minimum values. Values are based on 59 plots of 100 m² each. Because in some cases different species overshadow each other, the total coverage can be above 100%.

3.5). The density of *Microlepia speluncae* (L.) Moore differed significantly between the two sites and was related to topography, being highest on low slopes and mid slopes. The density of *Blechnum orientale* decreased with increasing slope.

Ferns first established in locations where smouldering logs had been consumed by fire, leaving a bed of ash. The long period of heat production (often in the order of several days) in these locations must have sterilised the soil. The fact that these sites were the first to be occupied by ferns implies that fern spores arrived after the fire from outside the burned area. Even though 6 months after the fire the plants were still small, they formed a dense cover in these sites. From this we infer that spores must have arrived in high densities, since there is no reason to believe that the sterilised sites would have received a higher than average influx of spores. Reaching a maximum height of 1.5 to 2 m, the fern cover had overgrown many of the seedlings and resprouts approximately one year after the fire.

Other non-woody species were much less abundant than ferns, which is the reason we did not include them in the

anova analyses. *Imperata cylindrica* was present in 61% of the 100 m² subplots, but the ground cover was never dense nor closed, with an average of $1.7 \pm 2.9\%$ per 100 m² plot (average \pm sd, n= 59). The vine species *Mikania scandens* was present in 72% of the subplots and formed a locally dense layer of vegetation with an average ground cover of $4.6 \pm 7.3\%$ and a maximum cover of 39%.

Light-demanding tree saplings

The community of tree saplings that established after the fire was predominantly formed by a few light-demanding species (Table 3.7). Based on a comparison with a complete inventory of seedlings in the burned Sungai Wain forest (Priadjati 1999) we estimate that the contribution of other species to the total density of saplings >1.30 m high was around 10%.

Sapling densities of *Vernonia arborea*, *Macaranga gigantea* and were considerable, given the density of adult trees in the plots which was low (respectively <0.5 and 0.8 trees ha⁻¹). The density of *Dillenia cf. borneensis* was 3.9 trees ha⁻¹ (>10 cm dbh).

Table 3.6. The density of taxa from the three main groups of growth forms in the burned forest explained by environmental factors and other components in the vegetation with the use of one multivariate anova for each functional group.

Dependent Variable	Corrected		Site		Topographic unit		Slope class		% dead trees		Seedling density		Total ba		Fern cover		<i>Pteridium</i> cover		Pre-fire stem density		Error df	
	Source	Model df	F	df	F	df	F	df	F	df	F	df	F	df	F	df	F	df	F	df		
		Sig.		Sig.		Sig.		Sig.		Sig.		Sig.		Sig.		Sig.		Sig.		Sig.		
FERNS																						
All ferns	10	3.25		1	0.56	4	2.22	2	5.89	1	1.01	1	7.36	1	3.77						48	
		<i>0.003 **</i>			<i>0.459</i>			<i>0.081</i>		<i>0.005** f,g>s</i>		<i>0.321</i>		<i>0.009** neg</i>		<i>0.058</i>						
<i>Pteridium caudatum</i>	10	5.42		1	4.54	4	2.72	2	1.57	1	14.46	1	2.85	1	3.46						48	
		<i>0.000 ***</i>			<i>0.038 * 2>1 \$</i>			<i>0.041 *</i>		<i>0.218</i>		<i>0.000 *** \$</i>		<i>0.098</i>		<i>0.069</i>						
Fine fern	10	3.64		1	5.55	4	3.31	2	0.18	1	0.02	1	0.57	1	2.51						48	
		<i>0.001 **</i>			<i>0.023 * 1>2</i>			<i>0.018 *</i>		<i>0.838</i>		<i>0.898</i>		<i>0.455</i>		<i>0.120</i>						
Simpel fern	10	2.61		1	0.00	4	0.85	2	7.70	1	0.44	1	2.60	1	0.15						48	
		<i>0.013 *</i>			<i>0.986</i>			<i>0.499</i>		<i>0.001** f,g>s</i>		<i>0.508</i>		<i>0.113</i>		<i>0.699</i>						
SEEDLINGS																						
All seedlings	11	1.98		1	1.31	4	1.44	2	6.42	1	0.70		1	2.68	1	4.69	1	0.47			47	
		<i>0.052 (*)</i>			<i>0.258</i>			<i>0.236</i>		<i>0.003** f>g,s</i>		<i>0.406</i>		<i>0.108</i>		<i>0.035* neg</i>		<i>0.495</i>				
<i>Macaranga</i> spp. #	11	4.27		1	6.30	4	3.38	2	0.39	1	0.21		1	0.01	1	0.32	1	0.99			47	
		<i>0.000 ***</i>			<i>0.016 * 1>2</i>			<i>0.016 * \$</i>		<i>0.682</i>		<i>0.649</i>		<i>0.915</i>		<i>0.576</i>		<i>0.325</i>				
<i>Macaranga gigantea</i>	11	2.61		1	4.43	4	3.44	2	6.00	1	1.38		1	3.52	1	2.15	1	2.84			47	
		<i>0.011 *</i>			<i>0.041 * 1>2</i>			<i>0.015 *</i>		<i>0.005 ** \$</i>		<i>0.246</i>		<i>0.067</i>		<i>0.150</i>		<i>0.099</i>				
<i>Vernonia arborea</i>	11	1.55		1	5.59	4	0.26	2	0.38	1	1.91		1	0.67	1	2.13	1	4.71			47	
		<i>0.145 NS</i>			<i>0.022* 2>1</i>			<i>0.905</i>		<i>0.685</i>		<i>0.174</i>		<i>0.416</i>		<i>0.151</i>		<i>0.035*</i>				
<i>Dillenia cf. borneensis</i>	11	1.29		1	0.11	4	1.07	2	2.78	1	0.28		1	0.07	1	2.76	1	0.03			47	
		<i>0.26 NS</i>			<i>0.745</i>			<i>0.38</i>		<i>0.072</i>		<i>0.602</i>		<i>0.793</i>		<i>0.103</i>		<i>0.869</i>				
SPROUTS																						
All sprouts	12	4.91		1	0.69	4	3.67	2	3.74	1	0.75	1	0.50	1	0.95	1	0.04	1	3.66	1	30.02	5
		<i>0.045 *</i>			<i>0.444</i>			<i>0.093</i>		<i>0.102</i>		<i>0.427</i>		<i>0.511</i>		<i>0.373</i>		<i>0.858</i>		<i>0.114</i>	<i>0.003 ** pos</i>	
<i>Fordia</i>	12	0.72		1	0.25	4	0.73	2	1.07	1	1.50	1	0.00	1	0.14	1	0.75	1	0.28	1	0.64	5
		<i>0.701 NS</i>			<i>0.639</i>			<i>0.607</i>		<i>0.412</i>		<i>0.275</i>		<i>0.958</i>		<i>0.726</i>		<i>0.426</i>		<i>0.617</i>	<i>0.459</i>	
All sprouts - <i>Fordia</i>	12	3.96		1	0.32	4	2.84	2	2.03	1	0.01	1	0.57	1	1.69	1	0.88	1	1.36	1	24.91	5
		<i>0.070 (*)</i>			<i>0.595</i>			<i>0.141</i>		<i>0.227</i>		<i>0.926</i>		<i>0.483</i>		<i>0.250</i>		<i>0.392</i>		<i>0.297</i>	<i>0.004 ** pos</i>	

Notes: #: All *Macaranga* tree species excluding *M. gigantea*. Abbreviations presented after the level of significance indicate: neg.: Negative relationship, pos.: Positive relationship. 1= East site, 2= West site. Slope classes: f= flat, g= gentle, s= steep. \$: see figure.

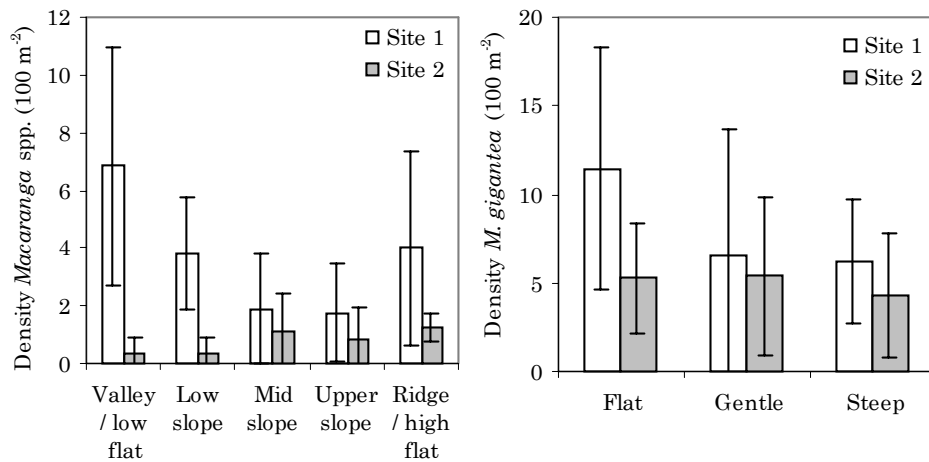


Figure 3.6. (a) Seedling density of *Macaranga* spp. per topographic unit in the burned forest. Included are all *Macaranga* tree species (but not shrubs, i.e. *M. trichocarpa*) except *M. gigantea*. (b) Seedling density of *Macaranga gigantea* per slope class in the burned forest.

The densities of *Macaranga* spp. and *Macaranga gigantea* differed between the two sites, and were related to respectively topographic unit (Figure 3.6 a) and slope class (Figure 3.6 b). Individual species did not show a significant relation with the percentage dead trees or with fern cover.

Light-demanding tree saplings

The community of tree saplings that established after the fire was predominantly formed by a few light-demanding species (Table 3.7). Based on a comparison with a complete inventory of seedlings in the burned Sungai Wain forest (Priadjati 1999) we estimate that the contribution of other species to the total density of saplings >1.30 m high was around 10%.

Sapling densities of *Vernonia arbo-*

rea, *Macaranga gigantea* and were considerable, given the density of adult trees in the plots which was low (respectively <0.5 and 0.8 trees ha⁻¹). The density of *Dillenia cf. borneensis* was 3.9 trees ha⁻¹ (>10 cm dbh). The densities of *Macaranga* spp. and *Macaranga gigantea* differed between the two sites, and were related to respectively topographic unit (Figure 3.6 a) and slope class (Figure 3.6 b). Individual species did not show a significant relation with the percentage dead trees or with fern cover.

Two years after the fire, saplings of the three most common light-demanding species had an average dbh varying from 1.8 to 3.0 cm (Table 3.7). The most rapid growth was observed in *Macaranga gigantea* and *Vernonia arborea*, which had produced individuals with a maximum

Table 3.7. Stem density and diameter at breast height (dbh) of characteristic light-demanding tree species that established after the fire in the burned forest. Data are based on 59 plots of 100 m², which were inventoried 21 months after the fire.

Species	Stem density per 100 m ² (> 1.3 m high)				Dbh (cm)			
	Average	sd	min	max	Aver.	sd	min	max
<i>Dillenia cf. borneensis</i> Hoogl.	3.3	5.8	0	33	1.8	0.6	0.5	3.5
<i>Ficus</i> spp.	1.6	2.1	0	8				
<i>Macaranga gigantea</i> (Reichb.f. & Zoll.) Mull.Arg.	6.7	5.3	0	22	3.0	1.4	0.8	7.4
<i>Macaranga</i> spp.	1.6	1.8	0	8				
<i>Mallotus paniculatus</i> (Lam.) Mull.Arg.	0.6	1.6	0	8				
<i>Vernonia arborea</i> Buch.-Ham.	3.2	3.3	0	17	2.7	1.3	0.6	6.8
Total	17.6	9.6	1	44				

Source	Dependent Variable	df	F	Sig.
Corrected Model	Dbh <i>Macaranga gigantea</i>	2	1.50	0.241
	Dbh <i>Dillenia cf. borneensis</i>	2	3.91	0.032 *
	Dbh <i>Vernonia arborea</i>	2	0.49	0.618
Perc. dead trees	Dbh <i>Macaranga gigantea</i>	1	2.88	0.101
	Dbh <i>Dillenia cf. borneensis</i>	1	7.79	0.009 **
	Dbh <i>Vernonia arborea</i>	1	0.38	0.541
All fern cover	Dbh <i>Macaranga gigantea</i>	1	0.28	0.604
	Dbh <i>Dillenia cf. borneensis</i>	1	0.24	0.628
	Dbh <i>Vernonia arborea</i>	1	0.70	0.411
Error	Dbh <i>Macaranga gigantea</i>	28		
	Dbh <i>Dillenia cf. borneensis</i>	28		
	Dbh <i>Vernonia arborea</i>	28		

Table 3.8. Average dbh per subplot 21 months after fire for three seedling species explained by the percentage dead trees and fern cover in the subplot. Multivariate anova.

dbh of respectively 7.4 and 6.8 cm. The average dbh per subplot of *Dillenia cf. borneensis* was related with the percentage dead trees, but not in *Macaranga gigantea* or *Vernonia arborea* (Table 3.8). Total fern cover and canopy openness were not related to the average dbh of the three species (Analysis not shown).

A group of species that did not properly fit any of the functional groups in our classification were the diverse shrub and liana species from the family Rubiaceae. These species had a mixed regeneration strategy. They were present in the understory of the unburned forest, and after the fire established resprouts (>50 cm high) in a density of 2.1 ± 1.4 per 100 m². Rubiaceae were also present in the seed bank. During the second census, the density of Rubiaceae saplings (>1.30 m high) was 4.6 ± 5.0 per 100 m². This suggests that more than half the Rubiaceae established

from the post-fire seed bank.

Resprouting of shade tolerant species

Nearly 24% (0.047 stems m⁻²) of all resprouts belonged to *Fordia splendidissima*, a shade tolerant shrub species. The remaining resprouts were mainly shade tolerant tree species (Table 3.9 & 3.10). Notwithstanding the dominance of *F. splendidissima*, the species diversity of the resprouting community was high. In a sample of 1416 individuals (parent stem >50 cm high), we recorded 39 families, 102 genera and 126 species (where 41% was identified up to species level, 32% up to genus level, 7% up to family level, and 20% remained unidentified). An equally sized random sample among trees >10 cm dbh from the unburned forest yielded 46 families, 131 genera and 216 species (where 61% was identified up to species level, 31% up to genus level, 5% up to

Table 3.9. Stem densities of common resprouting species in the burned forest. The density of resprouts is divided over two categories, based on the dbh of the parent stem. The lower limit was 50 cm plant height. Data are based on 60 subplots spread over 6 psp with a total area of 0.6 ha for parent trees <10 cm dbh and 6 psp with a total area of 2.4 ha for parent trees >10 cm dbh.

Species	WD (g cm ⁻³)	Density (ha ⁻¹)		
		< 10 cm dbh	> 10 cm dbh	All
<i>Fordia splendidissima</i> (Blume ex Miq.) Buijsen	0.881	510		510
<i>Gironniera nervosa</i> Planch.	0.603	55	2.1	57
<i>Aporosa lucida</i> (Miq.) Airy Shaw	0.999	53		53
<i>Macaranga lowii</i> King ex Hook.f.	0.810	43	0.4	44
<i>Eurycoma longifolia</i> Jack	0.642	38		38
<i>Durio acutifolius</i> (Mast.) Kosterm.	0.670 #	28	0.4	29
<i>Litsea firma</i> (Blume) Hook.f.	0.541	28	0.4	29
<i>Artocarpus anisophyllus</i> Miq.	0.718	15	0.4	15
<i>Eusideroxylon zwageri</i> Teijsm. & Binn.	1.066	13	3.8	17
<i>Rhodamnia cinerea</i> Jack		10		10
Other		1335	21	1356
Sum		2130	28	2158

Table 3.10. Stem densities of common resprouting genera in the burned forest.

Genus	Family	Density (ha ⁻¹)		All
		< 10 cm dbh	> 10 cm dbh	
<i>Fordia</i>	Palilionaceae	510		510
<i>Syzygium</i>	Myrtaceae	105	0.4	105
<i>Xanthophyllum</i>	Polygalaceae	70		70
<i>Aporosa</i>	Euphorbiaceae	65	0.4	65
<i>Litsea</i>	Lauraceae	57	1.3	58
<i>Urophyllum</i>	Rubiaceae	55		55
<i>Gironniera</i>	Ulmaceae	52	2.1	54
<i>Salacia</i>	Celastraceae	53		53
<i>Macaranga</i>	Euphorbiaceae	45	0.4	45
<i>Barringtonia</i>	Lecythidiaceae	40	0.4	40
<i>Eurycoma</i>	Simaroubaceae	38		38
<i>Artocarpus</i>	Moraceae	37	0.8	38
<i>Durio</i>	Bombacaceae	37	0.8	38
<i>Popowia</i>	Annonaceae	35		35
<i>Pternandra</i>	Melastomataceae	27		27
<i>Archidendron</i>	Mimosoidae	22		22
<i>Nephelium</i>	Sapindaceae	20		20
<i>Cotylelobium</i>	Dipterocarpaceae	18	0.4	19
<i>Eusideroxylon</i>	Lauraceae	13	3.8	17
<i>Lithocarpus</i>	Fagaceae	13	0.8	14
<i>Baccaurea</i>	Euphorbiaceae	13	0.4	14
<i>Dacryodes</i>	Burseraceae	13	0.4	14
<i>Polyalthia</i>	Annonaceae	13	0.4	14
<i>Ixora</i>	Rubiaceae	12		12
<i>Tetracera</i>	Dilleniaceae	12		12
Other		752	15.4	767
Sum		2127	28	2155

family level, and 3% remained unidentified).

Most of the sprouts on parent stems <10 cm dbh originated from the base of the stem (93%). The majority originated from (just) below ground parts (64%), whereas fewer originated from above-ground parts or from both above-ground and below ground parts (30%). The remaining 7% of the resprouting individuals

resprouted along the stem. Root sprouts were very rare. Small stems contribute enormously to the post-fire sprout density (Figure 3.7). Partly, this is caused by a ten-fold decrease in sprouting frequency between parent stems which range in size from 0-1.9 cm dah to >50 cm dbh (Figure 3.8). However, the pattern is mainly the result of an exponential decrease of stem density with size, which is found in most

Table 3.11. Wood density, stem density (>50 cm high) and the estimated percentage sprouting stems of six shade tolerant species in unburned forest and the density of resprouts in adjacent burned forest.

Species	Wood density (g cm ⁻³)	Stem density per 100 m ² in unburned forest		Sprout density per 100 m ² in burned forest		Estimated % sprouting
		Average	sd	Average	sd	
<i>Dipterocarpus confertus</i> Sloot.	0.803	2.0	2.9	0.05	0.22	2.5
<i>Durio acutifolius</i> (Mast.) Kosterm.	0.670 *	3.6	2.5	0.40	0.71	11
<i>Fordia splendidissima</i> (Blume ex Miq.) Buijsen	0.881	5.5	4.8	5.6	4.0	102
<i>Gironea nervosa</i> Planch.	0.603	4.4	5.1	0.68	1.07	15
<i>Macaranga lowii</i> King ex Hook.f.	0.810	10.2	11.0	0.55	0.81	5.4
<i>Shorea laevis</i> Ridl.	0.933	6.3	7.9	0.03	0.16	0.4

Note: * The value for the wood density of *D. acutifolius* is the genus average (0.670 ± 0.056 g cm⁻³ (average ± sd, n= 9)).

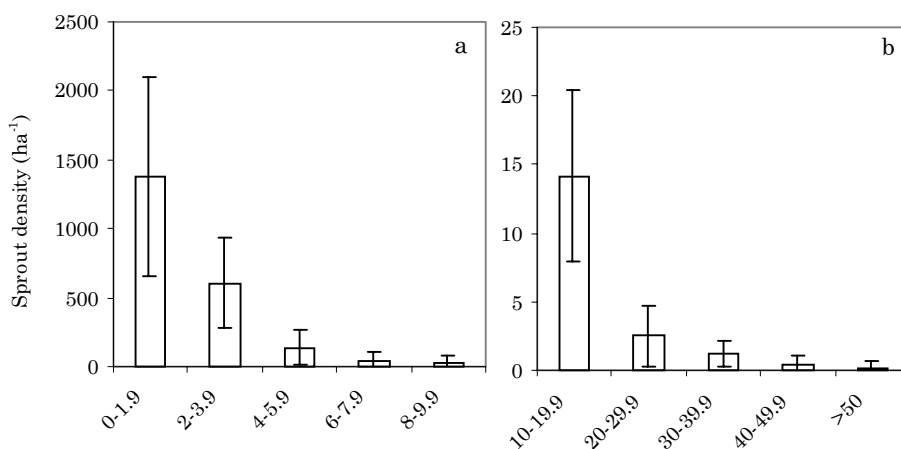


Figure 3.7. Density of resprouts per area (number ha⁻¹) in the burned forest originating from stems that were killed by the fire. Observations were made 8 months after the fire. Each size class refers to the size of the stem from which a sprout originated. In figure (a) size classes are delimited by diameter at ankle height (dah, measured at 25 cm above ground level), except for the smallest class, for which a minimum plant height of 50 cm is the lower limit, and the largest class, for which a maximum dbh of 9.99 cm is the upper limit. Figure (b) shows the sprouting frequency of stems >10 cm dbh at 10 cm size intervals. Here, all size classes are delimited by diameter at breast height (dbh).

forests. Sprout density per 100 m² correlated well with the density of stems >50 cm high before the fire (Table 3.6).

Based on a comparison of population densities of six species in unburned forest and burned forest, we observed that the frequency of resprouting varied greatly (Table 3.11). This comparison suggested a 100% sprouting frequency for *F. splendissima*.

For the whole community (<10 cm dbh) excluding *F. splendissima*, the average sprouting frequency was 13.5 ± 5.8% (n= 18). With a sprouting frequency below 3%, the dipterocarp species *Dipterocarpus confertus* Sloot. and *Shorea laevis* Ridl. remained well below the community average. Ranging from 5.4 to 15%, the other three species were at a

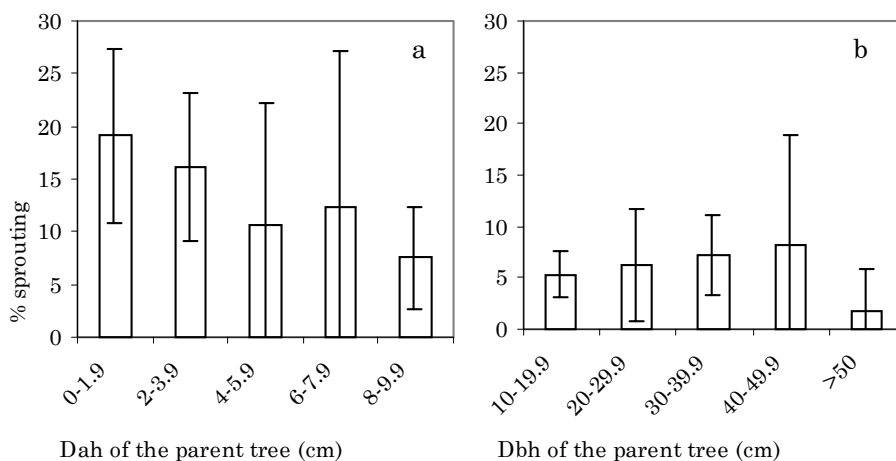


Figure 3.8. Relation between size of the pre-fire stem and the frequency of resprouting of stems that were killed by the fire. Observations were made 8 months after the fire. Size classes are defined as in figure 3.7 a and b.

sprouting level close to the community average. The five tree species in this comparison (i.e. excl. *Fordia splendidissima*) showed a strong negative relationship between sprouting frequency and wood density ($y = -38.9x + 37.1$, $R^2 = 0.89$).

Sprouts grew fast in the first 21 months after the fire. The average sprout length eight months after the fire was 25.1 ± 19.2 cm (3.1 ± 2.4 cm month⁻¹). Sprouts grew another 80.3 ± 71.3 cm (6.2 ± 5.5 cm month⁻¹) in the 13 months that followed. As predicted, length growth of sprouts was negatively related to specific wood density (Figure 3.9 a). Sprout survival was fairly high between the censuses 8 and 21 months after the fire: 83% of the sprouts survived, whereas the fate of another 11% remained unclear. Sprout survival was not significantly correlated to wood density (Figure 3.9 b).

Discussion

Spatial patterns in damage and light availability

In the current study, unburned patches were scarce, and so were very lightly burned patches that were observed in the field to have a largely intact canopy, and a vegetation development much more similar to unburned forest. Un-

burned patches and lightly burned patches were associated with low flat areas and low slopes and valleys. In a year with an average precipitation, many low flat areas are saturated with water. Low slopes and valleys experience a lower irradiation, lower wind speeds and a relatively high water influx. For these reasons they may have been slightly wetter than their surroundings at the time the fire arrived.

The percentage tree mortality explained little of the variation in the post-fire vegetation apart from the percentage cover of *Pteridium caudatum*. We assume that the spatial variation in fire-intensity was low, leaving a fairly homogeneously disturbed vegetation. This contrasts sharply with the effects of fire in temperate forests, where fire characteristically creates a landscape mosaic of disturbances (Turner et al. 1994).

Different processes determine the post-fire demographical dynamics of the three functional groups in this study. Non-woody species were probably present in the vegetation through establishment from the seed bank and post-fire seed rain. Light-demanding tree species established from the seed bank, although seeds of some species (notably *Vernonia arborea*) may have been wind-dispersed after the fire. Populations of shade tolerant

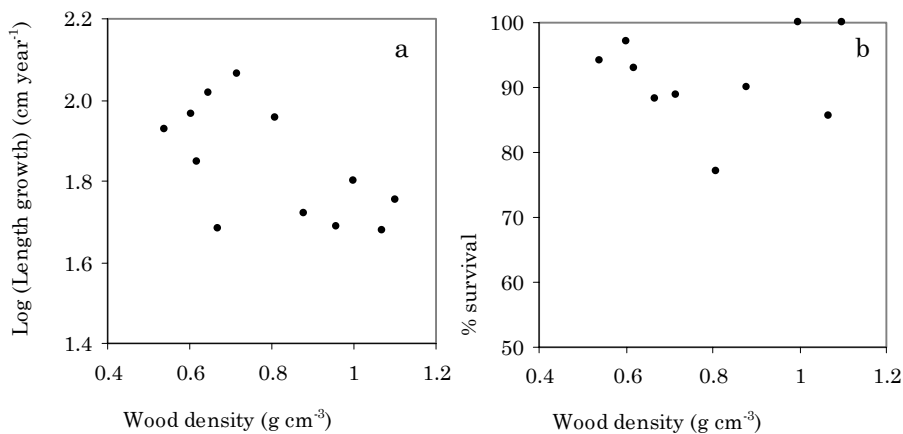


Figure 3.9. Wood density as an indicator for (a) length growth of sprouts and (b) sprout survival over the period from 8 months until 21 months after fire. One-tailed Pearson correlations reveal a significant correlation between wood density and sprout length growth (Pears. corr. -0.51 , $p = 0.05$, $n = 12$) and no significant correlation between wood density and survival (Pears. corr. 0.090 , $p = 0.40$, $n = 10$).

tree species were maintained through survival of stems and resprouting from basal parts, whereas post-fire seed dispersal was not observed.

Shade tolerant species

For shade tolerant species, post-disturbance seed dispersal is often implicitly expected to be an important factor in population development after a disturbance. Instead, the present study shows that in the first two years after fire, most of the stem density and species diversity actually resulted from resprouting stems. The local diversity of surviving adult trees was severely reduced up to a scale of at least several hectares. Since seed dispersal of large-seeded species is usually strongly skewed (Howe & Smallwood 1982), the local seed rain will be species-poor in the years to come. It is therefore most likely that the seed rain will contain fewer species than the already established local vegetation of resprouts. Moreover, shade tolerant trees were rarely observed to fruit in the two years after fire, which followed upon a mast-season a few months prior to the fires (Kiyono & Hastaniah 2001, G. Fredriksson, pers. com.). Thus, the seed rain appears to be much less important than expected. In this situation it becomes very important to understand species-specific differences in sprouting capacity.

On a per area basis, most of the resprouts originated from small stems. This is partly explained by the size-dependent ten-fold decrease in sprouting frequency. However, of much larger influence was the composition of the stem population before the fire, which showed a more than 7000-fold decrease in stem density over the same size range (Figure 3.7). The above ground living tissue of small individuals was at higher risk of mortality, because a thin bark is a less effective protection against fire heat (Gill & Ashton 1968, Vines 1968, Uhl & Kauffman 1990, Pinard & Huffman 1997). Thus, the relationship between tree size and sprouting frequency depended on the capability of seedlings and saplings to sprout from below ground parts.

Even though small individuals payed the largest contribution to the post-fire density of sprouts, the actual frequency of sprouting after fire was much lower than the sprouting frequency that has been observed for tropical trees after breakage of the main stem (respectively 14% after fire versus 65-100% after stem breakage, Guarigata 1998, Chapter 4). To understand potential limitations to sprouting ability after fire, we performed a preliminary experiment in which saplings were clipped at ground level, respectively at 10 cm above ground level (six species, n= 30 per treatment). Plants clipped at ground level had a sprouting percentage ranging from 0 to 41% (average 19%) relative to the sprouting frequency of plants clipped at 10 cm above ground level. This low ability of plants to sprout from below ground level explains the relatively low sprouting frequency of small individuals after fire. An intrinsically lower capacity of the root tissue to produce sprouting buds, or the stimulation of bud development by light availability could cause this low sprouting frequency.

We expected that wood density might be a useful proxy to predict specific sprout growth. Species with a high wood density had a lower relative growth rate, while sprout survival rate was not significantly related to wood density. Due to the species-specific differences in sprouting capacity, heavy-wooded species will be underrepresented in the post-fire resprout community. The species-specific sprouting capacity of saplings is analysed in more detail in chapter 4.

Light-demanding tree species

Macaranga gigantea, *Dillenia* cf. *borneensis* and *Vernonia arborea* were very rare as adult trees in the unburned forest, and yet they were common as saplings in the burned forest. *Macaranga gigantea* and *Dillenia* cf. *borneensis*, and to a lesser extent *Vernonia arborea*, produce quite large seeds which are probably not dispersed very far. Instead of being good dispersers in space, we presume that these species “disperse in time”, i.e. they survive for considerable periods of time in

the soil seed bank (review by Garwood 1989).

We found no significant relation between the percentage dead trees and sapling density. The relation between canopy openness or percentage dead trees and relative growth rate was only significant for *Dillenia cf. borneensis*. This suggests that within the range of light availability created by the fire (95% of the plots had a canopy openness above 15%), seed germination and sapling growth were rarely limited by light.

The post-fire demographic dynamics of the shrubs and lianas from the family Rubiaceae are the result of a mixed regeneration strategy. Rubiaceae established in roughly equal amounts as resprouts and as seedlings from the post-fire seed bank. This behaviour fits well with earlier descriptions of the regeneration niche of Rubiaceae. Species of this family often produce very small seeds, whereas at the same time they persist in the forest undergrowth (Metcalf & Grubb 1995, Metcalfe et al. 1998, Metcalfe & Turner 1998).

Non-woody species

The three most common fern species in the burned forest were not observed in the nearby unburned forest before or after the fire. Spores of these species must have originated from outside the reserve. However, the cultivated land surrounding the research forest burned in the months preceding the fires in Sungai Wain (Hoffmann et al. 1999) and was thus unlikely to have produced large quantities of fern spores. It is more likely that spores originated from unburned areas which lay at great distance from the research site. Spore input may have been especially high during the first rains following the fires, because a relatively high density of spores remained dispensed in the air during the preceding drought (Fletcher & Kirkwood 1979).

Total fern density was negatively related to the density of saplings (Figure 3.3). This suggests a certain level of competition between the two functional groups. Ferns and seedlings established

at approximately the same time, and both were capable of quickly forming a locally dense ground cover (MvN pers. obs.). Depending on the time of establishment and the initial population density, we regard both functional groups to have the potential to inhibit the establishment or growth of the other functional group.

Conclusion

The post-fire vegetation consists of several functional groups of plants, which show very different patterns of establishment and growth. Establishment from the pre-fire seed bank and from post-fire seed rain appear to be the most important processes determining the demographic dynamics of non-woody species and light-demanding tree species. The population density and local diversity of shade tolerant species, however, is mainly determined by the occurrence of resprouts.

The capacity of stems to resprout increases the resistance of the community to a fire disturbance. This allows for a relatively rapid recovery, because species do not have to recolonise the disturbed areas. If the resprouting plants are given the opportunity, a forest dominated by shade tolerant tree species may re-establish in a few decades. However, the threat of a forest fire does not come independently from the threat of other disturbances. In fact, repeated disturbances are very likely to occur, because (1) for at least a decade, the flammability of the post-fire vegetation is increased, and (2) an abundance of human sources of ignition is available during periods of drought. Also, burned forests in Indonesia have been disturbed in a government-backed move to exploit the forest for salvage wood (Chapter 6). Thus, a sequence of repeated disturbances is likely to follow the first fire (Cochrane & Schulze 1999, Cochrane et al. 1999, Siegert et al. 2001). Such repeated disturbances lead to a rapid degradation of the forest. Our research suggests that, with repeated disturbance, the time for recovery greatly increases because the density of resprouts will rapidly decrease.

Acknowledgements

We thank M.J.A. Werger, D. Sheil and F.J. Sterck for comments on an earlier version of the manuscript. H. Beukema and K.A.O. Eichhorn were helpful in the identification of respectively several species of ferns and shrubs. J. Helleman, N. Syah, F. Udin, S. Laysa Putra and numerous staff members of the In-

ternational Ministry of Forestry (MOF)-Tropenbos research station (Wanariset Samboja) provided much appreciated assistance in the field. This project was financially supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) with grant 84-408 to M.v.N., and by the Center for International Forestry (CIFOR) in Bogor.



Once-burned forest dominated by ferns and *Macaranga gigantea*. Resprouts, standing dead stems and living stems are found scattered throughout the vegetation. Sungai Wain, June 2000.



Postfire sprouts originating from below ground around a stem of *Eusideroxylon zwageri*. Sungai Wain, December 1998.

4

Resprouting capacity of tropical saplings after artificial stem breakage, and the storage of non-structural carbohydrates

Abstract

Resprouting of saplings after physical disturbance is a common phenomenon in the tropical rainforest, and plays an important role in the maintenance of populations in a disturbed environment. Little is known of resprouting behaviour after severe damage, and about the importance of stored total non-structural carbohydrates (tnc) in this respect. We studied the resprouting behaviour of saplings of six shade tolerant tree species in a lowland dipterocarp forest in Indonesia after artificial breakage of the main stem, inflicting the loss of all green leaves. We limited the study to the first six months after stem breakage, during which time the plants were predicted to develop through two stages, based on the origin of the invested carbohydrates. We predicted that the species-specific amount of carbohydrate reserves would correlate with the percentage of individuals that sprouted, as well as the total dry mass produced. We predicted that with increasing light availability, the concentration of tnc would be higher, and as a result the sprouting capacity would be higher. Sprout growth was expected to be correlated with specific wood density during the second stage of development, when sprouts have developed photosynthetically active tissue. Apical dominance was disrupted by the treatment. We observed how apical dominance was restored, and how this affected the architecture of the sprouts.

Tnc concentrations differed significantly between species. Tnc tended to be related to the percentage of individuals that sprouted and the total dry mass produced after six months. The concentrations of tnc thus seem to play a vital role in determining the sprouting capacity of a plant. Tnc concentrations were not related to light availability, nor were sprouting frequency or dry mass production. This suggests that even under low light conditions, plants give a high priority to the investment of carbohydrates into storage, relative to investing them in growth.

We observed two distinct phases in the development of resprouts. In the first phase sprout height growth was fast, and entirely dependent on tnc, because photosynthesising leaves were absent. In the second phase, sprout height growth was much slower for most species, and green leaves provided at least part of the photosynthates. Sprout growth in the second developmental stage (i.e. in the 5th and 6th month after clipping) tended to be negatively correlated with specific wood density.

Sprout height growth and the development of a dominant shoot varied considerably between species. Some species had a highly dominant shoot after six months, whereas in others all shoots were of almost equal length. We suggest that this variation reflects a trade-off between rapid lateral extension of the crown, which maximises light interception under shady conditions, and investment in height growth, which improves the relative height position in the vegetation, and consequently prolongs the duration of light capture following gap formation in the canopy.

Keywords: Apical dominance, East Kalimantan, Indonesia, lowland dipterocarp forest, physical damage, shade-tolerance, wood density.

Introduction

In tropical rain forest, the seedlings and saplings of shade tolerant tree species remain in the understorey for a long period of time. Many individuals experience severe damage during their life due to local disturbances by branch fall and tree fall or due to large-scale disturbances such as fire (Clark & Clark 1991, Paciorek et al. 2000, Chapter 3). Given the high incidence of stem breakage, the species-specific ability to resprout is likely to exert a major influence on the performance of individuals and the dynamics of populations (Bond & Midgley 2001). High persistence of individuals will limit the local changes in species composition after a disturbance has occurred, and is likely to sustain local species diversity after a large-scale disturbance that affects a large proportion of the individuals. The phenomenon of sprouting must be understood if we want to comprehend the dynamics of forests after disturbances such as logging (Kammesheidt 1999), hurricanes (Bellingham et al. 1994) or fire (Kauffman 1991, Kammesheidt 1998).

Sprouting responses of plants are variable, depending on the severity of the disturbance and the plant parts that are lost (Bond & Midgley 2001). In the current study we focus on resprouting in saplings after one of the most severe possible disturbances, breakage of the main stem below the crown, which causes the loss of all branches and all green leaves.

This treatment mimics decapitation of saplings by falling debris, or browsing by large herbivores. In the following text, it will be referred to as stem breakage. Several studies have investigated the sprouting behaviour of tropical trees over the course of a few years after such damage (Putz & Brokaw 1989, Bellingham et al. 1994, Guariguata 1998), but the recovery process shortly after breakage has scarcely been studied. We investigated the process of resprouting during this first period after breakage at both the population level as well as the individual plant level, focussing on the factors that determine sprout development, and focussing on how sprout growth patterns, in terms of sprout axis production, leaf production, length growth rate and the development of sprout dominance differ between species.

When sprouting occurs after stem breakage, sprout development goes through two phases. In the first phase, dormant buds are activated and sprouts emerge from the bark. Mature leaves are absent in this first phase, so the formation of new sprouts is dependent on stored total non-structural carbohydrates (tnc) (Chapin et al. 1990). In the transition to the second phase, the newly formed sprouts develop mature leaves, and start producing carbohydrates. Sprout growth gradually becomes independent of the stored tnc (Schier & Zasada 1973). We

Table 4.1. Description of the species in the study. n* is the number of individuals in the clipping experiment. The 95% dbh limit represents the dbh below which 95% of the individuals of a population are found, followed by the number of trees in the observed population. The growth form of the adult tree is categorised in 3 classes (Em= emergent, Up= Upper canopy, Mid= Mid-story). Wood densities were taken from the literature. The last three columns show the specific individual leaf mass of the saplings before clipping (slm_{sapl}) (average, sd and number of observations).

Species	Family	n*	95% dbh		Growth Form	Wood density (g cm ⁻³)
			limit (cm)	n		
<i>Dipterocarpus confertus</i> Sloot.	Dipterocarpaceae	108	95	55	Em	0.80
<i>Durio acutifolius</i> (Mast.) Kosterm.	Bombacaceae	93	25	41	Mid	0.67
<i>Gironniera nervosa</i> Planch.	Ulmaceae	96	30	83	Up	0.60
<i>Macaranga lowii</i> King ex Hook.f.	Euphorbiaceae	103	15	52	Mid	0.81
<i>Madhuca kingiana</i> (Brace) H.J.Lam	Sapotaceae	97	30	137	Up	0.79
<i>Shorea laevis</i> Ridl.	Dipterocarpaceae	102	105	149	Em	0.93

investigated how the phase of tnc-dependence and the photosynthesising phase are reflected in the patterns of height growth rate (hgr) of sprouts.

The principal objective of this research was to study the importance of energy reserves that are stored in the stem and roots on sprouting capacity of shade tolerant trees. A correlation between storage of carbohydrates and increased sprouting frequency has been documented in Australian heath lands (Pate et al. 1990, Bell et al. 1996) and South African fynbos (Bell & Ojeda 1999). We expect a similar correlation for tropical tree saplings, and hypothesise that sprout biomass production rate after stem breakage is correlated to the amount of stored tnc in roots and stem. If the rate of biomass production in resprouting saplings is limited by the amount of stored tnc, the relationship between these two factors will be strongest shortly after sprouts have started to photosynthesise. We expect that, when a species has a higher concentration of stored tnc in stem and roots, (a) a higher percentage of its population will produce sprouts and (b) its individuals will have a higher sprout dry mass production rate. Furthermore we predict that (c) within species, individuals which were growing under higher light conditions before breaking have a higher concentration of tnc. (d) If this is true, these individuals are expected to have a higher sprouting chance and a higher sprout dry mass production rate. This higher sprout production is reflected in an increase in the initial number of leaves and sprouts produced, and a higher total sprout length by the time sprouts have developed photosynthesising leaves.

In chapter 3 of this thesis, sprouting

Table 4.1. (Continued)

Slm sapl		
(g)	SD	n
2.6	1.2	15
0.33	0.15	15
0.53	0.38	15
0.34	0.15	15
1.5	1.1	15
0.23	0.13	15

capacity of a number of shade tolerant tree species, including the species that feature in this clipping experiment, was measured. In that research, a negative correlation was observed for 12 species of shade tolerant trees between sprout growth and wood density, whereas sprout survival was not significantly correlated to wood density. A similar association between wood density and maximum growth rate was found for tropical trees in Borneo and in Guyana (Suzuki 1999, H. ter Steege pers. com.). Our hypothesis is that in the second stage of development, when sprouts are no longer relying on stored energy supplies, sprout growth occurs under the same constraints as seedling growth, and is therefore negatively related to wood density. In this study wood densities were taken from the literature (Burgess 1966, Suzuki 1999).

Sprouting occurs because dormant buds are activated after apical dominance has been removed (Wilson 2000). During the resprouting process, apical control will be restored by one sprout, which becomes dominant over the others. We expect that apical dominance of one sprout will develop, which will form the main stem in the future. The development of the dominant sprouts is investigated over the first and second developmental phase.

Study area

Sungai Wain Forest (1°16' S and 116°54' E) is a forest reserve of roughly 100 km² in East Kalimantan, located 20 km North of Balikpapan and 15 km West of the Strait of Makassar. The forest is currently the subject of a study on the effects of forest fire, since a large part of the reserve burned in 1998. The forest fires did not destroy a core area of 30 km². Two-thirds of this core area are covered with lowland dipterocarp rain forest, with a canopy height of an estimated 45 m. The canopy is irregular and quite open, which is probably due to the frequent droughts that the region has experienced. The other one-third of the unburned area maintains an infrequently flooded forest with a lower and more closed canopy in which Dipterocarpaceae do not dominate.

Dawkins		
Category	score	Description
1. Low	1	No direct lateral or overhead light
	2-L	Some direct lateral light, no overhead light
2. Middle	2-M	Between 2-L and 2-H
3. High	2-H	Much direct lateral light, no overhead light
	3, 4, 5	Increasing amounts of direct overhead light

Table 4.2. Light categories based on Dawkins' crown illumination index (Dawkins & Field 1978), refined by Clark and Clark (1992).

The topography of the reserve consists of gentle to sometimes steep hills, and is intersected by several small rivers. The area varies in altitude from 40 to 140 m.a.s.l. Alisols form the major soil type (MacKinnon et al. 1996). For a more detailed description, see chapter 1.

Material and methods

The experiment was performed in four primary forest plots of 60 x 300 m each, which were spread over an area of 10 km². The plots were laid out as part of a larger research design on the effects of drought and fire on forest dynamics (Chapter 2). Plot topography was measured in 20 x 20 m subplots with a clinometer (Suunto).

Six tree species that are common in the understorey as saplings were selected (Table 4.1). Species will be referred to by their generic names. All six species (including *Macaranga lowii*) are shade tolerant, i.e. they commonly occur in the forest understorey as seedlings and saplings. Four of these species can be found in the upper canopy or as emerging trees, whereas the other two species are found in the mid-storey. Leaf size varies by a factor 11 between species. Per species, approximately 115 saplings with a diameter at breast height (dbh, measured at 130 cm) between 1.50 and 2.50 cm were labelled. Individuals with obvious stem deformations, including multiple stems and stems with signs of previous severe damage, were excluded. Individuals that were damaged by falling debris during the experiment were excluded as well. The co-ordinates of each individual were recorded, and the site topography for each individual was classified into three classes (1= ridge, 2= slope, 3= valley).

For each sapling the light availability was estimated by using the Dawkins'

crown index, which scores the source and relative amount of crown lighting (Table 4.2) (Dawkins & Field 1978, Clark & Clark 1992). For the analysis, class 1 and class 2-L were combined because they were sometimes difficult to distinguish. Because of low observation numbers in some classes, some other Dawkins scores were combined to form a total of three categories (Table 4.2).

Individuals (n= 93 to 108) were clipped at 1.30 m height in September 1999. At the time of clipping, stem length and number of leaves of each individual were measured. Analysis showed high correlations between dbh, stem length and number of leaves for all six species (n= 91-108, all 2-tailed Pearson correlations >0.38 and p< 0.001). Therefore only dbh was included in analyses as an indication of pre-clipping plant size. After the clipping treatment, sprouting behaviour was surveyed monthly over a period of six months. The monthly survey included both measurements of characteristics at the population level, as well as the individual plant level (Table 4.3). For clarity we refer to the stems of individual sprouts as axes were necessary, to distinguish them from the remnants of the saplings' main stems that remained after the clipping treatment.

Per species, six individuals in low light (light category 1) and six individuals in high light (light category 3) were randomly selected and excluded from the clipping treatment. In these individuals the concentration of total non structural carbohydrates (tnc, in mg/g) in the main stem and main root was measured. A sample was taken consisting of the sawdust of six transverse cuttings of the stem at 20, 40, 60, 80 and 100 cm above the ground. The root sample consisted of four transverse cuttings at three equal distances between the soil surface and the

Table 4.3. Plant traits recorded after stem breakage. Traits are either recorded monthly over the course of six months, or are measured once, six months after the time of stem breakage.

Level	Trait	Abrevia- tion	Unit	Description
Population				
	Sprouting frequency		%	The percentage of individual stems that produces sprouts
	Stem mortality		%	The percentage of individual stems that dies after having produced sprouts
Individual plant				
	Time to sprout emergence		month	Time lapse between breakage of the main stem and the emergence of the first sprout
	Number of sprouts		n	Number of sprouts per stem
	Sprout axis turn-over		%	Mortality among individual sprout axes per stem
	Number of immature leaves		n	Number of immature leaves per stem
	Number of mature leaves		n	Number of mature leaves per stem
	Average sprout axis length		cm	Average length of all sprout axes on a stem
	Largest sprout axis length		cm	Length of the sprout that was longest six months after clipping
	Height of implantation		cm	Distance between breakage point and point of implantation of each sprout
	Average height growth rate	hgr_{aver}	cm month ⁻¹	Length growth per sprout axis per month
	Maximum height growth rate	hgr_{max}	cm month ⁻¹	Length growth per month of the sprout axis which was largest at t= 6
	Variation in sprout length	cv	%	Coefficient of variation, indicating the variation in length between the sprout axes on a stem
	Axis mass per length	aml	g cm ⁻¹	Dry mass per unit length of the sprout
	Specific leaf mass	slm	g	Average dry mass of a mature leaf on a resprouting stem
	Specific immature leaf mass	slm_{imm}	g	Average dry mass of an immature leaf on a resprouting stem
	Total leaf mass	tlm	g	Total dry leaf mass of a resprouting stem
	Total axis mass	tam	g	Total dry mass of all sprout axes per individual stem
	Total sprout mass	tsm	g	Total dry mass of all sprouts on a stem (tlm + tam)
	Leaf axis mass ratio	lamr	g g ⁻¹	Total leaf dry mass divided by the total sprout dry mass

point at which the root diameter was 5 mm. Side roots were removed at the point of <5 mm diameter. Samples were dried at 70 °C for 48 hours. The concentration of tnc was measured by taking ± 25 mg oven dried plant mass. Samples were ground, extracted and hydrolysed with 3% HCl for at least 3h at 125 °C. Total glucose content was determined by the reduction of copper, using a modified Fehling method (Sawyer & Dixon 1968). A photo-spectrometer (Skalar auto-analyser) was used for the colorimetric determination of glucose.

At the level of the population, we recorded the sprouting frequency (the percentage of individual stems that sprouts) and stem mortality (Table 4.3). At the level of individual plants, we characterised the sprouting process by monitoring the number of sprouts (length >0.5 cm), the sprout axis length and the height of implantation of each individual sprout. From the fourth survey onwards, the number of immature and mature leaves was also recorded. Immature leaves were defined as leaves that had not yet unfolded (*Durio*, *Shorea*) or expanded (*Dipterocarpus*, *Girroniera*) and that were

Table 4.4. Three-way anova testing the effect of species, light class and storage organ (root or stem) on the concentrations of tnc. The average number of samples per species is 26 (range from 22 to 30).

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	180518	23	7849	6.97	0.000
Intercept	5129786	1	5129786	4558	0.000
Species	106539	5	21308	18.9	0.000
Storage organ	20097	1	20097	17.9	0.000
Light class	2713	1	2713	2.41	0.123
Species * storage organ	25981	5	5196	4.62	0.001
Species * light class	6959	5	1392	1.24	0.296
Storage organ * light class	4086	1	4086	3.63	0.059
Storage organ * species * light class	2486	5	497	0.44	0.819

densely pubescent (*Dipterocarpus*, *Gironniera*) or coloured brownish-red (*Madhuca*) or distinctly light green (*Durio*, *Macaranga*, *Shorea*). Mature leaves were defined as leaves that had unfolded and/or expanded and which were green, and which were therefore supposed to be capable of photosynthesis. Individual sprouts were monitored through time. From the data on sprout length, the height growth rate (hgr) per month was calculated for each individual sprout axis. The longest sprout axis after six months was identified on each stem, and its growth was more closely analysed. The variation in sprout length was expressed as the coefficient of variation (cv), corrected for small sample sizes (Sokal & Rohlf 1981).

Prior to our study, no data were available on the time-lapse between stem breakage and the emergence of the first sprouts and the development of the first mature leaves. During the course of the experiment, the start and the end of the tnc-dependent phase and the following photosynthesising phase were estimated, based on the time of first sprout emergence, the development of mature leaves, and a pronounced change in hgr of the sprouts.

Sprout development was characterised in terms of dry mass of leaves and sprout axes, six months after the clipping treatment, which was shortly after all species had developed green leaves (Table 4.3). Sprouts of five to eight randomly selected individuals were harvested for

measurement of the dry mass per unit length of the sprouts (sprout axis mass per length, aml, g/cm), specific leaf dry mass of immature leaves (slm imm, per individual leaf, in g) and specific leaf dry mass of mature leaves (slm, per individual leaf, in g). Dry masses were determined on a Satorius 210 BP balance.

These measured values of individual sprout dry mass were used to estimate the total dry mass of the stems of re-sprouts (total axis dry mass, tam, in g), total leaf dry mass (tlm, in g) and the sum of these two (total sprout dry mass, tsm, in g) of the sprout axes on the other individuals. This was achieved by multiplying the above mentioned average dry masses with respectively the total sprout length, number of immature leaves, and number of mature leaves six months after clipping. The leaf axis mass ratio (lamr, in g/g) was calculated by dividing the total leaf dry mass by the total axis dry mass.

SPSS 7.0 was used for the statistical analysis of the data. Species-specific differences in the concentration of tnc were analysed with a general multivariate analysis with the independent variables species, storage organ (main stem or main root), dbh and Dawkins light index (low light: category 1 in table 4.2, and high light: category 2 & 3 in table 4.2). Since dbh was not correlated with the tnc concentration, the same analysis was performed without this variable to include a post-hoc comparison test between species. Because the interaction between storage organ and light class was significant, we

analysed whether the tnc concentrations in root and stem of each species were significantly different with a paired t-test.

Differences in temporal patterns of first sprout emergence from each stem were tested with Kaplan-Meier survival analysis (n= 100 for each species, post-hoc comparisons between species made with Tarone-Ware statistics). The relationship between sprout mortality and topography and light climate was analysed with Kaplan-Meier analysis. Light categories and topographical units were compared using a log rank statistical comparison. The correlation between the species-specific average concentrations of tnc in root and stem versus the percentage of sprouting individuals was tested with a 2-tailed Spearman rank correlation.

Species-specific differences in production of number of sprouts and leaves, and sprout dry mass six months after clipping and the effect of light availability there upon were analysed with a two-way anova. Differences between species were tested with post-hoc Dunnett T3 tests (equal variances not assumed).

To assess the development of sprout dominance, height growth of the largest sprout versus average height growth was

analysed using a paired samples t-test. The analysis was not performed as a repeated measurement analysis because of missing values in the first and last time steps. To correct for the multiple use of measurements (i.e. sprout length was used to calculate hgr during two consecutive time steps) a Bonferroni correction was applied. An interspecific comparison of variation in sprout length, expressed as the coefficient of variation (cv), was made with a one-way anova.

Results

Pre-damage non structural carbohydrates

All six species had average tnc concentrations above 145 mg/g in both their roots and stem (Figure 4.1). Contrary to our prediction, the tnc concentration in the root and stem was not significantly related to the light environment (Table 4.4). *Dipterocarpus*, *Durio* and *Madhuca* had relatively high concentrations of tnc in both root and stem, with significantly higher tnc concentrations in the root than in the stem. The pattern of tnc storage in these three species was significantly dif-

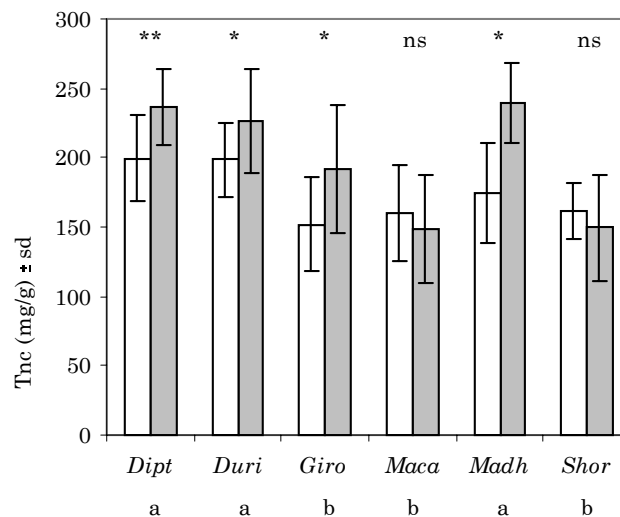


Figure 4.1. Concentrations of tnc in the stem (white bars) and the main root (hatched bars) of saplings (\pm sd). Letters below the bars show the significant differences between species, based on a Bonferroni post-hoc test ($p < 0.05$). The stars above the bars indicate differences between the root and the stem (* = $p < 0.05$, ** = $p < 0.01$, ns = not significant).

ferent from *Gironniera*, *Macaranga*, and *Shorea*. *Gironniera* tended to have lower tnc concentrations in both stem and root. The relatively low tnc concentrations in both the stem and the root of *Macaranga* and *Shorea* did not differ significantly from each other.

Survival and mortality

In all six species more than 50% of the individuals had sprouted within three months after clipping (Figure 4.2 a-f). Emergence of the first sprout through time was fastest in *Durio*, *Gironniera* and *Macaranga* ($p > 0.05$), intermediate in *Madhuca* and *Dipterocarpus* ($p < 0.01$ for comparisons with the other four species, and $p = 0.077$ for the comparison between the two species), and slowest in *Shorea* ($p < 0.01$ for all comparisons). The number of sprouting *Dipterocarpus* was still increasing after six months, and was expected to reach 100% after 9-10 months if the same trend continued. In *Macaranga* and *Shorea*, respectively 7% and 20% of the individuals never produced sprouts. None of the species showed a significant relation between light climate or topography and the emergence of sprouts through time.

Unexpectedly, we observed considerable levels of mortality among saplings that had produced sprouts in *Macaranga*, *Shorea* and *Madhuca*, which started in the second to fourth month after clipping (Figure 4.2 g-l). Resprouting individuals of *Shorea* died earlier when they grew under a higher light intensity (Kaplan-Meier analysis, $n = 82$, number of events = 29. Comparisons between Dawkins classes 1-2, 1-3, 2-3 yield respectively: $p = 0.000$, $p = 0.000$, $p = 0.908$). In *Macaranga* mortality was related to topography, being higher on the ridges and lower on slopes and in valleys (Kaplan-Meier analysis, $n = 98$, number of events = 23. Comparisons between topographical units 1-2, 1-3, 2-3 yield respectively: $p = 0.019$, $p = 0.018$, $p = 0.694$). The mortality of resprouting *Madhuca* saplings was independent of topography and light environment. We observed a fungus infection underneath the bark of a high proportion of the dead saplings of this species.

The mortality of individual sprout axes over six months was highest in *Shorea* (51%) and *Macaranga* (46%), intermediate in *Durio* (32%), *Diptero-*

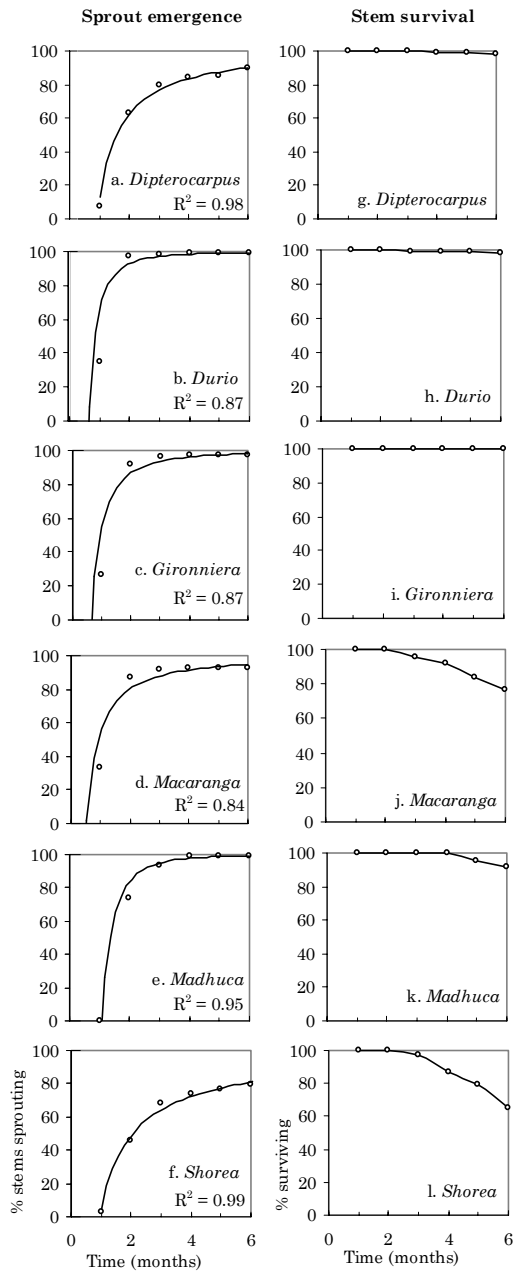


Figure 4.2. (a-f). First sprout emergence through time and (g-l) sapling survival (defined by the death of all sprouts on a stem) through time.

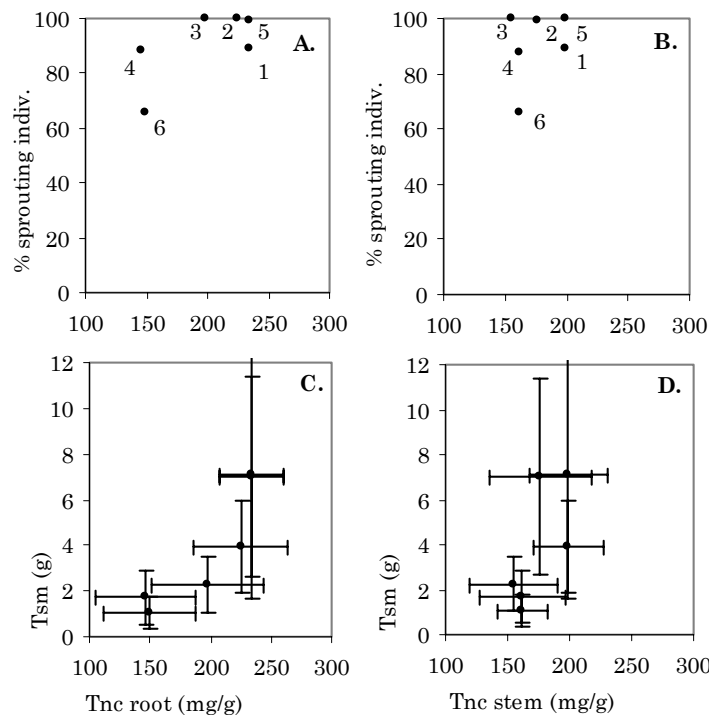


Figure 4.3. Relation between the average concentration of tnc in the main root and main stem, and (a, b) the percentage of individuals that had resprouted after six months and (c, d) total sprout dry mass production (Tsm) after six months. Label numbers refer to species. 1= *Dipterocarpus*, 2= *Durio*, 3= *Gironniera*, 4= *Macaranga*, 5= *Madhuca*, 6= *Shorea*.

carpus (28%) and *Gironniera* (34%), and lowest in *Madhuca* (17%). Sprout axis mortality per stem was often strongly aggregated in time, which suggested an external cause of mortality. In *Macaranga*, *Madhuca* and *Shorea*, 100% sprout axis mortality within one month was recorded in respectively 38%, 71% and 54% of the individuals that had produced more than one sprout and that had died by the end of the experiment. Such immediate death was associated with signs of a fungus infection in *Madhuca*, and accounted for half of the 17% sprout mortality recorded in this species.

The two species with the lowest tnc in both root and stem, *Macaranga* and *Shorea*, had the lowest percentages of sprouting individuals after six months (Figure 4.3 a & b), the highest levels of individual sprout axis mortality and the

highest levels of stem mortality during the experiment. However, the number of species was too low to reveal a significant relationship between the percentage of individuals sprouting and the concentration of tnc in the root (2-tailed Spearman rank correlation, $n = 6$, corr. coef. = 0.50, ns) or in the stem ($n = 6$, corr. coef. = 0.21, ns).

Two phases of sprout development

The two phases in the production of sprouts that were expected because of the absence of photosynthesising leaves in the first phase of sprout development were suggested by the peaked-curved pattern of the hgr in most species. In all species the production of sprout axes was highest in the second and third month (Figure 4.4). Hereafter, sprout production decreased, and dropped below the

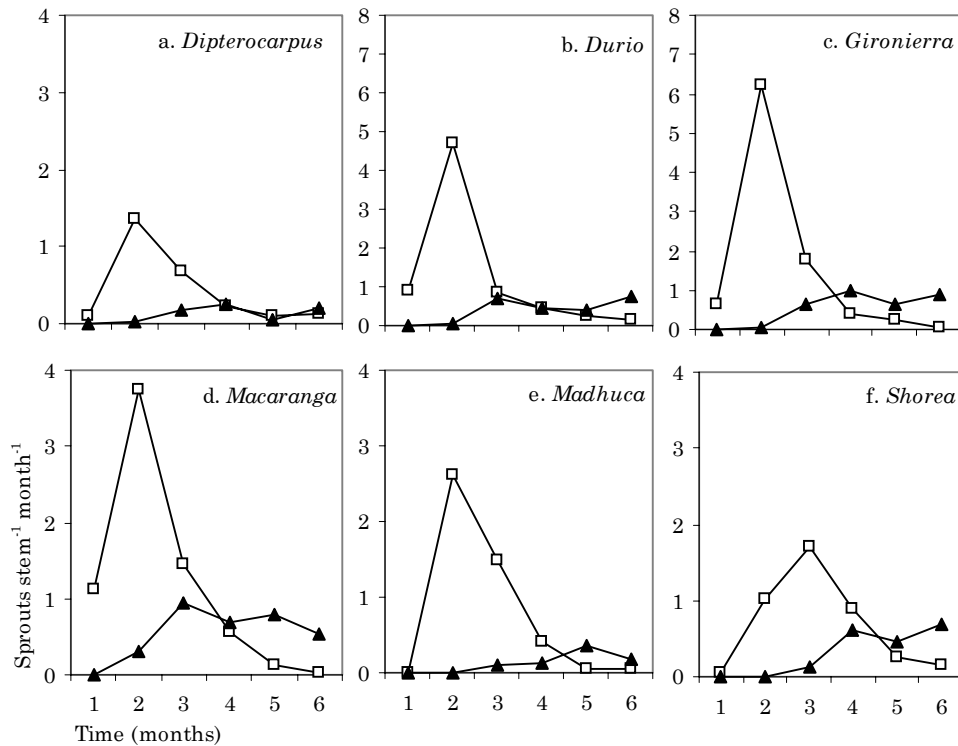


Figure 4.4. Sprout dynamics per stem during six months after clipping. Open squares: Average number of sprouts emerging per stem per month. Closed triangles: Average sprout mortality per stem per month. Note the different scales on the y-axis.

monthly sprout mortality in *Durio*, *Gironniera*, *Macaranga* and *Shorea*. Around the same time as we observed a peak in sprout emergence, a pronounced peak in hgr was found for most species (Figure 4.5). In the third and fourth month a transitory period between the first to the second phase followed, during which the hgr decreased, after which the hgr appeared to stabilise at a relatively low rate from the fifth month onwards. The pattern was pronounced for *Durio*, *Macaranga* and *Madhuca* and *Shorea*, whereas it was less obvious for the average hgr of *Dipterocarpus* and *Gironniera*.

Sprout growth, tnc, and wood density

The characterisation of sprouting behaviour revealed significant differences between species for all variables in the analysis (Table 4.5, 4.6). Light class had a very limited effect, and was strongest related to the number of leaves per sprout axis. Reviewed at a species-specific level,

the relation between light class and number of leaves per sprout axis showed a small increase in some species, which was negligible in comparison with the variation within one light class.

Total sprout mass varied by a factor 7, and the specific leaf mass by approximately a factor ten between species. The large leaf size produced by *Dipterocarpus* was associated with the production of a low number of leaves and low number of sprout axes. Specific leaf mass was strongly correlated with axis mass per length (One-tailed Pearson correlation = 0.98, $p < 0.001$, $n=6$). Considering the large variation in specific leaf mass, differences in leaf axis mass ratio were remarkably small. Only *Dipterocarpus* differed significantly from the other species in this respect.

The concentration of tnc in the root tended to be related to the total sprout mass production (Figure 4.3 c, $F=13.9$, $p=0.02$, $n=6$), but this was not the case for

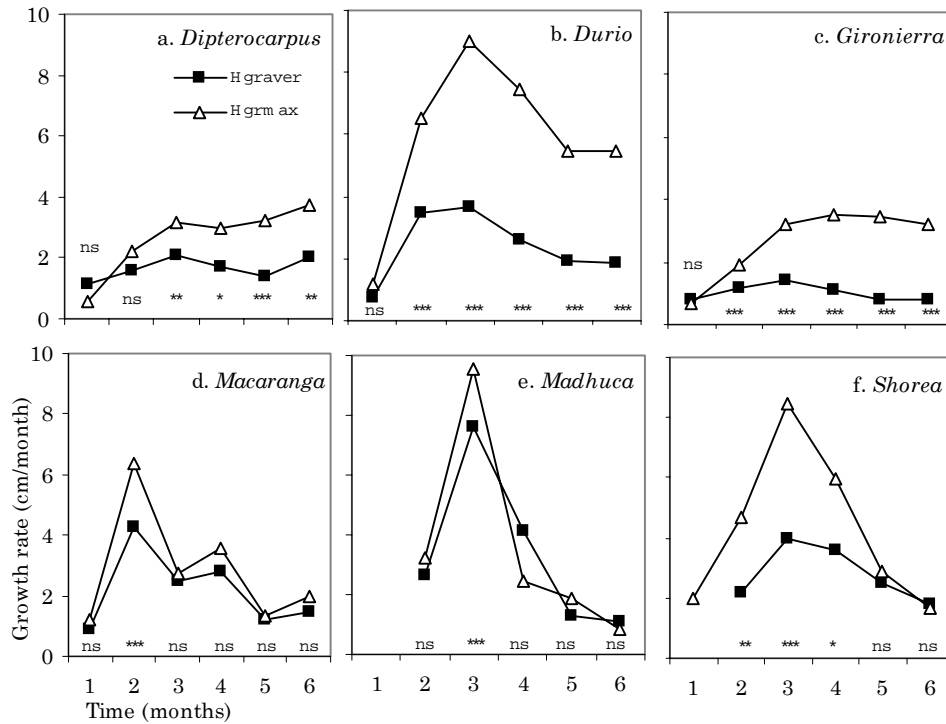


Figure 4.5. Average height growth rate (hgr_{aver}) per individual sprout through time (closed squares), and the hgr_{max} , of the sprout which was largest six months after clipping (open triangles). In the top three species, the hgr_{max} is persistently higher than the hgr_{aver} , whereas in the lower three species the hgr_{max} is higher only during the first phase of development.

tnic concentration in the stem (Figure 4.3 d, $F= 3.7$ $p= 0.13$, $n= 6$). Growth of the tallest sprout in the fifth and sixth month after breakage showed a tendency to be correlated with wood density (Figure 4.6).

Apical dominance

In all species the largest sprout after six months had a hgr which was significantly higher than average during at least one observation month after clipping (Figure 4.5). In three species, the hgr of the largest sprout was significantly higher than average both during the leafless first phase, as well as during the second phase. In *Macaranga*, *Madhuca* and *Shorea*, the hgr of the largest sprout was significantly higher only during the first one to fourth months of establishment, a difference which became insignificant by the time green leaves had developed on the sprout axes.

Variation in hgr between the individual sprouts on a single individual resulted in size differences between sprouts after six months. As a result the coefficient of variation (cv) in sprout length after six months differed considerably between species (Figure 4.7). The cv gives a standardised indication for the dominance of the tallest sprout. Such a dominant sprout developed in *Dipterocarpus*, *Durio* and *Gironniera*, whereas the variation in sprout length between the sprouts on each individual sapling remained low and even decreased over time in *Macaranga*, *Madhuca* and *Shorea*. In the case of *Madhuca*, we observed that the sprouts of each individual had a remarkably constant length after six months. The initial variation in sprout length in this species was due to variation in the time of emergence of the different sprouts on the same stem, which resulted in differences in stage of development at any particular time step.

Table 4.5. Two-way anova describing the effects of species and light class on sprouting behaviour six months after clipping. Sprouting behaviour is characterised in terms of number of leaves, number of sprouts, number of leaves per sprout, total sprout mass (Tsm), total leaf mass (Tlm), total sprout axis mass (Tam) the ratio between leaf mass and axis mass (Lamr). Results of the post-hoc analysis of species-specific differences are presented in table 4.6.

Source	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	
Species	Number of leaves	4893.3	5	978.7	13.2	0.000	***
	Number of sprouts	488.1	5	97.6	13.8	0.000	***
	Leaves per sprout	31.7	5	6.3	2.5	0.029	*
	Tsm	2666.8	5	533.4	54.5	0.000	***
	Tlm	1661.0	5	332.2	53.0	0.000	***
	Tam	149.3	5	29.9	51.9	0.000	***
	Lamr	475.3	5	95.1	20.3	0.000	***
Light class	Number of leaves	512.2	2	256.1	3.4	0.033	*
	Number of sprouts	8.8	2	4.4	0.6	0.539	
	Leaves per sprout	31.9	2	16.0	6.3	0.002	**
	Tsm	23.9	2	11.9	1.2	0.296	
	Tlm	8.5	2	4.3	0.7	0.507	
	Tam	4.5	2	2.3	3.9	0.020	*
	Lamr	15.1	2	7.5	1.6	0.202	
Species * light class	Number of leaves	713.6	10	71.4	1.0	0.478	
	Number of sprouts	87.7	10	8.8	1.2	0.263	
	Leaves per sprout	51.1	10	5.1	2.0	0.029	*
	Tsm	137.5	10	13.7	1.4	0.175	
	Tlm	83.9	10	8.4	1.3	0.207	
	Tam	10.0	10	1.0	1.7	0.071	
	Lamr	81.2	10	8.1	1.7	0.071	
Total	Number of leaves	115468.0	430				
	Number of sprouts	14067.3	430				
	Leaves per sprout	4777.1	430				
	Tsm	15723.4	430				
	Tlm	9670.6	430				
	Tam	857.1	430				
	Lamr	8686.6	430				

Discussion

Total non-structural carbohydrates and light

Ranging from 15 to 24% of the total dry weight, concentrations of tnc were considered high, considering that the studied plants were growing in the forest understorey. Comparable concentrations have been found for seedlings growing in temperate forests (Canham et al. 1999). Theoretical modelling studies (Iwasa & Kubo 1997, Iwasa 2000) have predicted that, if they grow under unfavourable

conditions and have a high chance of experiencing damage, the optimal strategy for plants is to make relatively large carbon investments to ensure their persistence, at the cost of investing in growth. Apparently, the saplings in our study act according to this model, storing considerable amounts of energy in order to ensure their survival under adverse circumstances.

Contrary to our prediction, there were no significant differences in tnc concentrations between individuals growing under different light conditions. Canham et al. (1999) found a small effect of light availability on tnc concentrations in a temperate forest, which suggested that

either seedlings were limited in their ability to respond to differences in light availability, or alternatively storage of tnc has a high priority, and is achieved even under limited light conditions. The lack of correlation between tnc concentrations and light conditions also suggests that

Table 4.6. Sprout characteristics six months after clipping. All values are for newly produced spouts only. Presented are: **(a)** Dry masses measured on a random subsets of five to eight individuals per species (n). **(b)** Sprout characteristics measured in the field of all individuals (n) of the six species in the experiment. **(c)** Calculated sprout characteristics of all individuals (n) of the six species in the experiment. Significant differences between pairs of species, based on a *post-hoc* Dunnett T3 test, are indicated in the table with letters.

		<i>Diptero-</i> <i>carpus</i>	<i>Durio</i>	<i>Giron</i> <i>niera</i>	<i>Maca-</i> <i>ranga</i>	<i>Madhu</i> <i>ca</i>	<i>Shorea</i> <i>ca</i>
(a) Measured dry mass							
	n (stems sampled)	6	7	6	8	6	5
Specific leaf mass (immature leaves)	Slm _{imm} (g)	0.72	0.075	0.031	0.021	0.049	0.007
	SD	0.83	0.057	0.020	0.021		
Specific leaf mass (mature leaves)	Slm (g)	1.29	0.24	0.11	0.11	0.42	0.10
	SD	0.90	0.08	0.09	0.03	0.24	0.07
Sprout axis mass per length	Aml (g/cm)	0.059	0.013	0.014	0.0077	0.034	0.0065
	SD	0.026	0.005	0.007	0.0025	0.011	0.0026
(b) Measured sprout characteristics							
	n	93	91	96	74	88	52
Number of leaves		4.9	14	17	14	13	9.3
	SD	4.2	8.5	9.9	10	8.7	8.0
	Sign.	a	cd	d	cd	bc	b
Number of sprouts		2.1	5.1	6.2	5.1	4.2	3.8
	SD	1.1	2.7	3.2	3.2	2.6	2.9
	Sign.	a	bcd	d	cd	bc	b
Leaves per sprout		2.5	3.3	3.0	2.9	3.2	3.5
	SD	1.3	2.3	1.4	1.5	1.3	4.4
	Sign.	a	ab	ab	ab	ab	b
(c) Calculated dry mass							
	n	93	91	96	74	88	52
Total dry mass of sprout axes	Tam (g)	1.1	1.0	0.52	0.41	2.0	0.29
	SD	1.0	0.4	0.28	0.27	1.4	0.20
	Sign.	b	b	c	c	a	d
Total leaf mass	Tlm (g)	5.9	3.0	1.7	1.3	5.1	0.74
	SD	4.5	1.7	1.0	1.0	3.2	0.59
	Sign.	a	b	c	d	a	e
Total sprout dry mass	Tsm (g)	7.1	3.9	2.3	1.7	7.0	1.0
	SD	5.4	2.0	1.2	1.2	4.4	0.7
	Sign.	a	b	c	d	a	e
Leaf axis mass ratio	Lamr (g/g)	0.84	0.73	0.76	0.74	0.72	0.66
	SD	0.06	0.10	0.07	0.10	0.09	0.19
	Sign.	a	b	b	b	b	b

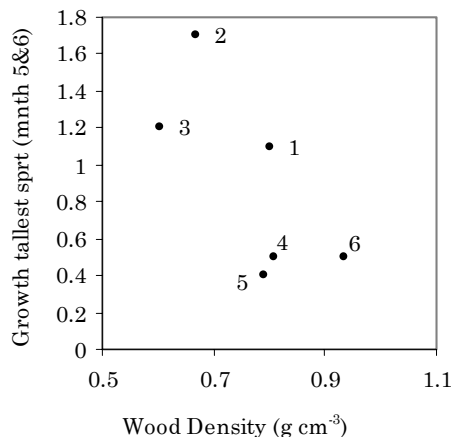


Figure 4.6. Sprout growth in the second stage of sprout development (in the presence of photosynthesising leaves) versus specific wood density. The one-tailed correlation between the two variables was -0.71 , $p = 0.056$, $n = 6$. Label numbers refer to species. 1= *Dipterocarpus*, 2= *Durio*, 3= *Gironierra*, 4= *Macaranga*, 5= *Madhuca*, 6= *Shorea*.

(undamaged) plants that grow under unfavourable light conditions make conservative use of their energy reserves, and differences in tnc concentration may only become apparent after a long period of very low light availability.

Sprouting frequency and sprout mortality

After clipping, the saplings of four out of six species in this study had a resprouting frequency close to 100%. A comparable frequency of sprouting has also been found in Panama (Guariguata 1998). We found that the sprouting frequency tended to be positively related to the tnc concentration in the root, while stem mortality and sprout turnover tended to be negatively related to the tnc concentration in the root. Sprouting frequency did not correlate significantly with tnc in the stem. This suggests that the measured tnc in the stem is not fully available for the plant, although the concentrations were considerable. In other studies it has been observed that the production of tissue may stop well before the reserves of tnc have been depleted, which has led to the suggestion that not all measured tnc are truly available to the

plant for the production of new tissue (Chapin et al. 1990).

Resprouting stems of *Macaranga*, *Shorea* and to a lesser extent *Madhuca* showed considerable levels of mortality, all sprouts on a stem frequently dying off over a single one-month observation period. This simultaneous mortality suggests an external mortality agent. In the case of *Madhuca*, an increased susceptibility to a fungal infection appeared to be the cause of mortality. Stem mortality in *Macaranga* and *Shorea*, which was respectively related to topography and light environment, seemed to be caused by water deficiencies. Also the turn-over of individual sprout axes (e.g. not causing the death of the individual) was highest in *Macaranga* and *Shorea*.

These patterns are remarkable, since *Macaranga* and *Shorea* species have heavy wood, a characteristic that has been associated with resistance to xylem cavitation (Hacke et al. 2001). Indeed, mature trees of heavy-wooded species survived a severe drought in our study area better than did species with lighter wood (Chapter 2). This contradictory result is possibly caused by the xylem vessel architecture at the points of attachment of sprouts to the main stem. Water transport resistance is locally increased at branching points (Bazzaz 1996) and at the attachment points of sprouts (Klugmann & Roloff 1999), as the result of a high number of xylem vessels ending in these locations. It seems that especially in heavy-wooded species, with their small vessel width and very thin sprout axes, this morphology frequently causes fatal xylem cavitation in recently formed sprouts.

Biomass production and the two phases of sprout development

All species but *Dipterocarpus* showed two phases in the average hgr of their sprouts. In the first phase, a high sprout emergence was observed and a high average hgr was achieved. In the second phase, the sprout emergence rate and the average hgr decreased. The first phase lasted until three to five months after

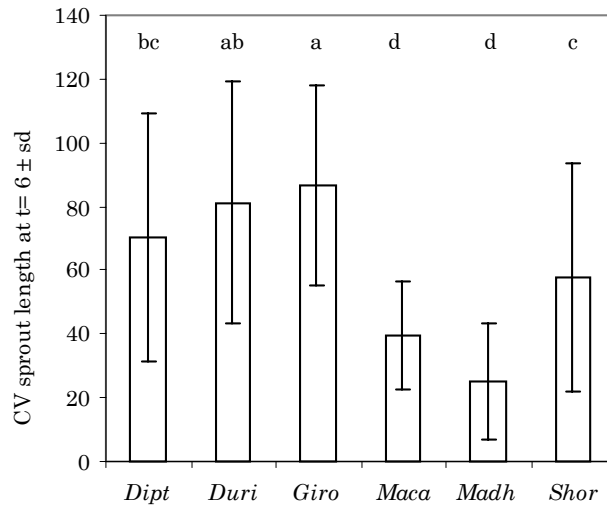


Figure 4.7. Coefficient of variance for the length of sprouts per stem, six months after clipping. Values are corrected for small sample size (Sokal & Rohlf 1981). Letters above the bars show the significant differences between species, based on a Bonferroni post-hoc test ($p < 0.05$).

stem breakage. Because green leaves were absent, sprout growth must have been entirely dependent on the stored tnc during the sprout initiation phase. The total dry mass produced by resprouting at the end of the experiment was positively related to the concentrations of tnc in the root. By this time, most of the biomass was produced using stored tnc. These observations suggest that the storage of tnc is indeed of vital importance for the successful resprouting of these saplings. Since many seedlings and saplings survive severe damage during their lives before reaching the canopy (Clark & Clark 1991, MvN pers. obs.) the high concentrations of tnc and the subsequent high persistence of individuals may be a common phenomenon in many forests.

The light environment prior to clipping did not explain intra-specific differences in sprouting frequency or sprout capacity six months after clipping. Because green leaves were absent during a large part of the experiment, and the hgr was low during the period that green leaves were present, the measured sprout production appears to be mainly based on stored tnc. Since the concentrations of tnc

were not related to the light environment, differences in sprouting capacity were not to be expected between saplings growing in different light environments. In a defoliation experiment with temperate seedlings, Canham et al. (1999) found a similar limited effect of light level on seedling growth rate, pattern of biomass allocation, tnc concentration, and survival. They concluded that this suggests a relative independence of seedling performance on external resource availability, whereas seedling survival seems to be strongly affected by disturbance factors that cause defoliation or loss of root or shoot tissue.

Green leaves had started to develop at the beginning of the second phase, which suggests that at this point, the sprouts were becoming more and more autonomous in their energy supply. In this phase, length growth of sprouts tended to be negatively correlated to specific wood density. Similar constraints on growth, such as a higher carbon investment per volume of wood tissue in heavy-wooded trees, may explain the similarity in the patterns of sprout growth and growth of undamaged seedlings.

Sprout dominance and crown architecture

One of the most striking inter-specific differences in sprout formation was the fast growth of a dominant sprout in *Dipterocarpus* and even more so in *Durio* and *Gironniera*. In these species, the dominant sprout had a higher than average hgr during the first as well as the second phase of development. This growth pattern contrasted with the sprout growth in the other three species, where the tallest sprout did initially have a significantly higher than average hgr, but did not maintain this during the second phase. The interspecific differences in the pattern of hgr resulted in sprouting behaviour that ranged from the formation of a single dominant sprout, to the production of a larger number of sprouts which were almost equal in size.

For the growth of undamaged saplings, a trade-off has been suggested between investment in lateral extension of the crown and investment in height growth (King 1990, Kohyama & Hotta 1990, Ackerly & Donoghue 1998). Lateral crown extension will maximise light interception under shady conditions. Investment in height growth increases the speed at which better-lit sites higher up in the canopy are reached (King 1990, Kohyama & Hotta 1990).

The observed variation in sprout formation after stem breakage may be the result of a similar trade-off. We observed that the production of many similar-sized sprouts coincided with more horizontally growing branches and a conspicuous wide lateral distribution of the leaf area in *Madhuca*, which corroborates the existence of a trade-off between height growth and lateral crown extension. We hypothesise that the alternative strategy, which comprises of quickly producing a dominant sprout which shows rapid height growth, improves the chances for a damaged plant to consolidate a dominant position in the relative size order with its neighbours. This is likely to increase the future growth of the individual as well as its survival chance if a vertical light gra-

dient exists, since the size of a sapling relative to its neighbours has been shown to be one of the main determining factors for the outcome of competition (Zagt 1997, Brown et al. 1999).

Sprouting strategy and persistence of individuals

The high levels of sprouting capacity found in this paper show that the persistence of individuals after a disturbance, including large-scale disturbances such as fire, is likely to play a pivotal role in determining the future forest structure and species composition. At current, knowledge of species-specific sprouting behaviour of tropical trees, and the factors that determine it, are virtually non-existent (Bond & Midgley 2001). We have shown that sprouting capacity is influenced by the amount of stored tnc, particularly in the root, and wood density. Marked differences in sprouting behaviour provide evidence for the existence of variation in recovery strategy. There are few impediments to validate the importance of variation in sprouting behaviour as a life-history characteristic on a large set of species, because it is relatively easy to make detailed assessments of sprouting behaviour in a standardised way.

Acknowledgements

I am grateful to M.J.A. Werger, J.A. Sayer, D. Sheil, D.W. Dijkman, T. de Kam, K. Sidiyasa, H.J. During, M. van Noordwijk, P. Frost, F. Sterck, J.W.F. Slik and G.M. Fredriksson for logistic support and fruitful discussions. The field work benefited from the dedicated assistance of J.A. Helleman, N. Syah, F. Udin and S. Laysa Putra. Carbohydrate analyses were done by J. van Rheenen. This research was performed at the International Ministry of Forestry (MOF)-Tropenbos-Kalimantan research station in East Kalimantan. Financial support was provided by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) with grant 84-408 and by the Center for International Forestry Research (CIFOR) in Bogor, Indonesia.

5

Vertical gradient in viable seed density and germination after fire in the seed bank of a lowland dipterocarp rain forest

Abstract

The vertical distribution of seeds in the top 4.5 cm of soil in a primary lowland dipterocarp forest in East Kalimantan and in an adjacent burned part of the forest were compared. In the primary forest the seed density was 292 - 397 seeds 0.1 m², which is higher than recorded values from most other studies on tropical rain forest. Seed density showed a rapid decline with depth. In the burned forest the viable seed density in the litter layer and the upper 1.5 cm of the soil was respectively 86% and 71% lower than in the primary forest, but lower layers were not significantly different. The vertical stratification pattern and changes therein were comparable for the two dominant families, Rubiaceae and Melastomataceae.

Sensitivity of dormant seeds to different combinations of light and temperature was tested experimentally. Light was shown to be a pre-requisite for the germination of very small-seeded species, whereas small-seeded *Macaranga* was able to germinate in complete darkness as long as there were daily fluctuations in temperature. In complete darkness, *Macaranga* seedlings etiolated and postponed the unfolding and colouring of the cotyledons. In contrast, very small-seeded species did not etiolate and always produced two green cotyledons immediately after germination. The combination of germination in the dark and stem elongation suggests that *Macaranga* is capable of successful seedling establishment from a greater depth in the soil.

Keywords: East Kalimantan, forest fire, germination trigger, seed bank, seedling establishment, tropical rain forest.

Introduction

A persistent soil seed bank, which includes herbs, shrubs, lianas and trees, is commonly found in tropical forests (Chin 1973, Cheke et al. 1979, Saulei & Swaine 1988, Garwood 1989, Dalling et al. 1994, 1997 a, Swaine et al. 1997). The density of viable seeds in the soil of an undisturbed forest decreases with increasing depth (Hopkins & Graham 1983, Young et al. 1987). This pattern results from a slow infiltration rate of seeds in the soil (Bekker et al. 1998), in combination with a low mortality rate for dormant seeds, which is commonly sigmoid or logarithmic over time (Roberts 1972, Dalling et al. 1997 a).

The germination rate of seeds at a certain depth in the seedbank and the subsequent chance of above ground establishment of seedlings are determined by different environmental factors (Vleeshouwers 1997). Germination is usually triggered by an external abiotic trigger, such as light (both the amount and the spectral composition (Pons 1992, 2000)) and daily fluctuations in temperature (Vázquez-Yanes & Orozco-Segovia 1982, Probert 1992, 2000, Vázquez-Yanes & Orozco-Segovia 1993). As light penetrates only a few millimetres into the soil (Wooley & Stoller 1978), only those light-sensitive seeds which are close to the soil surface are likely to respond to an above-ground change in the light regime (Molofsky & Augspurger 1992). Temperature-sensitive seeds may germinate at a greater depth, since temperature fluctuations are considerable up to a depth of approximately 10-15 centimetre when the soil surface is exposed to a full day of direct sun light (Rosenberg 1974).

The chance of successful establishment of a seed from a certain depth is determined by its size, which sets the maximum size of the seedling that can be produced (Grime & Jeffrey 1965). The initial size does not only affect the competitive ability of the seedling, but also the maximum burial depth from which emergence to the soil surface is possible (Haskins & Gorz 1975 in Vleeshouwers

1997, Bond & Wilgen 1996). The seed size of species with dormant seeds varies by at least an order of 3 in the Southeast Asian rain forest (Metcalf & Grubb 1995). Most Rubiaceae and Melastomataceae have a seed weight <1 mg or even <0.1 mg. *Ficus* seeds commonly weigh 0.1-0.4 mg, whereas *Macaranga* species typically have a seed weight of 10-30 mg (Metcalf & Grubb 1995).

It would be clearly advantageous to a seed to be sensitive to a germination trigger that penetrates the soil up to the maximum depth from which it is able to successfully establish a seedling. Thus, we expect that species with larger seeds are sensitive to triggers that penetrate deeper into the ground. More specifically, we predict the seeds of very small-seeded taxa (Rubiaceae, Melastomataceae, *Ficus*) to be triggered by light, whereas *Macaranga* seeds are also sensitive to daily fluctuations in temperature. In the present study, we tested how different combinations of light availability and daily fluctuations in temperature influence the germination of seeds from the soil seed bank.

The dependence for germination on an external trigger allows species with dormant seeds to commonly establish in natural forest gaps (Hopkins & Graham 1984, Raich & Gong 1990). The same mechanism ensures that the seedbank contributes significantly to the establishing vegetation after fire (Young et al. 1987, Riswan & Kartawinata 1989, Woods 1989, Nykvist 1996, Kammesheidt 1999). Due to the fire the above ground vegetation is disturbed which greatly increases the light availability and daily fluctuations in temperature at the soil surface, thus providing ample triggers for seed germination. However, seeds in the upper part of the seed bank are likely to be damaged (Ewel et al. 1981, Swaine et al. 1997) by the fire (Campbell et al. 1995). These two opposing variables determine the post-fire density of germination (Martin & Cushwa 1966, Whelan 1995). We investigated the vertical gradi-

ent of the seedbank in an undisturbed forest, and compared this with the vertical distribution of seeds in adjacent parts of the forest that were burned. This way we can make an estimate of how the fire affects the availability of seeds that have the potential to successfully establish a seedling after the fire.

Material and methods

Site description

The samples for this study were collected in the Sungai Wain forest reserve close to Balikpapan, East Kalimantan in Indonesia (1°16' S and 116°54' E). This reserve is covered mainly by lowland dipterocarp rain forest. It receives an average annual rainfall of 2790 mm. In March and April 1998, during an extremely long dry episode, a forest fire burned two-thirds of the reserve. A core area of the forest was saved from the fire by means of an extensive network of firebreaks. More details on the site description are given in chapter 2.

Inside the forest the fire was of low intensity, spreading over the ground at a rate of 10-15 m/h and with a flame height of 0.5 m. The fire was largely confined to the litter layer, which mostly did not burn completely. Although high rates of tree mortality occurred, nearly all dead stems, including small seedlings and saplings, were left standing (chapter 2).

Two experiments were conducted in this forest. The first experiment aimed at measuring the change in the vertical gradient of seed density in the seed bank as the result of fire. The second experiment focussed on differences in sensitivity of dormant seeds to light availability and daily fluctuations in temperature, which penetrate to different depths in the soil.

Seed density experiment

For the measurement of the viable seed density, soil samples were collected from six sites over an area of 9 km². Sampling took place from 5 to 10 October 1998. Samples were collected pair-wise, one sampling station being situated in burned forest and one in unburned forest. Sampling stations were at a distance of

15 to 30 m from the firebreak. At each sampling station, five sub-samples with a surface area of 10 x 20 cm each were taken in an area of 3 x 5 m. Each sub-sample was stratified into four horizontal layers, including the litter layer and three layers of mineral soil of 1.5 cm depth each. Per soil depth layer, these stratified sub-samples, were later homogenised to form a single sample. Thus we sampled up to 4.5 cm deep into the mineral soil. The volume of soil collected per sampling station was 0.90 l (excluding the litter layer). The layers were collected by using knife-edged metal plates, which delineated the vertical borders of the sub-sample, after which a single plate was driven into the soil horizontally to collect the layers separately. After collecting a layer, the depth to the soil surface was measured at the four corners of the sample pit, to ensure a correct stratification. These measurements showed that accurate stratification was achieved: From the soil surface downwards, the depth of the three soil layers was respectively 1.6 ± 0.2 cm (average \pm sd, n= 60), 3.1 ± 0.2 cm and 4.6 ± 0.2 cm.

Samples were stored in plastic bags in the dark and transported to the nursery within three days. Each sample was concentrated by rinsing with water and sieving through a mesh of 0.5 mm. Because very small seeds might be lost by this procedure, we combined the residues of the three layers of mineral soil from one sub-sample (excluding the litter layer) into one sample, which was washed through a sieve of 0.1 mm mesh wide. This control test was performed on the sub-samples of four sample points. All the residues were randomly placed in trays on a substrate of white sand in a layer with a maximum depth of 0.5 mm to ensure favourable germination conditions at all depths in the samples (Dalling et al. 1994). To control for viable seeds in the substrate and for wind dispersed seeds that might arrive during the experiment, an additional twenty trays which contained only white sand were placed randomly over the greenhouse area. The few samples that had remained relatively voluminous after rinsing and sieving were

Table 5.1. Description of the environmental conditions that were simulated in the germination trigger experiment. Four combinations were made of two potential germination triggers. The different combinations of these two factors mimic the conditions at increasing depth in the soil. The relative light intensity was measured with an overcast sky. For further details see text.

Treatment	Code	Triggers		Environmental conditions										
				Irradiance level (% of full light)			Percentage of the daily temperature fluctuation in the greenhouse							
				Aver.	SD	n	Aver.	SD	n	Aver.	SD	n		
Greenhouse				30.6	2.4	10	100							
High light x Fluct. temperature	HT	+	+	20.8	2.0	19	67	13	5					
Low light x Fluct. temperature	LT	±	+	0.5	0.2	18	63	20	6					
No light x Fluct. temperature	OT	-	+	0			54	10	6					
No light x Cons. temperature	OO	-	-	0			29	8	7					

spread over two trays, in order to ensure that all samples were spread in a thin layer. The trays were placed inside plastic greenhouses of 1 x 2 x 0.5 m, which were placed underneath a gallery of shadow-cloth, to avoid too much direct sunlight and too high mid-day temperatures. A small amount of fertiliser dissolved in water was added, and trays were kept moist by daily watering.

For 13 weeks the seedlings in each tray were counted and marked on a weekly basis. When seedlings were large enough to survive transplantation, one to five individuals per species were transplanted to individual bags for further rearing and identification. Additional seedlings that could be identified to one of the transplanted species or types were removed from the trays. Many seedlings could not be identified or could only be identified up to family level, due to a high predation rate on very small seedlings by insects, and due to the difficulty to recognise species on the basis of vegetative characteristics. Manuals by Ng (1991) and Bodegom et al. (1999) were used for identification.

SPSS 8.0 was used for the statistical analyses. To increase homoscedasticity, the data on seed densities were (log + 1) transformed (Sokal & Rohlf 1981). Average values were back transformed for presentation. The vertical distributions of the seed density in unburned and burned

forest were analysed with a two-way anova. T-tests with a Bonferroni-correction were employed to test for the effect of the fire on individual sample layers.

Germination trigger experiment

In the germination trigger experiment we investigated the importance of light and daily fluctuations in temperature as triggers for seed germination from the seed bank. We applied four treatments (Table 5.1), aiming to separate the effects of light and temperature, and at the same time mimicking the burial of seeds at different depths in the soil. The experiment was performed in a forest clearing of 0.5 ha, in a greenhouse with open sides. The roof of the greenhouse consisted of several layers of black shade-cloth, which reduced the light intensity to 31% of full light (Table 5.1). The average daily minimum and maximum temperature in the greenhouse were 22 ± 0.6 °C and 33 ± 3 °C (n= 11), respectively.

Light-tight frames of 30 x 30 x 10 cm were fitted into regularly spaced holes in the ground (cf. Wesson & Wareing 1969). The different environments were simulated by covering these frames with different lids. The daily maximum and minimum temperature inside the trays was measured with max-min thermometers and the relative light availability with linear light sensors (PAR, $W m^{-2}$).

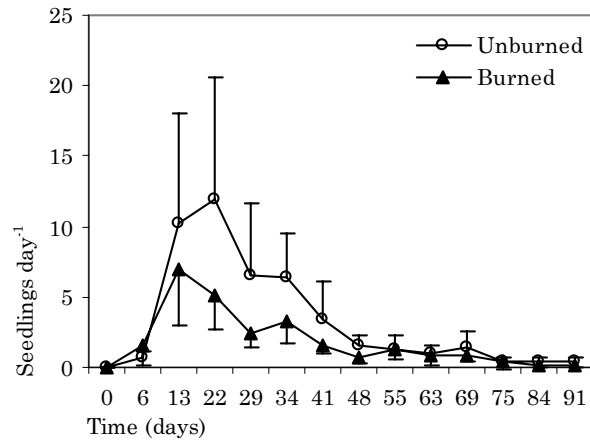


Figure 5.1. Daily seedling establishment (\pm sd) through time per sample point in the unburned samples and burned samples of the vertical seed distribution experiment, based on weekly observations. The experiment was started on 13 October 1998. The total sample volume per sample point was 0.9 l of soil plus a variable amount of litter.

The frames of the HT treatment had a cover of clear plastic, and the LT treatment was covered by a thin black cloth which allowed penetration of 0.5% of the full light (Table 5.1). The OT treatment was covered by a light-tight 2-mm thin triplex lid, which reduced the daily fluctuations in temperature to 54% of the above ground fluctuations in the greenhouse. The OO treatment was covered with a light-tight triplex lid and a 3-cm thick board of foam, which reduced the daily fluctuations in temperature to 29%. Great effort was made to prevent light leakage in the latter three treatments. Each treatment was replicated five times, and the OT treatment six times.

Since the seed dormancy of some species is broken by even a very short exposure to light (Wesson & Wareing 1969), soil samples were collected at night, in complete darkness and with the use of a torch that was covered with green plastic. Soil samples were collected from four different sites, at a depth of 1.5 - 4.5 cm. All samples were concentrated on the spot by washing and sieving. By collecting from one additional site underneath a mature tree of *Macaranga gigantea* (Reichb.f. & Zoll.) Müll.Arg., an effort was made to ensure the presence of a high density of

dormant seeds of this species. However, in the course of the experiment most of these seeds appeared to be unviable. The samples from all five sites were homogenised into one sample, which was sown in an equally thin layer (<0.5 mm) in the experimental trays. Trays were watered every second night, and seed germination was observed weekly for 12 weeks at night, using a torch with green cover. Germinated seeds were categorised into two size classes, 5 mm diameter being the limit between the two groups. In the present paper, seeds with a diameter below 5 mm will be called "very small", whereas seeds between 5 and 10 mm diameter will be called "small". Even though this limit is arbitrary, it allowed a functional division of the seeds into two groups, first because actually, few very small-seeded species had a seed size >2 mm, and second because the group with a seed size >5 mm consisted of a distinct set of species, mainly including the genera *Macaranga* and *Mallotus*.

Differences between the treatments were analysed with a one-way anova, using post-hoc Bonferroni comparisons between treatments. The OO treatment was not included in this analysis, because no seeds germinated there.

Table 5.2. Two-way anova for testing the log (seed density + 1) in the seed-bank between the unburned treatment versus the burned treatment over four horizontal layers of soil (a litter layer and three layers of mineral soil with a thickness of 1.5 cm each).

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	7.89	7	1.13	14.6	< 0.001
Intercept	119	1	119	1543	< 0.001
Treatment	1.56	1	1.56	20.2	< 0.001
Layer	5.42	3	1.81	23.4	< 0.001
Treatment * layer	0.99	3	0.33	4.28	0.011
Error	2.93	38	0.08		

Results

Vertical seed density

Seed germination was quick (Figure 5.1). Within two to three weeks after the start of the experiment, the highest level of germination was found and within eight weeks, 90% of the total recorded germination had taken place in both the unburned and the burned samples. The temporal pattern of seed germination in

the experiment was not significantly different between unburned samples and burned samples (repeated measures anova with 14 time-steps, $n = 12$, $MS = 0.0$, $F = 0.0$, ns).

The overall seed density in the top 4.5 cm of the soil plus the litter layer decreased from 292 (95% confidence limits 162 - 525) seeds per 0.1 m² in the unburned forest to 164 (95% confidence limits 148 - 199) seeds per 0.1 m² in the burned forest, a difference of 44%. The

difference in seed density between the unburned treatment and the burned treatment was significant, and was dependent on the depth of the soil sample (Table 5.2). In the burned samples, the seed density was significantly lower in the litter layer and the top 1.5 cm of the mineral soil, differing by 86% by 71% respectively with the unburned forest. Below a depth of 1.5 cm, differences were no longer significant, a result which is unlikely to be due to the low sample number, because the recorded average seed densities in unburned and burned forest were very similar.

In the unburned forest, we observed a gradual decrease in seed density with depth in the mineral soil (Figure 5.2), whereas in the burned forest, the highest seed density was found at a depth of 1.5 to 3 cm.

An average 0.5 ± 0.6 seedlings per tray (average \pm sd, range 0-2) emerged from the

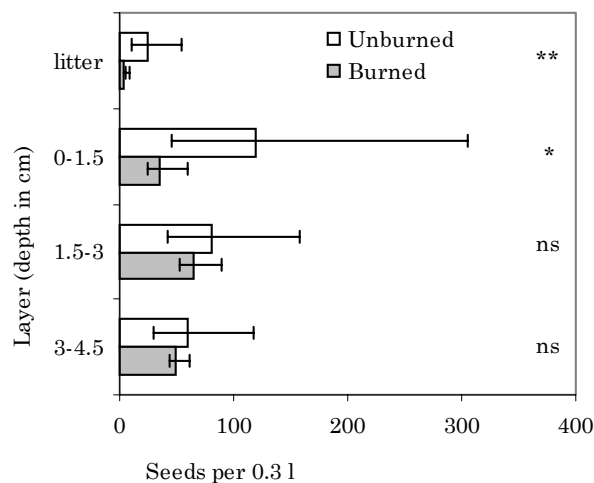


Figure 5.2. The vertical distribution of viable seeds in unburned forest (white bars) and burned forest (grey bars) (average \pm 95% confidence limits, $n = 6$). Values are based on the back-transformed averages of log (seed density + 1). Given is the seed density per soil layer of 1.5 cm. Because the thickness of the litter layer varied, the seed density of the litter layer is shown as the number of seeds per 0.10 m², which would equal a volume of 0.3 l if the sample depth were 1.5 cm. Significant decreases in seed density per layer are indicated. ns: non significant, *: $p < 0.05$ and **: $p < 0.01$.

Table 5.3. Species composition of the seed bank in unburned and burned forest. Given is the number of identified seedlings in all samples combined (5.4 l of soil + a varying amount of litter), and the relative frequency of each family or genus in the total sample, expressed as the percentage of all identified seedlings.

Family	Genus	Number of seedlings		% of all identified	
		UB	B	UB	B
Rubiaceae		285	56	44	30
	<i>Uncaria</i>	132	16	20	9
	Spp.	93	26	14	14
	<i>Urophyllum</i>	37	5	6	3
	<i>Timonius</i>	17	2	3	1
	<i>Psychotria</i>	6	7	1	4
Melastomataceae		229	71	35	38
	<i>Pternandra</i>	145	51	22	27
	<i>Sonerila</i>	81	17	13	9
	Spp.	3	3	0	2
Moraceae		45	22	7	12
	<i>Ficus</i>	45	22	7	12
Graminae		5	1	1	1
	<i>Imperata</i>	5	5	1	3
	Spp.	5	1	1	1
Others		89	39	14	21
Total		648	188		

control trays filled with white sand. Substantial numbers of seedlings emerged from the 0.1 mm-sieved samples (range 3-76, $n=4$), representing an average of $25\% \pm 11$ (average \pm sd) of the total number of seeds found in a sample. Correcting for the low number of seedlings that germinated in the control trays and for the substantial seed loss during the sieving treatment, we estimate that the true number of seeds in the top 4.5 cm of the soil plus the litter layer was 397 (95% confidence limits 191 - 824) seeds per 0.1

m^2 in the unburned forest, and 208 (95% confidence limits 120 - 361) seeds per $0.1 m^2$ in the burned forest. This indicates a slightly higher difference in seed density between the unburned and the burned forest of 48%.

The fresh weight of the litter layer was on average $10.5 \pm 3.6 \text{ kg } m^{-2}$ (\pm sd, $n=6$) in the unburned forest. Notwithstanding the fire, which consumed much of the original litter layer, $4.5 \pm 0.8 \text{ kg } m^{-2}$ litter was measured in the burned forest. Part of this originated from the highly in

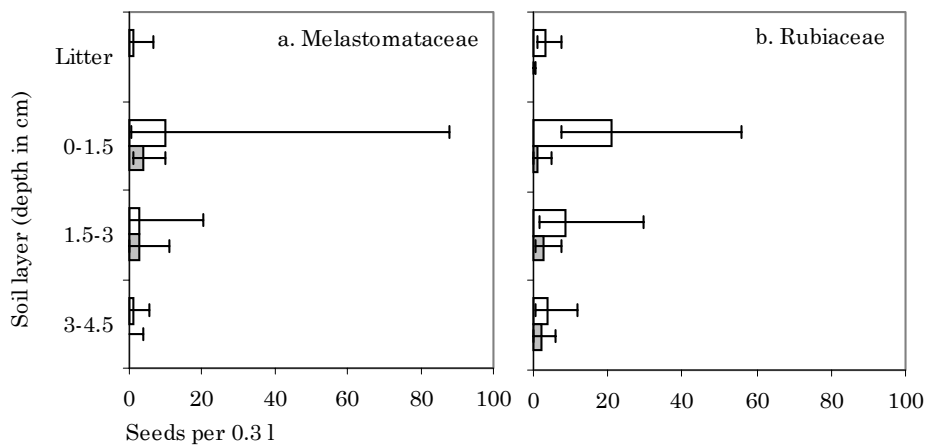


Figure 5.3. The vertical distribution of viable seeds of (a) Melastomataceae (mainly *Pternandra* sp.) and (b) Rubiaceae in unburned forest (white bars) and burned forest (grey bars) (average \pm 95% confidence limits, $n=6$). Values are based on the back-transformed averages of $\log(\text{seed density} + 1)$. The sample volumes are the same as in figure 2.

Table 5.4. Three-way anova for testing the log (seed density + 1) in the seed-bank of two families (Melastomataceae vs. Rubiaceae) between two treatments (unburned forest vs. burned forest) over four horizontal layers of soil, including a litter layer and three layers of mineral soil with a thickness of 1.5 cm each.

Source	Type III		Mean Square	F	Sig.
	Sum of Squares	df			
Corrected Model	10.3	15	0.68	3.74	< 0.001
Intercept	28.1	1	28.1	154	< 0.001
Family	0.59	1	0.59	3.23	0.076
Treatment	3.11	1	3.11	17.0	< 0.001
Layer	4.60	3	1.53	8.39	< 0.001
Family * treatment	0.75	1	0.75	4.11	0.046
Family * layer	0.26	3	0.09	0.47	0.702
Treatment * layer	1.12	3	0.37	2.03	0.116
Family * treatment * layer	0.19	3	0.06	0.35	0.788
Error	13.9	76	0.18		

creased leaf fall after the fire. In all burned plots but one we recorded viable seeds in the litter layer, although the litter layer formed the main source of combustible material.

Three families made up more than 85% of the identified individuals (Table 5.3). Nearly all the taxa that we found produce very small seeds (i.e. <5 mm diameter). Several species of small trees were found in the samples, including *Ficus grossularioides* Burm.f., *Ficus aurata* Miq. and *Vernonia arborea* Buch.-Ham. The only common species that reaches above 15 m was *Pternandra* sp. Only very few seedlings of *Macaranga* spp. were found in the samples, although they were common in the burned forest. Melastomataceae and Rubiaceae were present in sufficiently high densities to allow for a comparison of their vertical seed density distribution (Figure 5.3). The vertical

seed distribution of these two families was nearly identical both in the absence and presence of fire (Table 5.4). We found only a marginally significant interaction term between family and the fire treatment, which suggests that Rubiaceae might be slightly more sensitive to fire.

The spatial variation in seed density was high (i.e. see the 95% confidence limits in figure 5.2). We observed that this spatial variation in seed density was not just the result of the aggregation of seeds of a single species, but instead resulted from a correlation in the density of seeds from different taxa (Figure 5.4). This correlation was pronounced in both the unburned and the burned forest.

Germination triggers

We found significant differences in seed germination under different environmental conditions (one-way anova, df=

Table 5.5. Number of seeds germinated from soil samples from the primary forest, which were sown under different combinations of environmental conditions (See table 1). The number of replicates (n), the total number of seeds emerged (\pm sd), the number of seeds smaller than 5 mm diameter, and the number of seeds larger than 5 mm diameter are given.

Treatment	n	Total			Seeds < 5 mm		Seeds > 5 mm	
		Average	SD	Sign*	Average	SD	Average	SD
HT	5	88	19	a	87	19	1.2	0.8
LT	4**	40	9	b	40	9	0.5	0.6
OT	6	0.5	0.5	c	0.2	0.4	0.3	0.5
OO	5	0.0			0.0		0.0	

* Pairwise differences between treatments were tested with a post-hoc Bonferroni test (all $p < 0.013$). Because in the OO treatment no seeds germinated, this treatment was excluded from the statistical analysis. ** One replicate in the LT treatment was lost due to disturbance.

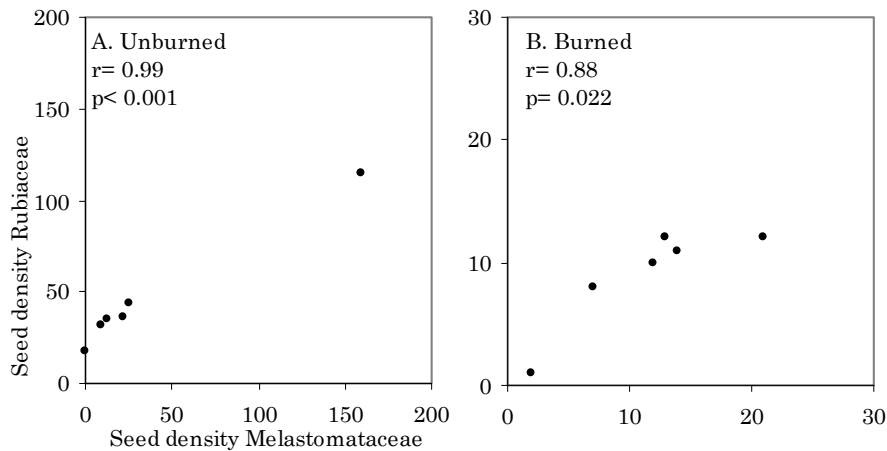


Figure 5.4. Correlation in the spatial seed density of Melastomataceae (mainly *Pternandra* sp.) and Rubiaceae in (a) unburned and (b) burned forest. Given is the total number of identified seedlings per sample which consisted of 5.4 l of soil plus a variable amount of litter. The Pearson correlation coefficient (r) and level of significance are given.

15, $F = 46.6$, $p < 0.001$). Post-hoc comparisons revealed significant differences between all treatments tested (Table 5.4). The highest number of germinating seeds was found in the HT treatment (Table 5.5). The very low light level of 0.5% in the LT treatment allowed substantial germination of seeds < 5 mm. Very low germination was observed in the OT treatment, and germination was zero in the OO treatment.

Even though considerable numbers of *Macaranga* seeds were present in the experiment, only very few germinated. During the course of the experiment, it appeared that a high percentage of the seeds was dead. Nevertheless, some seeds of the small-seeded *Macaranga gigantea* germinated in the complete darkness of the OT treatment. The seedlings showed a marked behaviour under these conditions: After germination the stem continued to elongate up to 8 cm, while the cotyledons remained pale yellow. This contrasted with the emerging seedlings of very small seeds in the LT treatment, where all seedlings did not etiolate but instead remained very small (less than a few millimetres) and immediately developed green cotyledons.

Discussion

The average density of 292 to 397 seeds per 0.1 m^2 in the top 4.5 cm soil + litter layer of the unburned forest is substantially higher than the seed densities found in other studies in tropical forests (review by Garwood 1989). Differences in methodology are likely to be at least partially responsible for the deviating outcome (Dalling et al. 1994). In most studies, soil samples are spread out at a thickness of 1 to 1.5 cm. Since light penetration into the soil is only a few millimeters, studies in which soil samples are not spread thinly are likely to underestimate the density of light-sensitive seeds (Dalling et al. 1994, TerHeerdt et al. 1996, Bossuyt et al. 2000). However, the thin spreading of samples often requires an impractically large area. Washing and sieving of soil samples may remedy this problem, but care should be taken not to remove seeds from the samples during this process. We found a substantial number of very small seeds in the residues which were sieved using a 0.1 mm mesh. Therefore we suggest that washing and sieving of soil samples using a 0.1 mm mesh is the preferable method, because it ensures that most seeds are cap-

tured whereas at the same time it allows the thin spreading of samples over an area of manageable size.

The species composition of the soil seed bank is an indicator for the regrowth potential after a fire. Only 28% of all seedlings could be identified up to some taxonomic level, partly because many very small seedlings (1-2 mm high at the time of emergence) died before identification was possible. Therefore, the relative abundance of different taxa should be interpreted cautiously. Rubiaceae and Melastomataceae both represented roughly one third of the identified seedlings. Shrubs, small trees and lianas are the common growth forms in these families.

The various seedlings germinating from the soil samples have been classified as light-demanding pioneer species (*Ficus aurata*, *Ixora* spp., *Macaranga* spp., *Melastoma* sp., *Trema* spp., *Timonius* sp.), while the samples also contained a number of very small-seeded shade tolerating species (*Ficus grossularioides* Burm.f., *Lasianthus* spp., *Pternandra* sp., *Urophyllum* spp.), which are dependent on a patch of bare soil for their establishment (Metcalf & Grubb 1995, Metcalf et al. 1998). *Pternandra* sp. was the most abundant species in the seed bank, probably as a result of the relatively high stem density of 3.1 trees ha⁻¹ (>10 cm dbh) in the unburned forest.

We observed a large spatial variation in seed density (see 95% confidence limits in figure 5.2), which, remarkably, in large part is the result of a correlation in seed density of the two dominant families (Figure 5.4). The majority of the recorded Rubiaceae can be categorised as short-lived light-demanding species, whereas *Pternandra*, the species that accounts for most of the seeds recorded within the Melastomataceae, is a longer-lived understory tree. Therefore, the local history of above-ground disturbance seems an unlikely explanation for the correlative pattern. Instead, there seems to operate a species-independent factor that influences the local seed density. Possible factors are either interactions with generalist seed consumers such as ants, which may cause

spatially clumped patterns of seed dispersal (review by Louda 1989) and post-dispersal seed predation (Louda 1989, Crawley 1992), or site-specific abiotic factors such as soil texture (Hopkins & Graham 1983) and soil humidity (Garwood 1989), which influence the movement of seeds or the local survival rate (Roberts & Abdalla 1968, Roberts 1972).

Comparison of the vertically stratified soil samples from the unburned forest and the burned forest shows that the fire damage was restricted to the uppermost layers: Only the litter layer and top 1.5 cm of the seed bank were significantly affected. Changes in seed density were also largely confined to the top 1.5 cm of mineral soil in a Ghanaian forest after being experimentally burned (Swaine et al. 1997). The pattern is in agreement with the short fire residence time and the low fire intensity inside the forest (MvN pers. obs.), and with the observation that peak temperature generally declines rapidly with depth (references in Whelan 1995, Swaine et al. 1997, Campbell et al. 1995).

Notwithstanding the superficiality of the damage, the fire may have profound consequences for the establishment potential of seedlings from the seed bank. Burial depth influences the chance of seed germination and seedling establishment and thus the chance that a seed contributes to the establishing vegetation after the fire. The trigger experiment that we performed, showed that all of the very small-sized seeds need light for their germination, even though that can be as low as 0.5% light. Such light levels may be available at 1 to 2 mm depth in a bare soil (Wooley & Stoller 1978). In agreement, a rapid decrease in germination rate of seeds deeper than 5 mm in the soil was found in a neotropical study (Dalling et al. 1994) in which approximately 90% of the seeds had a weight <1 mg.

A study in a neotropical rainforest in Costa Rica suggested much higher proportions of germination, with 85% of the seeds in the top 4 cm of the soil germinating and establishing a seedling after a patch of land was slashed and burned (Young et al. 1987). However, the seed

density prior to the disturbance may have been underestimated, due to the above-mentioned methodological problems. Tentatively we conclude that, unless disturbances occur at the soil surface that expose deeper soil layers, only the most superficially buried seeds of the strictly light-sensitive species will be triggered to germinate, and a substantial proportion of the seed bank probably remains unaffected by either the fire disturbance or the subsequent change in the above-ground light environment.

The seed store of the small-seeded *Macaranga* species may be affected quite differently by the disturbance. Some seeds of *Macaranga* germinated in complete darkness, probably as a response to daily fluctuations in temperature. After germination they showed a marked elongation of the stem (etiolation) up to at least 8 cm. Even though the number of germinating seeds was too low to provide statistical proof, these observations suggest that *Macaranga* seedlings are able to establish from deeper in the soil.

The consequence of the higher germination rate from deeper soil layers may be that, after a fire disturbance and the subsequent germination flush, a smaller part of the seed stores of small-seeded species like *Macaranga* remains than of very small-seeded species. Because a repeated disturbance may kill the re-establishing

individuals before a new seed-set has been achieved, *Macaranga* populations are expected to decline more rapidly than the populations of very small-seeded species after logging activities in a burned forest (Nieuwstadt et al. 2001) or after a recurring fire.

Acknowledgements

This research was performed at the Wanariset International Ministry of Forestry (MOF) - Tropenbos research station, East Kalimantan. I am indebted to many of the staff members working there, especially M. de Kam, A. Susilo and K. Sidiyasa for logistic support, and the research group of R. Effendi for maintenance of the greenhouse experiment. The research would have been impossible without a rewarding co-operation with G.M. Fredriksson and the dedicated assistance of J. Helleman, S. Laysa Putra, N. Syah, F. Udin and C.S.A. Vissers. Seedlings were identified by K.A.O. Eichhorn, P.B. Pelsler and J.W.F. Slik. M.J.A. Werger and H.J. During provided helpful comments on the manuscript. The research was supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) with grant 84-804 to M.v.N.



Repeatedly burned hill side, with a vegetation consisting of herbs, vines, shrubs, and a few scattered surviving trees. Wanariset re-search area, February 2000.

Note to Chapter 6

**" The ecological consequences of logging in
the burned forests of East Kalimantan,
Indonesia"**

(With Douglas Sheil and Kuswata Kartawinata)

Publ In: Conservation Biology 15(4): 1183-1186

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6

The ecological consequences of logging in the burned forests of East Kalimantan, Indonesia

With Douglas Sheil and Kuswata Kartawinata

In: Conservation Biology 15(4): 1183-1186

Keywords: repeated disturbance, resprouting, salvage logging, seed bank, South-East Asia, tree mortality, tropical dipterocarp forest.

Introduction

In 1997-1998 over 50,000 km² of East Kalimantan burned, and some 26,000 km² of natural forest concessions were affected. This is nearly one-quarter (24%) of the area of all natural forest concessions in the province (Hoffmann et al. 1999, Siegert et al. 2001). The biomass of the trees living at the time of the burn was little reduced by the fire which tended to be restricted to the litter and understory, and although many trees died, most stems remained standing after fire. These dead stems in the burned forest represent a significant timber resource. A government regulation was issued (Directorate of Forest Utilization 1999) indicating that in concessions where fires had occurred, "salvage felling" (harvesting of the remnant commercial dead timber by conventional methods) should precede any continuation of regular harvesting operations in unburned forest areas. The reason for this regulation was that the dead stems could still provide valuable timber if removed before

serious deterioration (Ulbricht et al. 1999). It was apparently assumed that such salvage activities would have little additional effect on the already degraded forest. There are good reasons, however, to be concerned about the ecological effects of salvage felling after fire.

Forest areas can recover after fire, but remain in a very sensitive state in which additional disturbances, such as salvage felling, will cause significantly increased levels of forest deterioration and loss. The results from our 2-year study on post-fire vegetation dynamics in the unlogged dipterocarp rainforest of Sungai Wain near to Balikpapan (1°16' S and 116°54' E; altitude 40 to 140 m.a.s.l.; average yearly rainfall 2790 mm (Vose et al. 1992), East Kalimantan, compel us to warn against the implications of salvage felling. We intend to publish a more detailed account of our study but the urgency of the situation makes it important that we disseminate our main conclusions as soon as possible.

Vegetation processes after single and repeated disturbance

The recovery capacity of forest vegetation after fire and other disturbances involves four main processes: tree survival, the resprouting of damaged trees, germination of seeds in the seed bank, and the seed rain. To study the relative contribution of these processes to vegetation development, we established permanent sample plots of 1.8 ha each in unburned forest and in forest that burned accidentally in March 1998 after several months of drought. Nine pairs of burned and unburned plots were established adjacent to each other over a human-made edge (a successful fire break that usually does not correspond to any topographical feature) between burned and unburned forest. The plots were spread over a total area of circa 20 km². Each pair of plots formed one contiguous transect of 60 x 600 m half in burned and half in unburned forest. In these plots, more than 3000 (both dead and living) stems larger than 28 cm dbh (diameter measured at 1.3 m height) were measured and labeled. In subplots of 0.4 ha, an additional 4700 trees between 8 cm and 28 cm dbh were measured and labeled. A total of 2190 (dead and living) seedlings and saplings (<8 cm dbh) and 445 living resprouts on stems smaller than 8 cm dbh were measured and labeled in 10 m² burned subplots. Living trees and sprouts and dead trees larger than 28 cm dbh belonging to 10 common species were identified by local experts.

Directly after the low intensity ground fire most of the trees remained standing, although a high proportion of the stems appeared to be dead. One year after burning < 1% of trees smaller than 8 cm dbh survived, but larger sizes generally fared better. Survival of trees larger than 30 cm dbh was circa 45%, with a range from 20 to 95% among species. Comparable levels of survival for trees larger than 10 cm dbh 1 month after fire have been found in a recently logged forest in Sabah (Woods 1988), whereas survival 6 months after fire was circa 25% higher in an unlogged forest in Kutai Na-

tional Park, East Kalimantan (Leighton & Wirawan 1986) and in Sumatra (Kinaird & O'Brien 1998). The surviving trees in the Sungai Wain forest appeared sensitive to wind. Of the 35% of the living stems that died in the second year, one-fifth had fallen. The remaining trees provided a sparse matrix, with a considerably impoverished species composition.

After the fire, some trees that were killed above ground sprouted from basal parts. This is a common phenomenon after slash and burn practices (Stocker 1981; Riswan & Kartawinata 1991 a & b; Kammesheidt 1998) and has been observed after fire in other tropical forests (Leighton & Wirawan 1986; Riswan & Yusuf 1986; Pinard et al. 1999). With a proportion of circa 17%, sprouting frequency was highest for above-ground-killed seedlings and saplings smaller than 8 cm dbh. This was enough to provide densities of 0.2 to 0.4 sprouting trees per m². Trees larger than 10 cm dbh that were killed above ground had a sprouting frequency below 10% and added little to the density of sprouting individuals.

In an experiment in the unburned forest we assessed the sprouting vigor of young trees of six primary forest species (*Dipterocarpus confertus* Sloot, *Durio acutifolius* [Mast.] Kosterm., *Gironniera nervosa* Planch., *Macaranga lowii* King ex Hook.f., *Madhuca kingiana* [Brace] H.J.Lam, *Shorea laevis* Ridl.), after clipping the main stem. Two hundred individuals from each species were checked monthly over 6 months for the number of sprouts produced, sprout length, and number of leaves. Sprouting occurred fast, with more than 90% of the individuals sprouted after 3 months in four of the six species. Several species were affected negatively by repeated disturbance. Plants that were clipped for a second time 2 months after the initial clipping showed a reduction in sprouting frequency ranging from 0 to 40% when the top of the remaining stem was removed to a 64 to 100% reduction when clipped at ground level. Thus, where the heavy machinery used for salvage felling damages resprouts, their survival is reduced.

Sprouts of primary tree species competed with ferns and secondary seedlings of pioneer trees and shrubs in the young vegetation and were often overgrown by these within 1 year. Most of the sprouts nevertheless survived for the first 2 years. After 2 years, 25% of the sprouts had outgrown the layers of ferns and shrubs. Therefore, they appeared to play an important role in the persistence of many primary forest species.

Stratified soil samples, taken in six replicates from unburned and burned areas in the Sungai Wain forest were placed in the nursery under high light conditions, which triggered abundant germination of seeds. The experiment revealed that the fire killed 85% of the seeds lying dormant in the litter layer and more than 60% of the seeds in the upper 1.5 cm of the soil. No reduced seed density was found in deeper soil layers. In the burned forest, the gap-like environmental circumstances induced the frequent germination of seeds from the seed bank (Vázquez-Yanes & Orozco-Segovia 1993). Notwithstanding the high seed mortality in the upper soil layers, a dense carpet of pioneer seedlings had established 4 months after the fire in those places where high densities of pioneer trees had been present prior to the burning. Because of the high mortality and the high germination incidence soon after the fire, the density of viable seeds remaining in the soil is greatly reduced (Hopkins & Graham 1984; Young & Brown 1987; Saulei & Swaine 1988). Under these circumstances the local seed bank has little potential for further regrowth. These areas, if further damaged, risk invasion by wind-dispersed species, including *Imperata cylindrica* [L.] Beauv. (Alang-alang, grass), *Pteridium caudatum* [L.] Maxon (Bracken fern), and *Dinochloa* sp. (Bamboo). It has previously been shown in East Kalimantan that complete conversion of a primary forest to Imperata grassland can take place rapidly after clearfelling and repeated burning (Kartawinata 1993). For the local seed production of woody species to become substantial takes 1 year or more for rapidly maturing shrubby species (e.g., *Homalanthus populneus*

[Geiseler] Pax, *Macaranga trichocarpa* [Reichb.f. & Zoll.] Müll.Arg., some *Ficus* spp.) and at least 4 years for the larger secondary tree species (e.g., *Dillenia* sp., *Mallotus paniculatus* [Lam.] Müll.Arg.) (Saulei & Swaine 1988).

Seed production by trees that survive either as individuals in the burned area or in pockets of unburned forest will ultimately be the main source of regeneration of many primary forest tree species. Initially the density and diversity of the seed rain will be impoverished due to the low availability of seed sources. Because the seed dispersal distance of many tree species is limited (Howe & Smallwood 1982; Whitmore 1984), the proximity and composition of relic unburned patches is anticipated to have a large effect on the persistence of fire-sensitive species in the burned forest.

Many species in the Sungai Wain forest fruited in 1997 during the long pre-fire drought and did not seed again during the first 2 years after the fire. As we described above, the burned forest was densely covered by ferns, pioneer seedlings, sprouts, and grasses by that time. Seedling establishment from the post-fire seed rain under these circumstances remains to be assessed, but it is evident that it will take a long time before seedlings of primary species will have established from the seed rain in numbers comparable to the post-fire density of resprouts. For that reason the presence and performance of resprouts is a more important factor in the initial restoration of the forest than is the density of tree seed sources.

Conclusions and recommendations

Fire does not in itself cause complete loss of forest cover. The survival and sprouting capacity of primary forest trees and the seedling establishment of pioneer trees and shrubs suppress the establishment of nonforest species. However, post-fire vegetation is certainly less resilient than might be assumed by anyone witnessing the vigorous post-fire regrowth. The post-fire undergrowth cannot withstand repeated disturbance: previously

sprouted individuals show reduced sprouting potential and survival after being damaged a second time, the seed-bank is largely reduced after the initial post-fire burst of germination, and the density of vital seed trees is low. The open areas created in the understory by the conventional heavy logging machinery used for salvage felling encourage the rapid development of nonforest vegetation, and seriously reduce the potential for recovery.

The genuine regenerative potential of burned tropical rain forest and the potential consequences of further disturbance caused by salvage felling need recognition. Our evidence implies that the maintenance of a productive permanent forest estate is likely to be served best by avoiding logging activities in burned areas. Further studies should be made in areas already harvested to further clarify the effects of salvage felling, but until such information is available caution is the only environmentally defensible option.

We have presented only ecological concerns so far, but there are other reasons to review current practices of salvage harvesting. In Indonesia concession holders cannot normally recut harvested

forest areas without waiting the statutory period (a 20-year cutting cycle is the norm). However, if fire occurs in a concession, this restriction is lifted and further cutting is allowed. Such incentives must be avoided.

Acknowledgements

This research was performed at the International Ministry of Forestry (MOF)-TROPENBOS-Kalimantan research station, East Kalimantan. We thank the many staff members working there for their support, especially M. de Kam, K. Sidiyasa, Ambriansyah, Z. Arifin, and A.K. Pakala. The field work benefited greatly from the dedication of N. Syah, F. Udin, and S. Laysa Putra. We are grateful to J.A. Sayer, M.J.A. Werger, M. van Noordwijk, D.W. Dijkman, G.M. Fredriksson, J.W.F. Slik and A. Hoffmann for their support and fruitful discussions. M.J.A. Werger, H. ter Steege, A. Hinrichs and 3 anonymous reviewers made valuable comments on earlier versions of the manuscript. The research was supported by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) with grant 84-408 to M.v.N.

7

Synthesis: Assessing the consequences of drought and fire in a lowland dipterocarp rain forest

“They wanted to be imperfect in order to always have something to strive towards, which is beauty. They wanted also to know wonder and to live miracles. Death is too perfect.”

Ben Okri, *The Famished Road*
1991

Introduction

This report describes vegetation dynamics in the first two years after drought and fire in a tropical lowland dipterocarp rain forest. The study followed upon large-scale fires which, during an exceptionally dry episode in 1997-1998, devastated extensive areas of forest in East Kalimantan, Indonesia (Hoffmann et al. 1999, Siegert et al. 2001). Fires are considered to be rare in the tropical rain forest, and are restricted to periods of exceptional drought. Nevertheless, occasional fires must have occurred for a long time in many of the Indonesian forests, because traces of historical fires have been reported throughout the entire length of many palynological sample cores (Dam et al. 2001 a & b, Hope 2001, Anshari et al. 2001, Suparan et al. 2001). Recently, the frequency and extent of fire disturbances in the dipterocarp rain forest has increased dramatically as the result of a synergism between logging activities, forest fragmentation, and the common use of fire for land clearing by concessionaires and farmers. In Kalimantan and Sumatra there are large areas of recently burned

forest, and remaining forests are under the threat of burning when new dry episodes occur.

Notwithstanding the astonishing size of the areas that are affected or threatened, very few studies have been carried out in Southeast Asia to assess the impact of fire on forest vegetation. Knowledge about the fate of a forest after burning is indispensable for sound forest management, both from a conservation as well as from an economic point of view. The fires also constitute an intriguing case for ecological science. Recently, the importance of large-scale disturbances in tropical rain forests has been acknowledged (Tanner et al. 1991, Bellingham et al. 1994, Whitmore & Burslem 1998, Cochrane et al. 1999). Understanding how the structure and composition of tropical rain forests is maintained in the wake of such disturbances constitutes a major scientific challenge (Sheil 1999).

Fire causes a multitude of biotic and abiotic changes in the structure and functioning of a tropical rain forest, and includes both direct and indirect effects. The most visible effect of fire is high tree

mortality (Leighton & Wirawan 1986, Woods 1989). Densities of animal populations change as the direct result of fire injury, and because of changes in availability of food sources and habitat suitability (Azuma 1988, Doi 1988, Suzuki 1988, Yajima 1988, Makihara et al. 2001). Changes in population density of herbivores, seed dispersers and pollinators may affect the growth and reproductive success of plants. Changes in the density and species composition of mycorrhiza after fire have been scarcely studied in Indonesia. Based on studies in Australia (Bellgard et al. 1994) and South Asia (Rashid et al. 1997), mycorrhiza populations may be able to recover rapidly after fire. Fire also causes changes in soil physical characteristics and nutrients (Holscher et al. 1997, Buschbacher et al. 1988, Ketterings & Bigham 2000, Ketterings et al. 2000, Kennard & Gholz 2001) and causes a temporarily increased erosion rate (Douglas 1999, Shimokawa 1988). Changes in the microclimate include an increase in light availability and temperature in the understorey, and a decrease in relative humidity (Toma 1999, Toma et al. 2001 a). Several of these phenomenae remain understudied and not very well understood. While acknowledging the variety of changes and possible interactive processes that may occur in all components of the ecosystem, the emphasis of this study is on successional changes of plants, with a focus on population demography and processes of plant establishment and persistence.

The objectives of this thesis are to assess the damage caused by fire and the subsequent recovery potential in a dipterocarp rain forest. After a short summary of the theoretical approaches to succession considered in this thesis and a description of the experimental set-up, I evaluate, respectively, the early establishment of different functional groups in the post-fire vegetation, the vegetation dynamics of functional groups, and the development of the group of shade tolerant tree species at species-level. The chapter continues with an analysis of several theoretical issues and an analysis of consequences for forest management.

Theoretical approaches

The vegetation changes that occur after fire disturbance can be described in terms of succession, which I define as a sequential change in species composition through time following a disturbance that opens up a relatively large space (sensu Connell & Slatyer 1977, Huston & Smith 1987, Chapter 1). Traditionally, several stages have been identified in patterns of succession. The first phase of succession is characterised by abundant establishment of individuals in the open space made available by the disturbance. After that follows a phase in which little open space is left and the vegetation develops through a process of plant growth and thinning (Connell & Slatyer 1977).

Succession may be best understood through study of the underlying processes and mechanisms (Connell & Slatyer 1977, Huston & Smith 1987, Pickett et al. 1987). A list of processes that potentially influence succession has been compiled by Pickett et al. (1987). The vegetational processes that are the main subject of this thesis include aboveground survival, sprouting and seed bank dynamics, while seedling performance and post-disturbance seed rain are also considered.

Theoretical approaches to succession taken by researchers studying fire-prone communities (hereafter referred to as fire theory of succession) and communities that are rarely affected by fire (non-fire theory of succession) exhibit some crucial differences (Bond & van Wilgen 1996). Central to much of non-fire theory of succession, which originates from studies on old fields after abandonment, are processes of species-specific rate of colonisation and competitive exclusion (Connell & Slatyer 1977, Tilman 1982, 1988, Huston & Smith 1987), even if many authors consider a complex set of factors to be of importance (Egler 1954, Connell & Slatyer 1977, Pickett et al. 1987).

In the study of old growth forests, small-scale gap dynamics resulting from treefall form the focus of successional development in the absence of large-scale disturbances (Bazzaz & Pickett 1980, Bro-

kaw 1985, Veblen 1992). An important difference with old-field succession and with succession after large-scale disturbances such as fire is, that post-disturbance colonization plays a limited role. Gap creation is such a low-intensity disturbance that it causes virtually no mortality of saplings (Uhl et al. 1988 c). The relative size distribution of individuals before the disturbance is an important determinant for the competitive ranking of individuals after the disturbance (Zagt & Werger 1998).

A form of succession in the tropics which is more similar to the old field studies from temperate areas is secondary forest development, which has been studied after fire disturbance in combination with other disturbances in the Neotropics (Uhl et al. 1981, 1988, Uhl & Jordan 1984, Uhl 1987, Finegan 1996, Kammesheidt 1998, 1999, Steiniger 2000, Peña-Claros 2001) and the Palaeotropics (Symington 1933, Riswan & Kartawinata 1988, 1989, Nykvist 1996, Toma et al. 2001 b). To analyse complex processes such as succession in these species-rich tropical forests, plant species which share life-history characteristics have been categorised into functional groups (Swaine & Whitmore 1988). The functional groups in the current study were recognised on the basis a combination of light requirement in the establishment phase, growth form and longevity (Denslow 1980, Whitmore 1984, Hubbell & Foster 1986, Swaine & Whitmore 1988). Our *a priori* categorisation included light-demanding non-woody species, light-demanding trees and shade tolerant trees.

Successional theory originating from research in fire-prone systems centres around the vital attributes approach (Noble & Slatyer 1980), in which competition plays a minor role (Bond & van Wilgen 1996). The vital attributes approach aims at determining the role of a plant in a vegetation replacement sequence. The population dynamics of a species are predicted by assessing three categories of plant characteristics, which include establishment requirements, mode of persistence and timing of critical life-history

attributes (Noble & Slatyer 1980, Chapter 1).

In this synthesis chapter, I will return to two aspects of post-fire vegetation dynamics which were introduced in chapter 1, and to which the two bodies of succession theory attribute differential importance. Using the two different theoretical approaches, I aim to answer two main questions:

(1) Which vegetation processes determine the early functional group composition of the vegetation?

(2) Which vegetation processes determine the population recovery and species composition of the group of shade tolerant tree species?

First, the two theories make different predictions about the composition of functional groups shortly after the disturbance. Non-fire theory assumes that the early vegetation composition after a severe disturbance depends on survival of propagules in the soil seed bank and on post-disturbance colonisation by propagules. Notably small-seeded, well-dispersed, light-demanding tree species possess these characteristics (Garwood 1989, Gómez-Pompa & Vázquez-Yanes 1981, Metcalfe & Grubb 1995, Dalling et al. 1998), and as a result they will be the first to establish and dominate the site, whereas large-seeded, slow-growing species with limited seed dispersal capacity will be absent from the early post-disturbance vegetation. In fire-theory, a more diverse array of persistence modes is explicitly considered to be of importance after a severe disturbance (Noble & Slatyer 1980). Besides the propagule-based modes of persistence that are emphasised in non-fire theory, also vegetative persistence is specified in the framework of vital attributes. It includes species which survive unaffected as juveniles or as mature individuals, and species which resprout from surviving tissue. Vegetative persistence limits changes in species composition in the wake of a disturbance, and in a tropical rain forest would ensure the maintenance of populations of slow-dispersing shade tolerant species that were present before the disturbance.

Table 7.1. Main life stages of a population as proposed by Noble and Slatyer (1980).

Population life stage	Description	Modes of persistence
Juvenile stage	Majority of the individuals are immature.	Vegetatively
Mature stage	Many (or all) of the individuals are reproductively mature *.	Sexually or vegetatively
Propagule stage	Only propagules remain. There no longer persists a significant number of juveniles or adults at the site.	Sexually
Locally extinct	No juveniles, adults or propagules are available at the site.	Long-distance dispersal of propagules

* Note that for this definition to apply to a tropical rain forest it should be interpreted liberally.

The second question concerns processes that determine the post-fire species composition within the functional group of shade tolerant tree species. In non-fire theory, composition of shade tolerant species is predicted to be determined by colonisation rate and competitive vigour. Fire-oriented theory assumes that these aspects may be of importance, but that the species composition is also determined by a more diverse array of vital persistence attributes, growth rate and longevity.

Experimental set-up

Following upon the fires of 1997 – 1998, we set up a post-hoc experiment comprised of replicated permanent sample plots (psp) in the partly burned Sungai Wain protection forest (1°16' S and 116°54' E) near to Balikpapan, East Kalimantan (Chapter 1). Before the fires, this reserve was largely covered by unlogged lowland dipterocarp rain forest. In the core of the reserve, nine pairs of psp were spread over an area of circa 20 km². Each pair of psp consisted of one unburned plot and one burned plot, which were separated from each other by a man-made firebreak. In the areas where the psp were located, the firebreak was independent of any specific topographical feature, which minimised the risk that a systematic difference would exist in the topography of unburned and burned plots (Eberhardt & Thomas 1991, Turner et al. 1997). Each psp had a size of 60 x 300 m,

in which all trees >28 cm dbh were assessed. In a subplot of 20 x 200 m within each psp, all trees >8 cm dbh were assessed. In each of six burned psp, ten subplots of 10 x 10 m were selected for the assessment of trees <8 cm dbh and non-woody plants. The plots were inventoried 8 and 21 months after the drought and fire to evaluate patterns of tree mortality (Chapter 2) and to study the development of the vegetation after fire through tree survival, seedling establishment and sprouting (Chapter 3).

Since 8 and 21 months after the fire, light-demanding non-woody species and light-demanding trees were virtually absent from the unburned forest, while they were abundant in the burned forest, a detailed comparison of these functional groups between the two treatments would have been redundant. Evaluation of the light-demanding functional groups therefore focussed on the burned forest, whereas the performance of shade tolerant trees was investigated in both unburned and burned forest.

Two additional experiments were carried out to elucidate the workings of particular processes after disturbance. Species-specific sprouting capacity was studied experimentally by removing the crown from saplings of six species of shade tolerant trees (Chapter 4). The effect of fire on the seed bank was studied by comparing seed germination in vertically stratified soil samples that were taken from unburned forest and burned forest (Chapter 5).

Successional patterns after drought and fire

Early presence of light-demanding functional groups: Seed bank and propagule dispersal

A few months after the fire, we observed that the early composition of the vegetation was determined by a variety of processes. The plants that established in the open spaces were categorised in four functional groups. Light-demanding non-woody species, light-demanding trees and shade tolerant trees were recognised *a priori*. The principal mode of persistence varied between these groups (Table 7.1). A fourth group of shade tolerant shrubs was defined *a posteriori* (Chapter 3). This group, notably formed by many species of Rubiaceae, exhibited a dual persistence strategy: The very small seeds were present in high densities in the post-fire seed bank (Chapter 5), whereas established individuals were observed to survive in the shade of the unburned forest, and were capable of sprouting from basal stem parts in the burned forest (Chapter 3). Because these species have been found to require openings in the litter layer for successful establishment while the seedlings are shade tolerant (Metcalf and Grubb 1995, Metcalfe & Turner 1998, Metcalfe et al. 1998), this functional group will be referred to as litter-gap demanding species.

Light-demanding non-woody plants dominated the early post-fire undergrowth, due to an abundantly establishing fern cover, dominated by three species (*Blechnum orientale* L., *Pteridium caudatum* (L.) Maxon. and *Microlepia speluncae* (L.) Moore). Ferns established first in locations where smouldering logs had been consumed by fire. The soil in these sites must have been sterilised by the prolonged heat produced by the fire. From this it was inferred that ferns arrived through post-fire dispersal of propagules. Reaching a maximum height of 1.5 to 2 m, the fern cover had overgrown many of the seedlings and sprouts approximately one year after the fire. Other light-

demanding non-woody species, including the grass *Imperata cylindrica* and the vine *Mikania scandens*, were much less abundant than ferns.

With a combined density of 17.6 ± 9.6 seedlings (>1.30 m high) per 100 m², light-demanding trees (*Macaranga* spp., *Mallotus* spp., *Dillenia* cf. *borneensis*) formed a prominent element in the post-fire vegetation, notwithstanding the very low densities of mature trees in the unburned forest (Chapter 3). Surviving seeds in the soil seed bank formed the main source of establishment after the fire (Chapter 5). The light-demanding functional groups were able to establish from the seed bank because the mortality caused by the fire was only superficial (Chapter 5). Seed density was reduced in the top 1.5 cm of the mineral soil, whereas the insulation properties of the soil assured that at greater depths, few seeds were killed.

Small seeds of light-demanding tree species such as *Macaranga* spp. do potentially have large enough energy resources to establish from deeper in the soil, whereas very small-seeded light-demanding shrub species such as Melastomataceae and *Ficus* spp. are only capable of successful establishment when they are at the soil surface. In line with these differential establishment capacities from a certain depth, seeds of the two groups of species appeared to be sensitive to different sets of germination triggers (Chapter 5). Our experiments showed that very small-seeded species required at least some light to trigger their germination. *Macaranga* may be sensitive to daily fluctuations in temperature, which penetrate up to a few centimeters deep into the soil. This allows *Macaranga* to detect gap-like conditions in the above-ground vegetation while remaining in complete darkness. Etiolation of the stem allows *Macaranga* seedlings to successfully establish from such a depth.

Due to the pre-requisite of very small-seeded species to be at the soil surface in order to germinate, the part of the seed bank that has the potential for post-fire seedling establishment will be more seriously affected for these species than is the

case for the seed bank of *Macaranga* species.

Early presence of the functional group of shade tolerant trees: Above-ground survival and sprouting

Shade tolerant trees persisted in the vegetation through above-ground survival, mainly of individuals >10 cm dbh (Chapter 2), as well as through resprouting from basal stem parts, mainly from individuals <10 cm dbh (Chapter 3).

In our study on tree mortality we investigated both mortality caused by drought and mortality caused by drought x fire (Chapter 2). Subtraction of the mortality rates caused by these two treatments provided us with an estimate of exclusive fire mortality, which could not be observed directly in the field. Both drought and drought x fire caused high levels of mortality among stems >10 cm dbh eight months after disturbance, and high levels of retarded mortality were observed in the second year after the disturbance. After 21 months, drought and drought x fire had caused 28% and 74% mortality, respectively. Exclusive fire mortality accounted for roughly 2/3 of the mortality in the burned psp.

The relative contribution of drought and fire-disturbance to the total mortality may be event-specific, and depends on the duration of the drought and the timing and intensity of the fire. To assess the effect of drought duration on tree mortality, we analysed mortality data from several studies in perhumid tropical forest (defined as forest which, on average, did not experience a monthly rainfall <100 mm) (Chapter 2). Drought severity was defined as the cumulative water deficit (cwd). From this comparison we inferred the relation between the intensity of a drought, and drought-induced levels of mortality. Tree mortality increased only slowly below a cwd of 100 - 200, whereas it rapidly increased when the cwd became larger than 200, so that a relatively small prolongation of a drought causes a large increase in mortality.

Twenty-one months after the fire, the stem density of surviving trees (>10 cm

dbh) was $128 \pm 65 \text{ ha}^{-1}$ (average \pm sd, $n=9$) in the burned forest. This is approximately one fifth of the total stem density (dead + living stems) of $594 \pm 76 \text{ ha}^{-1}$ that was measured in the adjacent unburned plots. The basal area of living stems was $9.9 \pm 1.9 \text{ m}^2 \text{ ha}^{-1}$ after 21 months, which was a decrease of 70% relative to the original $33.1 \pm 6.1 \text{ m}^2 \text{ ha}^{-1}$.

After the fire, shade tolerant sprouts originating from small parent stems (<10 cm dbh) were present in a density of 22 ± 9.6 stems per 100 m^2 , which is 17% of the density of stems <10 cm dbh in the unburned forest (Chapter 3). The high density of resprouts was mainly due to the sprouting ability of the abundant small pre-fire stems ("parent stems"). The local density of resprouts was related to the local density of parent stems. Much of the sprouting occurred from basal stem parts, below-ground or just above-ground, indicating that small stems retained sprouting capacity because the soil protected tissue with sprouting capacity from the fire-heat.

Factors structuring functional group succession after initial occupation

Following upon the first successional phase of plant establishment in unoccupied spaces, the vegetation rapidly increased in density. After one year, the understorey formed a nearly closed ground cover. The rate of establishment of all functional groups diminished. Very few shade tolerant species fruited in the two years following the drought and fire. Colonisation through seed dispersal did not occur and, contrary to the common expectation, seeds were not an important source of regeneration for shade tolerant tree species.

We found no significant relation between the percentage dead trees (used as a proxy for the local light availability) and seedling density. The relation between canopy openness or percentage dead trees and growth rate was significant for *Dillenia cf. borneensis*, but not for the other two light-demanding tree species that we investigated. These observations suggest that seed germination and seedling

growth of light-demanding tree species were rarely limited by shading from the remaining tree cover in the burned forest.

Twenty-one months after the fire, total fern cover was negatively related to the density of light-demanding tree seedlings. This suggests a certain degree of competition between the two functional groups. Ferns and seedlings established approximately at the same time, and both were capable of quickly forming a locally dense carpet which cast deep shade on the ground. Such high local densities were much more common for ferns than for light-demanding tree seedlings to occur. Large local variation in the composition of the vegetation may result from subtle differences between functional groups in timing of establishment and in initial densities, which prevent the establishment of other light-demanding individuals.

Pteridium, one of the dominant fern species, is known world-wide for its ability to dominate a vegetation after severe disturbance, keeping the vegetation in a stage of "arrested development" (den Ouden 2000). *Pteridium* is capable of inhibiting tree seedling establishment through the deep shade it casts on the ground, by smothering plants under collapsing dead fronds, and through the formation of a thick litter layer which inhibits the establishment of seedlings from small seeds (Finegan 1984, Molofsky & Augspurger 1992, Tolhurst & Turvey 1992, Humprey & Swaine 1997, den Ouden 2000). Although ferns had been very abundant two and five years after a forest fire in Sabah, they had virtually disappeared after eight years (Nykqvist 1996), apparently as the result of diminished light availability due to shading by emerging trees. Little is known of the autecology of the other two common fern species. Close to our research site, in a forest that burned 15 years ago, we did not observe ferns although the local abundance of mature trees of *Macaranga gigantea* and *Macaranga trichocarpa* indicated high light conditions after the fire. It is not clear whether ferns were outcompeted there, or they never estab-

lished after the fire occurred. Since in Sungai Wain some of the seedlings and sprouts were growing above the fern layer two years after the fire, we expect that ferns will not persist, but eventually will be outshaded by other plants.

The density of sprouting individuals was not related to the density of light-demanding functional groups. Instead, the density of pre-fire stems with a dbh <10 cm largely explained the density of sprouts. Sprouts generally had a lower growth rate than light-demanding tree seedlings and ferns, and were usually outshaded by these one year after the disturbance. Sprout survival was between 83% and 94% over the census period from 8 months to 21 months after the fire.

Patterns within the functional group of shade tolerant tree species

Ultimately, forest recovery is determined by the speed with which shade tolerant trees regain dominance of the vegetation, and the species composition in which they do so. Since vegetative plant survival after disturbance is substantial, persistence abilities form an important component of shade tolerant species' abilities to maintain a population. Here, I evaluate patterns of species diversity (Chapter 3), species-specific survival (Chapter 2) and sprouting capacity (Chapter 3, 4) within the functional group of shade tolerant trees and analyse how these modes of persistence contribute to the shade tolerant vegetation.

Only data on post-disturbance patterns of species diversity were collected. These allow assessment of the effect of delayed drought mortality on species diversity, and for the comparison of drought versus drought x fire disturbance. As a result of the drought, the number of species (>10 cm dbh) in the unburned forest decreased from 70.1 ± 5.3 per 0.4 ha plot (average \pm sd, n= 9) in the first census to 62.8 ± 7.8 in the second census. The number of species in the burned forest at the second census was only 20.8 ± 10.6 per 0.4 ha. Over a range of spatial scales from 0.01 ha to 3.6 ha, the species number in the burned forest was at least a factor of

two lower than in the unburned forest. In contrast, the number of species per number of stems was nearly identical between the unburned forest and the burned forest. The difference in species number per area must therefore be caused by the drastically reduced stem density in the burned forest.

The specific survival rate of shade tolerant trees depends on a species' sensitivity to both drought and the subsequent fire. For the community as a whole, drought mortality was positively correlated to dbh, while the opposite was true for fire mortality. Fire accounted for two-thirds of the overall mortality, but above 70 cm dbh, mortality in the burned psp was not significantly higher than mortality in the unburned psp. To assess the specific whole-plant persistence capacity of smaller trees, we should focus on fire resistance, whereas for larger individuals, sensitivity to drought forms the principal constraint.

Species-specific drought mortality could only be assessed for trees >30 cm dbh. For these trees drought mortality was negatively related to specific wood density (Figure 2.6). Such a pattern was expected because wood density is linked to wood traits that prevent xylem cavitation under drought stress (Hacke et al. 2001). Our observation contrasts with the commonly assumed association of high wood density in environments subject to very little disturbance (ter Steege & Hammond 2001). We do not dispute that very low rates of disturbance may result in forests with an average high wood density. However, our data suggest that under certain conditions a regime of severe droughts might favour the dominance of heavy wooded species. It is possible that the high local dominance of *Eusideroxylon zwageri* in Kalimantan and Sumatra (Whitten et al. 1987, MacKinnon et al. 1996) is the result of such specific climatic circumstances (Leighton & Wirawan 1986), since this dominance occurs in areas which suffer from occasional droughts similar to the drought that we investigated, to which *Eusideroxylon* appeared to be highly resistant (Figure 2.9). This pattern calls for a cautious use of vegeta-

tion characteristics as a way to infer the disturbance history of a site. It suggests that the assumption in the intermediate disturbance theory (Connell 1979, Huston 1979) and the dynamic equilibrium hypothesis (Huston 1994), that disturbances facilitate the maintenance of diversity by selecting against species with a K-strategy (sensu Pianka 1970), is not necessarily correct.

For the community as a whole, average bark thickness per dbh class was a fair predictor for fire-induced mortality. Thus, the proportional loss of individuals from a population by exclusive fire disturbance depends on the size-distribution of stems and on the species-specific pattern of bark increment with size (Chapter 2). Several species of Dipterocarpaceae combine a population structure characterised by an abundance of large individuals (Table 1.3 & 1.4) with a rapid increase in bark thickness with size (Figure 2.11). This combination of characteristics may explain why the relative dominance of this family in the burned forest is higher than in the unburned forest (Table 3.4).

Local diversity of shade tolerant trees shortly after the fire was mainly determined by sprouting of small stems: 18% of the pre-fire stems did so. Sprouts formed such an important component of the post-fire vegetation because their density (excluding *Fordia splendidissima*, a dominant shade tolerant shrub) was 13 times higher than the density of surviving stems, and their species diversity per number of stems was similar to that of pre-fire stems >10 cm dbh. Moreover, their early establishment after the fire may have given these resprouts an advantage over shade tolerant seedlings that may establish when dispersed seeds start to arrive, because it allows them to overgrow the potentially inhibitive fern-cover in an earlier stage of development.

Species showed different levels of sprouting capacity, which was expressed in terms of sprouting frequency (the percentage of individuals producing sprouts after being damaged), and the growth and survival of sprouts. Species-specific sprouting frequency after fire correlated

well with the sprouting frequency of those same species in a clipping experiment in the unburned forest (Chapter 4).

The clipping experiment provided insight in the question, which factors determine specific sprouting capacity. One pre-requisite for the maintenance of sprouting ability is the availability of sufficient energy reserves (Chapin et al. 1990, Pate et al. 1990, Bell et al. 1996). The six species in the clipping experiment proved to contain such reserves in the form of high concentrations of stored total non-structural carbohydrates (tnc) in the stem and root, forming 15-23% of the total dry weight. The species in our study appear to make large investments to secure their persistence. Carbohydrate reserves were high even when individuals were growing under a low light intensity. On theoretical grounds, such a persistence-oriented strategy is to be expected when individuals have to survive for long periods in an environment where resources are limited, while the risk of damage is high (Iwasa & Kubo 1997, Iwasa 2000). The ability of seedlings and saplings to resprout after a singular occurrence of fire probably is a side effect of the adaptive capability of juveniles to sprout after stem breakage. However, it appears that sprouting after fire is impeded by other factors than tnc availability as well, since the sprouting frequency after fire was approximately five times lower than the sprouting frequency after clipping.

After establishment in the burned forest, sprouts grew fast in the first 21 months after the fire. The average sprout length eight months after the fire was 25.1 ± 19.2 cm (3.1 ± 2.4 cm month⁻¹). Sprouts grew another 80.3 ± 71.3 cm (6.2 ± 5.5 cm month⁻¹) in the 13 months that followed. Length growth of sprouts was negatively related to specific wood density (Figure 3.9). The same pattern was observed in the clipping experiment when wood density was related to length growth of the tallest sprout in the fifth and sixth month after clipping, when growth had stabilised and depended on photosynthesis of the newly formed leaves (Figure 4.6).

Sprout survival was fairly high between the censuses 8 and 21 months after the fire: 83% of the sprouts survived, whereas the fate of another 11% remained unclear. Sprout survival in the clipping experiment appeared to be influenced by water constraints in two species. *Macaranga lowii* (a shade tolerant species) had a higher mortality on ridges than on slopes and in valleys, and *Shorea laevis* had the highest mortality under high light conditions. It is remarkable that the two species with the highest wood density would show the highest drought-related mortality, since wood density is related to the ability of a tree to withstand water stress (Chapter 2, Hacke et al. 2001). Water transport resistance has been found to be highest in the joints of branches (Bazzaz 1996), in the joints of sprouts (Klugmann & Roloff 1999), and in thin distal branches in general (Yang & Tyree 1993). I believe that such locally high resistance was the culprit for the observed mortality in these two species which formed very thin sprout axes (Chapter 4). In the burned forest, sprout survival was not significantly correlated to wood density. Sample sizes may have been too low to detect such patterns, or possibly the individuals that suffered from the constraint of high water resistance in sprout joints had died before the first inventory.

Competitive interactions between shade tolerant individuals will probably not occur until they have reached a height of several meters. The density of shade tolerant tree sprouts in the burned forest is less than one fifth of the pre-fire density of stems <10 cm dbh. At a small scale (i.e. 0.1 – 10 m) sprouts were evenly distributed (MvN pers. obs.). We infer that local shade tolerant species composition will be mainly determined by initial floristics (Egler 1954), i.e. the community composition of the surviving sprouts, and very little by competitive interactions. Heavy-wooded species will probably be underrepresented in the post-fire resprouting community, due to the species-specific differences in initial persistence ability through sprouting and subsequent sprout survival and growth rate.

The predictive power of non-fire and fire-based theoretical approaches

The research in Sungai Wain shows that a variety of persistence modes contribute to the population build-up of species after fire disturbance. Several of these modes of persistence have been largely ignored in non-fire successional theory after severe disturbance, which has a traditional focus on long-distance seed dispersal and survival of propagules in the soil. This focus on propagule-based processes is adequate when the disturbance regime is severe enough to kill most of the later-successional individuals on the site. Therefore, the traditional theory provides a good description of old field succession in the temperate regions from which the theory originates (Clements 1916, Glenn-Lewin & van der Maarel 1992). Disturbance treatments in tropical forest succession experiments have often been small in scale and of severe intensity to an extent which would not occur in the absence of human interference (e.g. Uhl et al. 1982, 1988, Uhl 1987, Uhl & Jordan 1984, Riswan & Kartawinata 1989, Kammesheidt 1998, 1999, Peña-Claros 2001). This bias unintentionally promoted the relative importance of propagule dispersal and propagule survival in the seed bank above vegetative modes of persistence, causing a reasonable fit of the data to traditional succession theory.

Both non-fire ecologists and fire ecologists recognise a great diversity of successional patterns and processes (Connell & Slatyer 1977, Pickett et al 1987, Bond & van Wilgen 1996). However, the idea of a predictable sequence of plant species replacement, the relay floristic model of succession, is still central to much of traditional ecological thinking (Bond & van Wilgen 1996). Connell and Slatyer made an attempt to distinguish the different mechanistic processes driving succession, proposing that succession occurred along one of three alternative pathways, which were named the facilita-

tion model, the tolerance model and the inhibition model. It has been argued that these alternative models are not mutually exclusive and cannot be discriminated from one another by experiments (Pickett et al. 1987). Nevertheless the framework remains an important reference point for successional studies.

The tolerance model, in which “the modifications wrought on the environment by the earlier colonists neither increase nor reduce the rates of recruitment and growth to maturity of later colonists” (Connell & Slatyer 1977, p. 1122), might appear to fit the characteristics of the early post-fire vegetation patterns in our study. However, the emphasis is fundamentally different between the tolerance model and the processes that appear to determine the functional group composition after fire. The discriminating emphasises of the models of Connell and Slatyer is on interactions between individuals, and aims at assessing whether establishment of later arriving species is either enhanced, reduced or unaffected by earlier established species. In contrast, our results show that, in order to understand early vegetation composition, it is not the interactions between species that are of central importance, but the abilities of species to persist in the seed bank, to regenerate vegetatively from surviving tissue or even to avoid any significant loss of biomass. This perspective asks for the explicit incorporation of species’ sensitivity to the disturbance treatment.

In traditional succession theory, the influence of the “initial floristics” on succession (Egler 1954) has been acknowledged for a long time. In tropical gap-dynamical studies, the importance of the pre-gap composition of the vegetation has been identified as a determinant of gap-phase succession (for example Zagt & Werger 1996, Wright 2002). Although different terminology is used, the essence of these studies is similar to the “initial floristics” approach of Egler. Nevertheless, species persistence capabilities (persistence here referring to the ability of a population to survive a particular disturbance) remain essentially unspecified in theoretical non-fire succession models

Table 7.2. Schematic overview of the relevance of different plant vital attributes for the four main functional groups after a single fire disturbance. The functional groups, including an a-posteriorly defined group of litter-gap demanding shrubs and a refinement of light-demanding non-woody species into two taxonomic groups, are ordered in an approximate sequence from early to late successional. The number of crossmarks indicates the relative importance of a vital attribute, a circle indicates the potential importance of a vital attribute after repeated disturbance. A question mark indicates a lack of information to assess the importance. Attributes which are considered of importance in traditional non-fire succession theory are underlined. A detailed description of the vital attributes is given in table 1.2.

Functional group (+ taxonomical subdivision)						
<i>Approximately ordered from early successional to late successional</i>						
		Light-demanding non-woody species	Grasses, herbs	Light-demanding trees	Litter-gap demanding shrubs	Shade-tolerant trees
Vital attribute						
Establishment requirements						
T	Tolerant species				<u>xxx</u>	<u>xxx</u>
I	Intolerant species	<u>xxx</u>	<u>xxx</u>	<u>xxx</u>		
R	Requiring species					?
Mode of persistence of the population						
D	Dispersed species	<u>xxx</u>	<u>xx</u>	<u>x</u>	<u>x</u>	<u>xx</u>
S	Soil-stored species	?	<u>xx</u>	<u>xxx</u>	<u>xxx</u>	
G	Germinating species			?		
C	Canopy-stored species					
V	Vegetative species	o	o	o	xx	xxx
U	Unaffected species					x
W	Mature stage unaffected					x
Y	Juvenile stage unaffected					
Time for the population to reach a certain life history stage						
<i>m</i>	Time to reproductive maturity	Very short	Very short	Short to long	Short	Long
<i>l</i>	Life span of individuals	Highly variable	Very short	Short to long	Short	Long to very long
<i>e</i>	Time for all propagules to be lost from the community in the absence of disturbance	Probably short	Probably short	Long	Long to infinite	Long to infinite

(Connell and Slatyer 1977, Pickett et al. 1987). The plant vital attributes approach developed by Noble and Slatyer (1980) appears to be the only commonly cited theoretical framework that may be suited to analyse the importance of plant persistence capabilities. The main assets of the vital attributes model are that it explicitly incorporates the predisturbance vegetation as a factor determining post-disturbance succession, and that it incorporates interactions between the distur-

bance regime and plant persistence capacities.

Vital attributes are defined as characteristics of a species which are vital in determining the role of a species in vegetation replacement sequences (Noble & Slatyer 1980). It is important to notice that vital attributes are defined relative to a particular disturbance type. Thus, vital attributes are not necessarily fixed characteristics, but may differ depending on the form of disturbance. Noble and

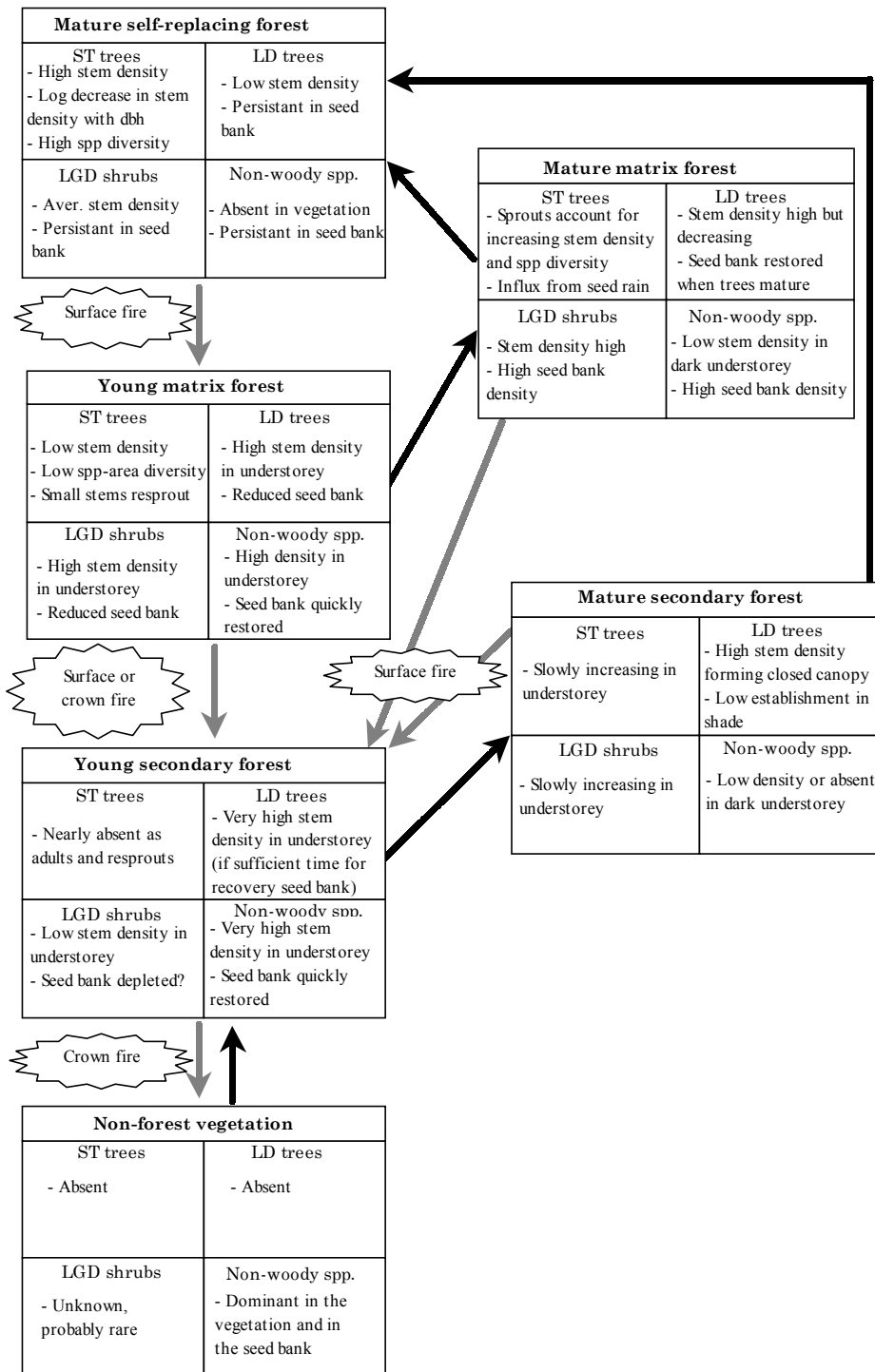


Figure 7.1 a.

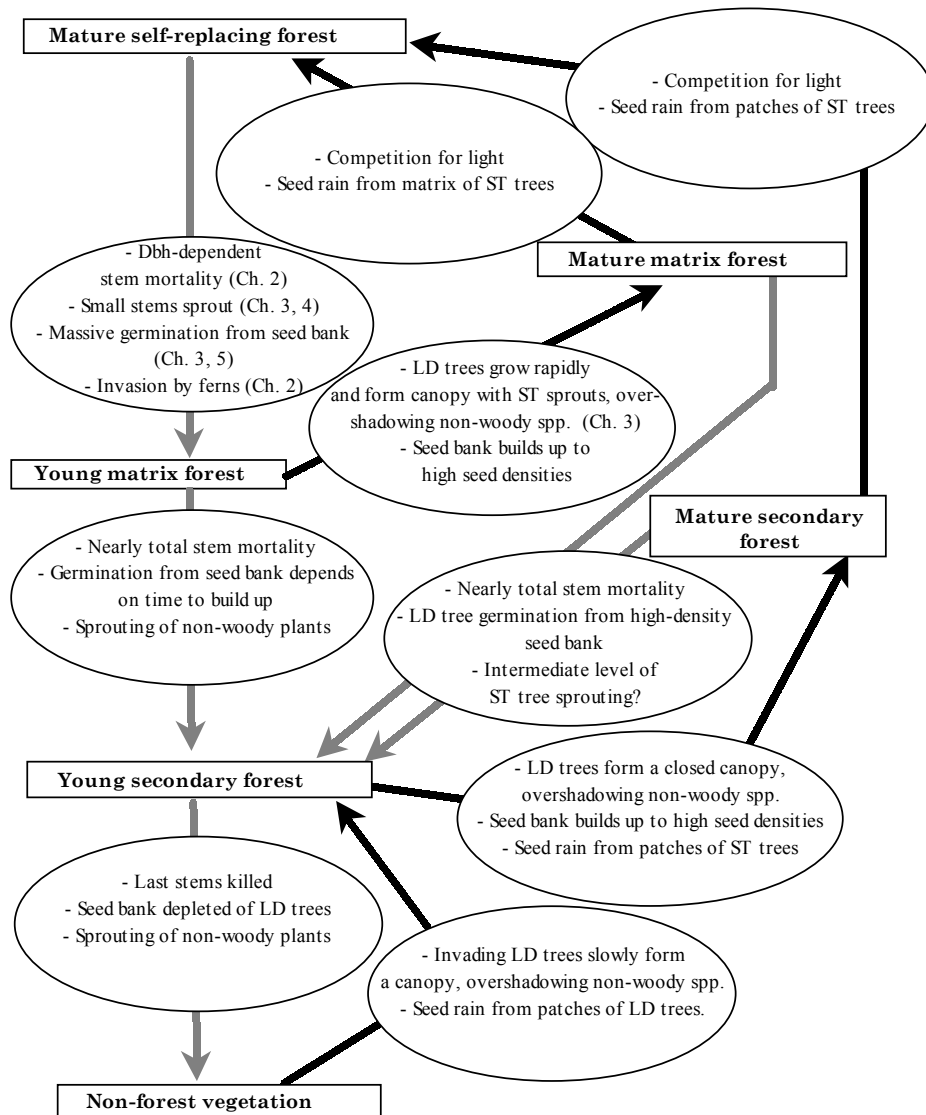


Figure 7.1 b.

Figure 7.1. Schematic representation of the transitions of a tropical rain forest that is affected by repeated fire disturbance. In figure (a), the main forest types are shown, and the population characteristics of the main plant functional groups which define the forest type are described. ST= Shade tolerant, LD= Light demanding, LGD= Litter-gap demanding. The functional attributes of each plant functional group are described in table 1.1. Matrix forest is distinguished from secondary forest by the presence of surviving mature trees from before the disturbance. Time to recovery increases from the top to the bottom of the figure. In figure (b), the biotic and abiotic processes are described that determine the transitions from one forest type to another.

Slatyer consider three groups of vital attributes (Table 7.1). Here, I focus mainly on the group of persistence attributes, for which the approach provides a comprehensive framework.

Persistence modes are based on either propagule-based mechanisms (where a propagule is defined as “a structure produced by an organism, either sexually or asexually, which becomes detached from the parent and gives rise to another individual (Noble & Slatyer 1980, p. 21)), or vegetative mechanisms, which are asexual. Vital persistence attributes are categorised according to their occurrence in four major life stages (Table 7.1). These life stages apply to the state of a population at a certain moment in time and not to particular individuals. The resulting framework renders 20 theoretical modes of persistence, eight of which are likely to occur in nature, according to Noble and Slatyer (Table 7.2).

Table 7.2 shows, which persistence modes and other vital attributes play a role in the population dynamics of the different functional groups that we studied. Using vital attributes, one can summarise the vegetation development as the result of population dynamics driven by different mechanisms of persistence, establishment and life stage characteristics. The successional pathway that occurs after fire in the dipterocarp rain forest of East Kalimantan is visualised in figure 7.1 a. Also indicated in the same figure are pathways as they may be expected after repeated fire disturbance. Figure 7.1 b shows the various mechanisms that appear to structure the dynamics of the four main functional groups studied in this thesis. Given a lack of information on many aspects of the performance of the functional groups, it is not yet possible to provide the full detail that is given by the vegetation replacement models in the tradition of Noble and Slatyers’ paper.

Figure 7.1 emphasises the importance of tree survival and sprouting of small stems as a factor contributing to the recovery of shade tolerant trees in the vegetation. The figure also indicates how, following repeated disturbances, recovery of shade tolerant tree populations will

depend ever more on long-distance seed dispersal. Infrequent seed production (Janzen 1974, Curran & Leighton 2000, Wich & van Schaik 2000) and often short dispersal distances (Hubbell 1979, 1980, Howe & Smallwood 1982, Dalling et al. 1998) make that the recovery process of shade tolerant populations will be much longer when they depend on seed dispersal.

Egler (1954) presented the concept of initial floristics in old field succession. White (1979) observed that “much of the persistent controversy surrounding succession stems from the very different starting points or pioneer states following varied kinds and degrees of disturbance, from which the seral sequence begins”. Many papers subsequently published on the subject of succession make reference to these authors (e.g. Connell & Slatyer 1977, West et al. 1981, Huston & Smith 1987, Pickett et al. 1987, Glenn-Lewin et al. 1992). Given this long-time recognition of initial floristics as a factor determining successional development, it is remarkable that the persistence characteristics defined in the vital attributes approach were never firmly integrated into general succession theory. It appears that succession theory would gain in comprehensiveness from an integration of the strong aspects of non-fire and fire approaches.

Possibly, the impediment to integration lies in the fact that most vital attributes in the vital attributes classification are determined only qualitatively. Noble and Slatyer did so deliberately in order to keep the approach simple. Thus, the main innovating aspects of the vital attributes approach, i.e. the explicit inclusion and modes of persistence and their interaction with the type of disturbance both remain unquantified in the theory. In non-fire theory it is common practice to define many plant characteristics quantitatively. This difference may be the reason that the vital attributes approach is cited in most papers on succession theory, but its ideas are never truly integrated in the conceptual framework.

The disadvantage of a quantitative approach is that the model system be

comes increasingly complex. Only computer supported simulation models may be able to handle such complexity. Recent succession simulation models already included a greater variety of life-history traits to explain vegetation dynamics and species diversity (Pacala et al. 1996, Clark 1996, Loehle 2000). As Pacala et al. (1996) showed, it is possible with these models to disentangle the effect of different life-history traits on the dynamics of populations. Individual-based succession models may allow the testing of how imaginary species would perform if they differed only in persistence characteristics.

Drought and fire persistence as life-history traits

Life history and physiological traits determine the performance of individuals, and structure the dynamics of a population. Plant traits occur in a limited number of combinations, as the result of character convergence (Cody 1973). The implication of this limited variation is that successional patterns are constrained to a restricted number of patterns (Grime 1979, Huston & Smith 1987). Insight in how plant traits correlate and which trade-offs determine the occurring combinations of traits helps to understand patterns of succession and is a subject which returns in many theoretical approaches (Grime 1979, Noble & Slatyer 1980, Tilman 1982, 1988, Huston & Smith 1987, Swaine & Whitmore 1988, Hubbell 1998). Understanding the correlations and trade-offs between persistence traits and other life-history characteristics is needed to assess the dynamics of populations in the successional development of a vegetation.

Correlative patterns between the mechanisms of persistence of shade tolerant trees and other traits have been scarcely studied. The research in Sungai Wain indicates that several such correlations exist, e.g. we found correlations between drought survival and wood density, fire survival and bark thickness, concentration of total non-structural carbohydrate reserves (tnc) and sprouting

frequency, wood density and sprout survival, and wood density and sprout growth.

Wood density is a variable which returns in several of these correlative relations. Even though wood density may be a derived characteristic in these analyses, lacking a simple mechanistic relationship with the other plant traits in the correlation, it provides a suitable way of characterising tree types because it correlates with a multitude of plant traits. These include growth characteristics (structural investments per unit volume, water transport capacity, xylem cavitation resistance, photosynthetic assimilation rate, growth rate, shade-tolerance, asymptotic height (Borchert 1994, Thomas 1996, Lucas et al. 1997, Hubbell 1998, Tyree et al. 1998, Suzuki 1999, Hacke et al. 2001)), and reproductive characteristics (seed size, seed dispersal mode (ter Steege & Hammond 2001)).

Inclusion of persistence abilities will increase the complexity of succession theory. However, the observed correlations between persistence abilities and other plant traits suggest that the number of possible life-history combinations is limited. Thus, the number of successional patterns (sensu Huston & Smith 1987) will not increase proportionally.

Nature conservation, forest management and the threat of repeated disturbances

Analysis of the successional pathways of dipterocarp rain forest after fire may help to determine the potential capability of the forest to recover, to assess its sensitivity to additional disturbances and to assess the need for specific management measures. As was observed in several other studies (Stocker 1981, Kammerheidt 1998, 1999), tropical rain forests possess a higher level of resilience to fire disturbance than was foreseen. Since many shade tolerant tree species are able to persist through whole-plant survival or resprouting from basal stem parts, recolonisation from unburned forest areas is not always required.

Notwithstanding the moderately optimistic results that come out of this study, persistence of the forest cover is highly threatened. It should be noted that this study was done in an old growth forest, whereas a large part of the fires in 1997-1998 occurred in selectively logged forest, which both had a higher risk of burning and probably experienced a higher fire intensity. Depending on logging intensity and the period of recovery between logging and burning, logging followed by fire probably results in a greater reduction in tree density, lower densities of resprouting stems, and a greater reduction of the soil seed bank.

Following a first disturbance such as selective logging or fire, the synergy between increased flammability of the forest and continuing threats posed by human activities is likely to result in a sequence of fire disturbances (Cochrane & Schulze 1999, Cochrane et al. 1999, Cochrane 2001). Following a first fire, the vegetation will remain much more flammable over a period of several decades. The canopy is opened, allowing for the rapid drying-up of fuel (Uhl et al. 1988, Holdsworth and Uhl 1997). Trees which were killed by the first fire provide ample coarse woody fuel (debris), while invading ferns and *Imperata cylindrica* form a highly flammable understorey.

The persistence mechanisms of shade tolerant trees and light-demanding trees

are not sufficient to ensure that forest cover is maintained in the wake of repeated fires. Following recurrent disturbances the vegetation rapidly deteriorates, and the pathway to recovery changes fundamentally (Figure 7.1). Instead of recovering locally through sprouting, shade tolerant tree populations will depend on the slow process of long-distance seed dispersal for their recovery. This takes a much longer time, and the species composition will be much more severely altered than in a resprouting forest. In chapter 6 we warned for a similar scenario if burned forests are further disturbed by logging (van Nieuwstadt et al. 2001).

Even though from a conservationists' point of view the burned forests of East Kalimantan form a poor substitute for unburned forest, their sustained diversity, surviving populations of timber species and evident recovery potential make them worth maintaining. An active protection program which minimises any subsequent disturbances is necessary to take advantage of their potential for recovery.

Acknowledgements

I am grateful to M.J.A. Werger, J.A. Sayer and D. Sheil for their comments on an earlier version of the manuscript.

Nederlandse samenvatting

Achtergrond

Tropische bosbranden als nieuw fenomeen

Wereldwijd worden tropische bossen in hoog tempo door de mens vernietigd. Tot voor kort vormden houtkap en ontginning voor landbouw de voornaamste redenen voor ontbossing. Gedurende de afgelopen decennia is daar een nieuwe bedreiging bijgekomen in de vorm van ongecontroleerde branden. In tegenstelling tot wat men lange tijd veronderstelde, blijken tropische regenwouden brandbaar te zijn gedurende ongewoon lange droogtes, die ontstaan in zogeheten el Niño jaren. Met name selectief gekapte bossen zijn voor brand vatbaar, maar ook ongeschonde bossen blijken vlam te kunnen vatten. De ecologische en economische schade hiervan is grootschalig: Alleen al in de Indonesische provincie Oost-Kalimantan verbrandde zo'n 2.6 miljoen hectare bos gedurende een aanhoudende droogte in 1997-1998.

Ondanks de enorme schaal waarop tropische bosbranden plaatsvinden, is er weinig onderzoek verricht naar de consequenties voor de ontwikkeling van het bos. Verbrande gebieden kunnen nog steeds een potentiële waarde voor houtproductie en natuurbescherming hebben. Deze waarde hangt af van de mogelijkheid van een verbrand bos om zich te herstellen, en de snelheid waarmee dit gebeurt. Evenmin zijn er pogingen ondernomen om de vegetatieontwikkeling na brand in een breder theoretisch kader te plaatsen. Men heeft lange tijd aangenomen dat de hoge soortendiversiteit in het tropisch regenwoud in stand blijft als gevolg van een langdurig stabiele omgeving, waar slechts lokale verstoringen in voorkomen. Uit palynologisch onder-

zoek is gebleken dat veel tropische bossen ook in het verleden sporadisch brandden. Het is een wetenschappelijke uitdaging om het voorkomen van grootschalige verstoringen, zoals bosbranden, te integreren in het theoretisch raamwerk dat de soortensamenstelling en de hoge soortendiversiteit in de tropen verklaart. Een complicerende factor hierbij is het feit dat ook de ongewone droogte zelf, die noodzakelijkerwijs aan een brand voorafgaat, effect op de vegetatie heeft.

Verskillende benaderingen in successietheorie

Successietheorie vormt het wetenschappelijk raamwerk waarbinnen de ontwikkeling van een vegetatie na verstoring wordt beschreven. Successie kan men definiëren als een voorspelbare opeenvolging van vegetatietypes die zich na een verstoring ontwikkelen. Successietheorie is inmiddels zo'n 100 jaar oud en was aanvankelijk gericht op het beschrijven van vegetatieontwikkeling op verlaten landbouwgronden. In die situatie spelen verschillen tussen soorten in koloniesnelheid, concurrentiekracht en levensduur een belangrijke rol in het verklaren en voorspellen van de opeenvolging van vegetatietypes. Omdat het beginstadium van de successiereeks uit een nagenoeg complete afwezigheid van vegetatie bestaat, spelen de overlevingskansen van planten gedurende de verstoring (het in cultuur brengen van de grond) nauwelijks een rol.

In de loop van de tijd werd vanuit het theoretisch raamwerk van successie de ontwikkeling van vegetaties in steeds meer verschillende situaties geanalyseerd. In bossen wordt successie bestudeerd na kleinschalige verstoringen in

het kronendak, meestal als gevolg van een omvallende boom. Een dergelijke verstoring veroorzaakt in het algemeen weinig schade aan de vegetatie en wordt meestal gekwantificeerd in termen van de toegenomen beschikbaarheid van bronnen die limiterend zijn voor de groei (met name licht). Successionele veranderingen worden voorspeld aan de hand van de concurrentie-rangorde tussen individuen in de opening in de vegetatie.

In het onderzoek dat zich richt op successie na brand in brandgevoelige vegetaties heeft zich een andere theoretische benadering ontwikkeld. Deze benadering ontstond toen men zich realiseerde dat in mediterrane struikvegetaties alle soorten, die gedurende verschillende stadia van de successiereeks domineren, al direct na een brand aanwezig zijn door middel van lokaal aanwezige zaden of door het uitlopen van overlevende wortels. Successie is hier niet het gevolg van verschillen in kolonisationsnelheid of concurrentie, maar simpelweg het gevolg van verschillen in levensduur.

In een poging om de dynamiek van soorten in een brandbare vegetatie integraal te beschrijven werd het raamwerk van "vitale plant attributen" (VPA) ontwikkeld. In deze aanpak wordt niet alleen de "regeneratie-niche" van soorten gedefiniëerd (de omstandigheden waaronder een soort zich succesvol kan vestigen), maar ook de "persistentie-niche" (de omstandigheden waaronder een gevestigd individu kan overleven) en de tijd die een soort nodig heeft om een aantal karakteristieke fasen te doorlopen (o.a. de tijd om volwassen te worden en de maximale overlevingsduur van gevestigde individuen). In tegenstelling tot de traditionele successietheorie, spelen verschillen in concurrentiekracht tussen soorten in VPA theorie nauwelijks een rol.

Successie in de tropen

Een grote verscheidenheid aan plantensoorten in een vegetatie bemoeilijkt het vinden van algemene patronen. Om analyse en interpretatie van processen zoals successie in een tropisch regenwoud

te vergemakkelijken heeft men het begrip functionele plantengroepen geïntroduceerd. Een functionele groep is een groep van soorten die een aantal karakteristieke kenmerken delen. In mijn onderzoek heb ik vantevoren drie functionele groepen onderscheiden, zijnde lichtbehoevende niet-houtige soorten, lichtbehoevende boomsoorten, en schaduwtolerante boomsoorten, terwijl *a posteriori* een vierde groep werd gedefiniëerd, zijnde soorten, die zich alleen kunnen vestigen op plekken waar een opening ontstaat in de strooisellaag.

In de bestaande theorie wordt de successiereeks in een tropisch bos na een zware verstoring tot een opeenvolging van de eerste drie functionele groepen geabstraheerd. Aanvankelijk bestaat de vegetatie uit lichtbehoevende soorten, die zich na een verstoring snel kunnen vestigen omdat ze een goede zaadverspreiding hebben en als zaad in de bodem overleven. De niet-houtige soorten domineren gedurende een korte beginperiode, waarna lichtbehoevende bomen boven hen uitgroeien. Geleidelijk aan wordt de vegetatie steeds meer door schaduwtolerante soorten gedomineerd, die later arriveren omdat ze een minder efficiënte zaadverspreiding hebben, maar die in de schaduw van een gevestigde vegetatie kunnen overleven.

Diverse onderzoeken in Borneo en in andere delen van de tropen beschrijven de effecten van brand op de ontwikkeling van de vegetatie. Deze onderzoeken geven echter geen goed totaalbeeld van de successionele ontwikkeling van een bos na brand, omdat de verstoringsregimes erg varieerden en deze vaak complex en intens waren (bv. kleinschalige kaalslag gevolgd door brand en landbouwgebruik). Mogelijkerwijs is het bestaande inzicht in vegetatieontwikkeling na brand gekleurd door deze nadruk op intensieve en kleinschalige verstoringen, die nooit zouden optreden in de afwezigheid van mensen. Door dergelijke verstoringen is de kans op lokale overleving van planten namelijk klein, terwijl het gewoonlijk nabijgelegen onverstoorde bos een bron van zaden vormt. De lokale overleving van planten kan een veel belangrijkere rol spelen

wanneer de vegetatie door een enkele, grootschalige brand wordt verstoord.

Onderzoeksopzet

Het onderzoek werd in het bos Sungai Wain uitgevoerd, een beschermd waterwingebied van zo'n 100 km² aan de oostkust van Oost-Kalimantan ten noorden van de stad Balikpapan. Dit gebied is grotendeels begroeid met laagland dipterocarp bos, een term die verwijst naar de meest kenmerkende familie van boomsoorten. Het gebied heeft een tropisch nat klimaat met een gemiddelde jaarlijkse regenval van 2790 mm en een gemiddelde maandelijkse regenval die gedurende het hele jaar boven de 100 mm ligt. Deze karakterisering is echter enigszins misleidend, omdat met een zekere regelmaat extreme droogtes van een of enkele maanden voorkomen, die ten dele samenhangen met het el Niño fenomeen.

De droogte die voorafging aan de branden die het onderwerp van deze studie zijn, bestond uit twee extreem droge episodes van ieder 12-14 weken, in de tweede helft van 1997 en de eerste helft van 1998. De 14 weken tussen deze twee droge episodes waren natter, hoewel er nog altijd minder neerslag viel dan gemiddeld. De meeste bosbranden vonden gedurende de tweede droge episode plaats. De branden in het bos waren van een lage intensiteit, met vlammen van zo'n 0.5 meter hoog die zich als een lang lint over de bosbodem verplaatsten met een snelheid van 10-15 meter per uur. Hoewel de sterfte van bomen hoog was, zorgde de lage vuurintensiteit ervoor dat zelfs de dunste stammetjes ook na de brand nog overeind stonden.

Het onderzoek richtte zich op een vergelijking van het centrale, onverbrande bos met het daaromheen gelegen eenmaal verbrande bos. Deze waren van elkaar gescheiden door een smalle brandgang die tijdens de branden werd aangelegd. De onderzoeksopzet bestond uit 18 permanente proefvlakken van ieder 60 x 300 m (1.8 ha), die over een gebied van zo'n 20 km² waren verspreid. De proefvlakken werden paarsgewijs uitgezet, het ene proefvlak in onverbrand en het an-

dere in verbrand bos. In totaal omvatten de inventarisaties in deze proefvlakken ruwweg 3000 bomen van meer dan 28 cm dbh, 5000 bomen tussen 8 en 28 cm dbh, en 5000 individuen van minder dan 8 cm dbh.

Resultaten en discussie

Sterfte van bomen na droogte en brand

Zowel droogte als brand bleken een hoge sterfte van bomen tot gevolg te hebben (Hoofdstuk 2). De sterfte nam gedurende het tweede jaar na verstoring substantieel toe. De waargenomen sterfte onder bomen (> 10 cm dbh) van 29%, 21 maanden na de droogte, is de hoogste die ooit in de wetenschappelijke literatuur over de tropen werd geregistreerd. Dikkere bomen hadden een grotere kans om als gevolg van de droogte te sterven. Soortspecifieke sterfte na droogte van bomen boven 30 cm dbh werd door verschillen in houtdichtheid verklaard. Zoals uit morfologisch onderzoek werd voorspeld, waren soorten met zwaar hout het minst gevoelig voor de droogte. Dit is opmerkelijk, omdat het voorkomen van zwaarhoutige soorten met hun langzame groei vaak met de langdurige afwezigheid van grote verstoringen geassocieerd wordt.

Eenentwintig maanden na de brand was de sterfte 74%. Door sterfte uitsluitend als gevolg van droogte af te trekken van sterfte na droogte en brand, werd geschat dat in het verbrande bos 2/3 van de sterfte door brand werd veroorzaakt. Bovengrondse sterfte van bomen na droogte en brand was bijna 100% voor individuen dunner dan 10 cm dbh. Met toenemende dikte hadden bomen een steeds kleinere kans om als gevolg van de brand te sterven. Boven de 70 cm dbh werd er geen significante toename in sterfte als gevolg van de brand waargenomen. De correlatie tussen boomgrootte en sterftekans wordt veroorzaakt door een betere isolatie van het levende weefsel naarmate bomen dikker zijn, als gevolg van een toenemende bastdikte. Bastdikte verklaart echter niet de soortspecifieke

verschillen in sterfte van bomen boven de 30 cm dbh als gevolg van de brand.

De combinatie van droogte en brand veroorzaakten vooral zo'n grote sterfte, omdat de twee verstoringen deels aangrijpen op verschillende grootteklassen. Het hoge niveau van "vertraagde" sterfte na zowel droogte als na droogte plus brand laat zien dat langlopende observaties noodzakelijk zijn om de consequenties van deze verstoringen voor de vegetatie te kunnen meten.

Vegetatiedynamiek van functionele plantengroepen na brand

In hoofdstuk 3 werden patronen van functionele plantengroepen in de vegetatie onderzocht. Tevens werd ruimtelijke variatie in het brandregime gemeten, als wel het effect van de brand op de lichtbeschikbaarheid en het verband tussen de lokale sterfte van bomen en de lichtbeschikbaarheid.

Onverbrande stukjes bos vormden slechts 4 tot 7% van het niet door de brandgang beschermde bos en waren ongelijkmatig verdeeld over de proefvlakken. Met name valeitjes hadden een lagere kans om te verbranden. De openheid van het kronendak in het verbrande bos was gemiddeld 24%, vele malen meer dan de 5% in het onverbrande bos. De openheid van het kronendak was aan het lokale percentage dode bomen gerelateerd. Ondanks de flinke variatie in lichtbeschikbaarheid in het verbrande bos, was de vegetatie die zich na de brand ontwikkelde hiermee nauwelijks gerelateerd, wellicht omdat kort na de brand de lichtbeschikbaarheid vrijwel nergens in het verbrande bos limiterend was.

De dichtheid aan varens was gemiddeld 61% in het verbrande bos. Op veel plekken vormden varens een aaneengesloten vegetatie van 1 tot 2 meter hoog. Lichtbehoevende jonge boompjes (> 1.30 m hoog) hadden een aanzienlijke dichtheid, variërend van 0.6 tot 6.7 stammen per 100 m², ondanks het feit dat volwassen individuen vóór de brand schaars waren. De dichtheid aan varens was negatief gecorreleerd met dichtheid aan lichtbehoevende jonge boompjes en was

niet gecorreleerd met de dichtheid aan uitlopende schaduwtolerante stammetjes.

De soortendiversiteit van bovengronds overlevende bomen (> 10 cm dbh, op een oppervlak van 0.4 ha) in het verbrande bos was slechts 30% van de onverbrande vegetatie. De soortendiversiteit per aantal stammen in onverbrand en verbrand bos was echter nagenoeg gelijk. De dichtheid aan schaduwtolerante soorten (in alle grote klassen) werd vooral door een hoge dichtheid aan herspruitende stammetjes dunner dan 10 cm dbh bepaald. Deze bleken een belangrijke factor in het herstel van het bos te vormen, en een relatief snel herstel van de populaties van schaduwtolerante soorten mogelijk te maken. De soortendiversiteit per aantal herspruitende stammen was vergelijkbaar met de soortendiversiteit per aantal stammen (> 10 cm dbh) in het onverbrande bos. Van een beperkt aantal schaduwtolerante soorten werd het verband tussen soortspecifieke houtdichtheid, spruitfrequentie, groeisnelheid en overleving in het tweede jaar na de brand onderzocht. Dergelijke verbanden kunnen helpen om veranderingen in de soortensamenstelling van de functionele groep van schaduwtolerante soorten te voorspellen.

Uitlopen van jonge boompjes na het afknippen van de stam: een experiment

In hoofdstuk 4 beschrijf ik een experiment, waarin de capaciteit van jonge boompjes om uit te lopen ("spruiten") na zware beschadiging bepaald wordt. Om zware beschadiging te simuleren werden jonge boompjes (1.5-2.5 cm dbh) van zes schaduwtolerante soorten op 1.30 meter hoogte afgeknipt, zodat er geen groene bladeren achterbleven. Gedurende zes maanden werd maandelijks het aantal spruiten en de lengte van iedere spruit gemeten. Doel van het onderzoek was om te onderzoeken hoe groot soortspecifieke verschillen in de capaciteit om te spruiten zijn, en hoe deze verschillen samenhangen met energiereserves ("totale niet-structurele carbohydraten", tnc) die door

deze soorten in de stam en de wortel worden opgeslagen.

De concentratie aan tnc varieerde van 15 tot 25% van het drooggewicht en verschilde significant tussen de zes soorten. De twee soorten met de laagste tnc concentratie in de wortel hadden een lager percentage spruitende stammen en een hoger percentage stammen waarvan alle spruiten stierven, dan de soorten met hogere tnc concentraties. Ook was er een tendens zichtbaar dat soorten met lagere tnc concentraties na zes maanden een lager drooggewicht aan spruiten hadden gevormd. De hoeveelheid energiereserves blijken dus een belangrijke factor te zijn die de capaciteit van soorten om na beschadiging opnieuw uit te lopen bepaalt.

Zodra spruiten fotosynthetiserende bladeren hadden gevormd, nam hun groeisnelheid af. In deze fase vertoonden de spruiten van zwaarhoutige soorten een tendens om langzamer te groeien. Dit patroon komt overeen met de verwachtingen voor het verband tussen houtdichtheid en groeisnelheid van onbeschadigde jonge boompjes. Dergelijke patronen helpen te voorspellen hoe verschillende populaties zich na zware verstoring zullen ontwikkelen.

Effecten van brand op de zaadvoorraad in de bodem

Door een vergelijking te maken tussen bodemmonsters uit zowel het onverbrande als het verbrande bos, onderzocht ik in hoofdstuk 5 de effecten van brand op de zaadvoorraad in de bosbodem. Om te kunnen analyseren tot welke diepte de brand effect heeft op de overleving van zaden werden bodemmonsters in vier lagen gestoken. Het bovenste monster bestond uit de strooisellaag, en de overige drie monsters uit laagjes minerale bodem van 0-1.5 cm, 1.5-3.0 cm en 3.0-4.5 cm diep. De zaaddichtheid in deze monsters werd bepaald door in een kwekerij gedurende 13 weken de kiemplantjes die opkwamen in de dun uitgespreide bodemmonsters te tellen en te identificeren.

De zaaddichtheid in het onverbrande bos nam snel met de diepte af. De schade aan de zaadvoorraad als gevolg van de brand beperkte zich tot de strooisellaag en de bovenste 1.5 cm van de bodem.

In een tweede experiment onderzocht ik, door welke factoren zaden in de bodem tot kiemen worden aangezet. Dit experiment toonde aan dat licht een voorwaarde voor de kieming van heel erg kleinzadige soorten (<5 mm doorsnede) was, terwijl de kleinzadige *Macaranga* (>5 mm doorsnede) ook in de duisternis kiemde, mits de dagelijkse temperatuur fluctueerde. In de duisternis strekten *Macaranga* zaailingen zich tot een lengte van zo'n 8 cm, terwijl de kiembladen zich gesloten hielden. Heel kleinzadige soorten vertoonden dit gedrag niet. De combinatie van kieming in het donker en het strekken van de zaailing suggereert dat *Macaranga* zich met succes vanaf een grotere diepte in de bodem kan vestigen. Als gevolg hiervan is de zaadvoorraad als geheel minder gevoelig voor brandschade.

Schade veroorzaakt door het kappen van dode bomen in een verbrand bos

Na de branden van 1997-1998 werd door de Indonesische overheid een richtlijn uitgevaardigd, waarin stond dat kapmaatschappijen prioriteit moesten geven aan het kappen van dode bomen met economische waarde in verbrand bos, boven de gewone kapactiviteiten in onverbrand bos. Kennelijk werd verondersteld dat het kappen van dode bomen geen negatieve invloed had op de regeneratie van de verbrande bossen, die immers toch al zwaar beschadigd waren. Ons onderzoek in Sungai Wain suggereert echter, dat het kappen van deze bomen een groot risico voor het herstel van het bos met zich meebrengt.

Een enkele brand veroorzaakt niet het volledig verdwijnen van de oorspronkelijke vegetatie. Lichtbehoevende boomsoorten komen kort na de brand op uit de zaadbank, die hierdoor tijdelijk in dichtheid vermindert. Schaduwtolerante boomsoorten, die karakteristiek zijn voor een onverstoord bos, behouden een rede

lijke dichtheid omdat ze voor hun regeneratie met name afhankelijk zijn van het opnieuw uitlopen van stammen die bovengronds door de brand zijn gedood.

Na deze eerste verstoring is de vegetatie kwetsbaar voor verdere verstoringen: Herspruitende planten hebben een lagere spruitkans wanneer ze een tweede keer worden beschadigd, de dichtheid van zaden in de zaadbank is als gevolg van de massale kieming kort na de brand sterk afgenomen, en de dichtheid aan bomen die als zaadbron dienst kunnen doen is laag. Wanneer in een dergelijke situatie de zich herstellende vegetatie wordt beschadigd door de zware machines die bij de kap gebruikt worden, ontwikkelt zich gemakkelijk een niet-bos vegetatie en wordt het potentiële tot herstel van het bos sterk verminderd. Onze resultaten wijzen erop dat kapactiviteiten in verbrand bos moeten worden vermeden wanneer men op de lange termijn het behoud van een bosvegetatie of de houtproductie van een concessie veilig wil stellen.

Conclusie

Uiteindelijk wordt het herstel van het bos bepaald door de snelheid waarmee schaduwtolerante soorten hun dominante positie in de vegetatie heroveren, en de soortensamenstelling waarin zij dit doen. De overleving van schaduwtolerante individuen, hetzij in ongeschonden toestand danwel door uitlopers na bovengrondse sterfte, is aanzienlijk. Daarom spelen deze "persistentie-processen" een belangrijke rol in de populatiedynamiek van schaduwtolerante soorten. Dergelijke persistentie-processen zijn in belangrijke mate veronachtzaamd in de traditionele niet-vuur gerelateerde successietheorie, waarin de nadruk op zaadverspreiding en overleving van zaden in de zaadbank ligt. Een dergelijke nadruk is voldoende wanneer het verstoringsregime dermate intens is, dat de meeste laat-successionele individuen op de site worden gedood. Om die reden vormt de traditionele theorie een goede basis voor de beschrijving van successie op verlaten landbouwgronden. In de tropen zijn veel successie-

experimenten gebaseerd op intensieve en kleinschalige verstoringen, die alleen kunnen ontstaan als gevolg van menselijk ingrijpen. Onbedoeld begunstigde deze aanpak het relatief belang van kolonisatie door zaad verspreiding en overleving van zaden in de bodem boven vegetatieve wijzen van persistentie.

Zowel niet-vuur ecologen als vuur ecologen onderkennen het bestaan van een grote diversiteit aan patronen en processen in de successionele ontwikkeling van een vegetatie. Desalniettemin vervult het idee dat soorten elkaar in de vegetatie in een voorspelbare sequentie van soorten opvolgen, gedreven door verschillen in kolonisatie snelheid en concurrentie, nog altijd een centrale rol in de niet-vuur gerelateerde theorie. Deze nadruk is fundamenteel verschillend van de aanpak die door vuurecologen wordt gevolgd, waarin een successiereeks wordt beschreven aan de hand van een aantal gecorreleerde plantkarakteristieken die in een VPA raamwerk worden ondergebracht. In deze aanpak speelt de wijze van persistentie gedurende een verstoring een belangrijke rol.

Gezien de belangrijke rol die in ons onderzoek door verschillende persistentie-processen wordt gespeeld, ligt het voor de hand om de principes van zowel de traditionele niet-vuur theorie als de VPA benadering op de vegetatie-ontwikkeling na brand toe te passen. Een dergelijke integratie van deze twee benaderingswijzen heeft tot dusver niet plaatsgevonden. Het obstakel om beide theoriën te integreren zit hem wellicht in het feit dat de VPA-theorie in grote mate kwalitatief is, om deze aanpak eenvoudig te houden. In de niet-vuur gerelateerde theorie is het daarentegen gebruikelijk om diverse plantkarakteristieken te kwantificeren. Het nadeel van een kwantitatieve aanpak van de VPA-theorie is dat het model bijzonder complex kan worden. Een dergelijke complexiteit kan enkel met behulp van computersimulaties worden bestudeerd.

Door diverse fysiologische en morfologische limiteringen komen planteigenschappen in een beperkt aantal combinaties voor. Dit principe speelt een

belangrijke rol in diverse theoretische benaderingen van ecologische problemen. Voor een integratie van de beide benaderingswijzen van successie zal het nodig zijn om de verbanden tussen persistentie en andere karakteristieken van soorten te begrijpen. Uit dit proefschrift komen verschillende verbanden naar voren, waarbij de houtdichtheid van soorten een nuttig soortenkenmerk blijkt te zijn om dergelijke verbanden te onderzoeken.

De integratie van persistentiekarakteristieken zal de complexiteit van successietheorie verhogen, maar de geobserveerde verbanden tussen persistentie en andere plantkarakteristieken suggereren dat het aantal mogelijke combinaties beperkt is. Daarom zal het aantal successionele patronen niet proportioneel in complexiteit toenemen.

Natuurbescherming, bosbeheer en het risico van herhaalde verstoringen

Analyse van de successionele ontwikkelingspatronen van een dipterocarp bos na brand helpen om de potentie van het bos om te herstellen te bepalen, de gevoeligheid voor bijkomende verstoringen te analyseren, en de noodzaak voor specifieke beheersmaatregelen vast te stellen.

Omdat schaduwtolerante soorten na een enkele brand een redelijke mate van lokale persistentie hebben, hoeft een verbrand bos niet opnieuw door deze soorten te worden gekoloniseerd. Hierdoor is een relatief snel herstel van het bos mogelijk.

Ondanks deze gematigd positieve conclusie, blijft het voortbestaan van een verbrand bos uitermate onzeker. Dit komt omdat een verbrand bos snel verder zal degenereren wanneer een bijkomende verstoring optreedt. Daar komt bij dat de brandbaarheid van een eenmalig verbrand bos gedurende enkele decennia sterk verhoogd is. Dit komt omdat er meer brandstof in de vorm van dode biomassa aanwezig is en omdat het bos sneller uitdroogt als gevolg van de open structuur van het kronendak. Bovendien zorgen landbouwactiviteiten voor een frequente bron van nieuwe brandhaarden. Studies in Latijns-Amerika hebben laten zien dat een veel voorkomend vervolg op een eerste brand is, dat er een reeks van branden optreedt. De persistentiemechanismen van schaduwtolerante soorten zijn niet voldoende om in een dergelijke situatie hun lokale overleving te bewerkstelligen. Dat heeft een snelle degradatie van de vegetatie tot gevolg.

Vanuit een natuurbeschermingsoogpunt vormen de verbrande bossen van Oost-Kalimantan een magere vervanging van onverbrand bos. Desalniettemin maken hun soortendiversiteit, overlevende populaties van commerciële boomsoorten en onmiskenbare herstelpotentieel het waard om ze te behouden. Een actief beleid dat erop gericht is om herhaalde verstoringen te voorkomen, is nodig om dit herstelpotentieel maximaal te benutten.

Percobaan oleh Kebakaran

Pembangunan paska-kebakaran hutan dipterocarp tropis

Ringkasan

Selama dekade terakhir, kebakaran hutan yang tidak terkendali meningkatkan ancaman terhadap hutan tropis, seringkali menyebabkan kerusakan ekologi dan ekonomi dalam skala besar. Hutan-hutan yang terbakar kemungkinan masih memiliki nilai potensial untuk produksi kayu dan konservasi alam, tergantung dari kemampuan hutan-hutan tersebut untuk pulih. Mengintegrasikan terjadinya gangguan-gangguan skala besar seperti kebakaran ke dalam kerangka-kerja teoritis merupakan tantangan ilmiah yang menjelaskan keragaman spesies dan komposisi spesies di hutan penghujan tropis.

Teori-teori suksesi membentuk kerangka-kerja yang menjelaskan perkembangan vegetasi setelah gangguan. Konsep sentral dalam teori-teori yang berkaitan dengan non-kebakaran (*non-fire theories*) adalah bahwa spesies saling menggantikan dalam urutan yang dapat diduga, terdorong oleh perbedaan laju kolonisasi, persaingan dan umur panjang. Penekanan ini secara mendasar berbeda dari pendekatan suksesi pada vegetasi mudah terbakar, dimana suksesi dijelaskan berdasarkan karakteristik tumbuhan, yang terbungkus dalam atribut vital tumbuhan. Dalam pendekatan ini, persistensi semasa gangguan memainkan peran penting, seperti juga waktu peristiwa sejarah kehidupan tumbuhan tertentu.

Dalam penelitian yang ada mengenai suksesi di hutan-hutan tropis, kompleksitas dan intensitas rejim gangguan pada umumnya tinggi. Kemungkinan ini mempengaruhi persepsi yang ada mengenai perkembangan vegetasi setelah kebakaran, karena setelah gangguan skala kecil yang parah, daya tahan hidup lokal tumbuhan menjadi rendah, sementara biasanya hutan yang tak terganggu di dekat hutan terbakar tersebut menyediakan sumber benih yang berlimpah. Per-

sistensi lokal tumbuhan dapat memainkan peran yang lebih penting saat vegetasi terganggu oleh kebakaran tunggal skala besar.

Penelitian ini dilaksanakan di Sungai Wain, yang berupa hutan dipterocarp daerah rendah, juga merupakan daerah suaka tangkapan air seluas 100 km² dekat pantai Kalimantan Timur. Wilayah ini beriklim tropis lembab, kekeringan ekstrim berbasis supra-annual, yang sampai derajat tertentu terkait dengan fenomena El Niño. Mengikuti kebakaran-kebakaran sebelumnya yang merupakan subyek thesis ini, wilayah tersebut mengalami dua kali kekeringan ekstrim masing-masing selama 12 sampai 14 minggu antara tahun 1997-1998. Riset ini berfokus pada perbandingan bagian sentral hutan Sungai Wain yang kering namun tidak terkakar, dengan hutan sekelilingnya yang satu kali mengalami kebakaran dengan intensitas rendah. Rancangan percobaan *posteriori* terdiri dari 9 permanen plot yang tidak terbakar dan 9 yang terbakar, masing-masing berukuran 60 x 300 m, membentang berpasangan di areal seluas 20 km². Plot-plot pada tiap pasangan terpisah satu sama lain oleh penghambat kebakaran buatan yang kecil.

Kekeringan dan kebakaran menyebabkan 29% dan 74% mortalitas pohon secara berurutan. Dalam hutan yang terbakar, 2/3 dari mortalitas disebabkan oleh kebakaran. Sebagian besar dari mortalitas yang tercatat terjadi di tahun kedua setelah gangguan. Setelah kekeringan, mortalitas pohon spesies-spesifik berukuran > 30 dbh berkorelasi negatif dengan kepadatan pepohonan kayu. Hal ini luar biasa, karena terjadinya spesies pepohonan berkayu-berat biasanya berkaitan dengan tidak adanya gangguan yang parah. Dengan dbh yang meningkat, pohon memiliki peluang yang lebih rendah dari kematian karena kebakaran,

karena kulit kayu yang lebih keras menyediakan insulasi yang lebih baik.

Pada hutan yang tidak dilindungi penghambat kebakaran, hanya 4 sampai 7% yang selamat dari kebakaran. Terbukanya kanopi pada hutan terbakar rata-rata 24%, sementara pada hutan tak terbakar 5%. Kepadatan tumbuhan pakis di hutan yang terbakar tinggi, dan secara negatif berkorelasi dengan kepadatan pohon muda atau anak pohon yang memerlukan sinar matahari, tetapi tidak dengan kepadatan batang-batang yang bertunas kembali dari spesies yang toleran terhadap keteduhan (toleran-teduh). Keragaman spesies pohon per wilayah yang bertahan dari kebakaran di atas tanah hanya 30% dari keragaman pada hutan tidak terbakar. Namun demikian, keragaman spesies per jumlah batang secara praktis sama pada hutan tidak terbakar dan hutan terbakar. Persistensi lokal dari spesies toleran-teduh terutama ditentukan oleh tingginya kepadatan batang yang bertunas kembali berukuran <10 cm dbh. Keragaman spesies per jumlah batang yang bertunas kembali di hutan yang terbakar serupa dengan keragaman per jumlah batang (>10 cm dbh) di hutan yang tidak terbakar.

Kapasitas tumbuh-tinggi dari pepohonan muda spesies-spesifik setelah gangguan parah diketahui dari percobaan dengan klipng individu pada ketinggian 1,30 m. Konsentrasi karbohidrat non-struktural total (tnc) berbeda secara nyata antara spesies, dan merupakan faktor penting dalam penentuan kapasitas tumbuh-tinggi. Pada tahap kedua dari perkembangan tumbuh tinggi, saat dedaunan pelaku fotosintesis sudah terbentuk, laju tumbuh-tinggi pepohonan muda dari spesies-spesies kayu-berat cenderung lebih rendah. Pola ini membantu memperkirakan pertumbuhan populasi spesies setelah gangguan.

Untuk menilai dampak kebakaran terhadap ketersediaan benih, kami membandingkan hutan yang terbakar dan tidak terbakar dengan mengumpulkan sampel tanah yang secara vertikal distratifikasi dalam empat lapisan tanah mineral masing-masing setebal 1,5 cm. Sinar matahari tampaknya merupakan

prasyarat untuk berkecambah bagi spesies-spesies berbiji sangat kecil (diameter <5 mm). Sebaliknya, *Macaranga* berbiji kecil (diameter >5 mm) berkecambah dalam kegelapan, dengan suhu harian yang berfluktuasi. Kemampuan berkecambah sebagai respon terhadap fluktuasi suhu, serta kemampuan etiolasi setelah berkecambah, menunjukkan bahwa biji *Macaranga* menunjukkan kemampuan untuk berhasil tumbuh dari kedalaman tanah yang lebih dalam. Dengan demikian, cadangan biji *Macaranga* di dalam tanah kurang peka terhadap kerusakan akibat kebakaran daripada spesies-spesies berbiji sangat kecil.

Baik ahli ekologi non-kebakaran maupun ahli ekologi kebakaran mengenali sejumlah besar keragaman pola dan proses yang berperan selama suksesi. Namun demikian, persistensi selama gangguan hanya memperoleh perhatian yang sedikit sekali dalam teori non-kebakaran sebagai faktor yang menentukan komposisi vegetasi paska-gangguan; padahal berperan penting dalam studi-studi suksesi setelah kebakaran. Asimilasi dari karakteristik persistensi ke dalam pendekatan tradisional akan meningkatkan aplikabilitas umum teori suksesi. Integrasi seperti ini akan menghasilkan pendekatan yang lebih kompleks, yang kemungkinan hanya dapat dianalisis oleh model-model simulasi komputer. Akan tetapi, korelasi yang diamati antara persistensi dan karakteristik tumbuhan lain menyatakan bahwa kompleksitas dalam pola suksesi tidak akan meningkat secara proporsional.

Persistensi lokal yang diamati dari spesies toleran-teduh setelah kebakaran tunggal memiliki implikasi penting untuk manajemen hutan-hutan yang terbakar. Sebagai hasil dari persistensi lokal, rekolonisasi spesies toleran-teduh tidak diperlukan, sehingga memungkinkan pemulihan hutan yang cepat. Tidak seperti kesimpulan yang cukup positif ini, pemeliharaan tutupan hutan dalam jangka panjang sangat tidak pasti setelah kebakaran terjadi. Mekanisme persistensi tidak cukup untuk memastikan daya tahan hidup lokal spesies toleran-teduh

segera setelah gangguan berulang, menyebabkan degradasi vegetasi yang sangat cepat. Potensi pemulihan yang diamati dalam penelitian kami secara serius terhambat apabila terjadi gangguan-gangguan tambahan yang disebabkan oleh pembalakan komersil terhadap pepohonan yang mati setelah kebakaran; atau apabila kebakaran berulang. Gangguan-gangguan semacam ini harus dihindarkan apabila tujuan jangka panjang adalah memelihara hutan

dan menjamin kelangsungan produktivitas konsesi kayu. Dari sudut pandang konservasi, hutan-hutan Kalimantan Timur yang terbakar membentuk substitusi yang amat kecil bagi hutan yang tidak terbakar. Namun demikian, keanekaragaman yang tinggi dari spesies-spesies yang tersisa, populasi spesies kayu yang bertahan hidup dengan potensi pemulihan yang jelas menjadikan hutan-hutan ini layak untuk secara aktif dilindungi.



Deforested area after prolonged cultivation, dominated by *Imperata cylindrica*. Area bordering Sungai Wain, November 1997.

References

- Ackerly, D.D. and M.J. Donoghue (1998) Leaf size, sapling allometry, and Corner's rules: Phylogeny and correlated evolution in Maples (*Acer*). *Am. Nat.* 152(6): 767-791.
- Adam, P. (1992) Australian rainforests. *Oxford biogeography series no. 6*. Pp. 308. Oxford University Press, New York, USA.
- Alder, D. and T.J. Synnott (1992) Permanent sample plot techniques for mixed tropical forest. *Tropical forestry paper 25*. Oxford Forestry Institute, University of Oxford, UK.
- Alexander, M.E. (1982) Calculating and interpreting forest fire intensities. *Can. J. Bot.* 60: 349-357.
- Alvarez-Buylla, E.R. and M. Martinez-Ramos (1990) Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia* 84: 314-325.
- Anshari, G., A.P. Kershaw and S. van der Kaars (2001) A Late Pleistocene and Holocene pollen and charcoal record from peat swamp forest, Lake Sentarum Wildlife Reserve, West Kalimantan, Indonesia. *Palaeo* 171(3-4): 213-228.
- Azuma, S. (1988) Distribution and abundance of primates after the forest fire in the lowland forest of East Kalimantan 1983-1986. Pp. 94-116. In: Tagawa, H. and N. Wirawan (eds.) *A research on the process of earlier recovery of tropical rain forest after a large scale fire in Kalimantan Timur, Indonesia, Occasional paper no. 14*, Research Center for the South Pacific, Japan.
- Bazzaz, F.A. (1996) *Plants in changing environments. Linking physiological, population and community ecology*. Pp. 320. Cambridge University Press, Cambridge, UK.
- Bazzaz, F.A. and S.T.A. Pickett (1980) Physiological ecology of tropical succession: A comparative review. *Ann. Rev. Ecol. Syst.* 11: 287-310.
- Bekker, R.M. et al. (1998) Seed size, shape and vertical distribution in the soil: indicators of longevity. *Funct. Ecol.* 12: 834-842.
- Bell, T.L. and F. Ojeda (1999) Underground starch storage in *Erica* species of the Cape floristic region – differences between seeders and resprouters. *New Phytol.* 144: 143-152.
- Bell, T.L., J.S. Pate and K.W. Dixon (1996) Relationships between fire response, morphology, root anatomy and starch distribution in South-west Australian Epacridaceae. *Ann. Bot.* 77: 357-364.
- Bellgard, S.E., R.J. Whelan and R.M. Muston (1994) The impact of wildfire on vesicular-arbuscular mycorrhizal fungi and their potential to influence the reestablishment of postfire plant-communities. *Mycorrhiza* 4(4): 139-146.
- Bellingham, P.J., E.J.V. Tanner and J.R. Healy (1994) Sprouting of trees in Jamaican montane forests, after a hurricane. *J. Ecol.* 82: 747-758.
- Berlage, H.P. (1949) Regenval in Indonesia. *Koninklijk Magnetisch en Meteorologisch Observatorium te Batavia. Verhandelingen no. 37*.
- Bodegom, S., P.B. Pelser and P.J.A. Keler (1999) Seedlings of secondary forest tree species of East Kalimantan, Indonesia. *Tropenbos-Kalimantan series 1*. Tropenbos Foundation, Wageningen, The Netherlands.
- Bond, W.J. and J.J. Midgley (2001) Ecology of sprouting in woody plants: the persistence niche. *TREE* 16(1): 45-51.
- Bond, W.J. and B.W. van Wilgen (1996) *Fire and plants*. Pp. 263. Chapman and Hall, London, UK.
- Borchert, R. (1994) Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75(5): 1437-1449.
- Bossuyt, B., M. Heyn and M. Hermy (2000) Concentrating samples estimates a larger seed bank density of a forest soil. *Funct. Ecol.* 14(6): 766.
- Bremen, H. van, M. Iriansyah and W. Andriess (1990) Detailed soil survey and physical land evaluation in a tropical rain forest, Indonesia. Pp.188. *Tropenbos technical series 6*. Stichting Tropenbos, Wageningen, The Netherlands.

- Brokaw, N.V.L. (1985) Treefalls, regrowth, and community structure in tropical forests. Pp. 53-69. In: Pickett, S.T.A. and P.S. White (eds.) *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, US.
- Burgess, P.F. (1966) Timber trees of Sabah. *Sabah forest record no. 6*. Forest department, Sabah, Malaysia.
- Burslem, D.F.R.P, T.C. Whitmore and G.C. Brown (2000) Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *J. Ecol.* 88: 1063-1078.
- Buschbacher, R., C. Uhl and E.A.S. Serrao (1988) Abandoned pastures in Eastern Amazonia. II. Nutrient stocks in the soil and vegetation. *J. Ecol.* 76: 682-699.
- Campbell, G.S., J.D. Jungbauer, K.L. Bristow and R.D. Hungerford (1995) Soil temperature and water content beneath a surface fire. *Soil Science* 159(6): 363-374.
- Canham, C.D., R.K. Kobe, E.F. Latty, and R.L. Chazdon (1999) Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots vs. carbohydrate reserves. *Oecologia* 121: 1-11.
- Cavender-Bares, J. and F.A. Bazzaz (2000) Changes in drought response strategies with ontogeny in *Quercus rubra*: Implications for scaling from seedlings to mature trees. *Oecologia* 124(1): 8-18.
- Chapin III, F.S., E.D. Schulze and H.A. Mooney (1990) The ecology and economics of storage in plants. *Annu. Rev. Ecol. Syst.* 21: 423-447.
- Cheke, A.S., W. Nanakorn and C. Yankoses (1979) Dormancy and dispersal of seeds of secondary forest species under the canopy of a primary tropical rain forest in Northern Thailand. *Biotropica* 11(2): 88-95.
- Chin, L.T. (1973) Occurrence of seeds in virgin forest topsoil with particular reference to secondary species in Sabah. *Malay. For.* 36(3).
- Christensen, N.L. (1985) Shrubland fire regimes and their evolutionary consequences. Pp. 86-100. In: Pickett, S.T.A. and P.S. White (eds.) *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Florida, USA.
- Clark, D.A. and D.B. Clark (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecol. Monogr.* 62(3): 315-344.
- Clark, D.B. and D.A. Clark (1991) The impact of physical damage on canopy tree regeneration in tropical rain forest. *J. Ecol.* 79: 447-457.
- Clark, D.B. and D.A. Clark (1996) Abundance, growth and mortality of very large trees in neotropical lowland rain forest. *For. Ecol. Manage.* 80: 1-3.
- Clark, J.S. (1996) Testing disturbance theory with long-term data: alternative life-history solutions to the distribution of events. *Am. Nat.* 148(6): 976-996.
- Clements, F.E. (1904) The development and structure of vegetation. *Botanical Survey of Nebraska* 7. Studies in the vegetation of the state, Lincoln, Nebraska, USA.
- Clements, F.E. (1916) *Plant succession*. Carnegie Institute Washington Publication 242, Washington, D.C., USA.
- Cochrane, M.A. (2001) Synergetic interactions between habitat fragmentation and fire in evergreen tropical forests. *Cons. Biol.* 15(6): 1515-1521.
- Cochrane, M.A. and M.D. Schulze (1998) Forest fires in the Brazilian Amazon. *Cons. Biol.* 12(5): 948-950.
- Cochrane, M.A. and M.D. Schulze (1999) Fire as a recurrent event in tropical forests of the Eastern Amazon: Effects on forest structure, biomass, and species composition. *Biotropica* 31(1): 2-16.
- Cochrane, M.A. et al. (1999) Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* 284: 1832-1835.
- Cody, M.L. (1973) Character Convergence. *Ann. Rev. Ecol. Syst.* 4: 189-211.
- Condit, R., S.P. Hubbell and R.B. Foster (1995) Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecol. Monogr.* 65(4): 419-439.
- Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.

- Connell, J.H. and R.O. Slatyer (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111: 1119-1144.
- Corner, E.J.H. (1949) The durian theory or the origin of the modern tree. *Ann. Bot.* 13: 317.
- Crawley, M.J. (1992) Seed predators and plant population dynamics. Pp. 157-192. In: Fenner, M. (ed.) *Seeds. The ecology of regeneration in plant communities*. C.A.B. International, Willington, UK.
- Curran, L.M. and M. Leighton (2000) Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* 70(1): 101-128.
- Dalling J.W. and J.S. Denslow (1998) Soil seed bank composition along a forest chronosequence in seasonally moist tropical forest, Panama. *J. Veg. Sci.* 9(5): 669-678.
- Dalling J.W., M.D. Swaine and N.C. Garwood (1994) Effect of soil depth on seedling emergence in tropical soil seed bank investigations. *Funct. Ecol.* 9: 119-122.
- Dalling, J.W., M.D. Swaine and N.C. Garwood (1997 a) Soil seed bank community dynamics in seasonally moist lowland tropical forest, Panama. *J. Trop. Ecol.* 13: 659-680.
- Dalling, J.W., M.D. Swaine and N.C. Garwood and K.E. Harms and R. Aizprua (1997 b) Seed damage tolerance and seedling resprouting ability of *Prioria copaifera* in Panama. *J. Trop. Ecol.* 13: 481-490.
- Dalling, J.W., S.P. Hubbell and K. Silveira (1998) Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *J. Ecol.* 86(4): 674-689.
- Dam, R.A.C., J. Fluin, P. Suparan and S. van der Kaars (2001 a) Palaeoenvironmental developments in the Lake Tondano area (N. Sulawesi, Indonesia) since 33,000 yr B.P. *Palaeo* 171(3-4): 147-183.
- Dam, R.A.C., S. van der Kaars and A.P. Kershaw (2001 b) Quaternary environmental change in the Indonesian region. *Palaeo* 171(3-4): 91-95.
- Davies S.J. and P.S. Ashton (1999) Phenology and fecundity in 11 sympatric pioneer species of *Macaranga* (Euphorbiaceae) in Borneo. *Am. J. Bot.* 86(12): 1786-1795.
- Dawkins, H.C. and D.R. Field (1978) A long-term surveillance system for British woodland vegetation. *Occasional papers no. 1*, Oxford University, Oxford.
- den Ouden, J. (2000) *The role of bracken (Pteridium aquilinum) in forest dynamics*. Ph.D. thesis, Wageningen University, Wageningen, The Netherlands. Pp. 218.
- Denslow, J.S. (1980) Gap partitioning among tropical rain forest trees. *Biotropica* 12: 47-55.
- Directorate of Forest Utilization (1999) Penyempurnaan surat edaran direktur jenderal pengusahaan hutan produksi nomor 259/IV-BPH/1999 tentang tebang penyelamatan di areal HPH bekas kebakaran. Departemen Kehutanan dan Perkebunan, Direktorat Jenderal Pengusahaan Hutan Produksi Republik Indonesia. Jakarta, Indonesia.
- Doi, T. (1988) Present status of the large mammals in the Kutai national park, after a large scale fire in East Kalimantan, Indonesia. Pp. 82-93. In: Tagawa, H. and N. Wirawan (eds.) *A research on the process of earlier recovery of tropical rain forest after a large scale fire in Kalimantan Timur, Indonesia*, Occasional paper no. 14, Research Center for the South Pacific, Japan.
- Douglas, I. (1999) Hydrological investigations of forest disturbance and land cover impacts in South-East Asia: a review. *Phil. Trans. R. Soc. Lond. B* 354(1391): 1725-1738.
- Eberhardt, L.L. and J.M. Thomas (1991) Designing environmental field studies. *Ecol. Monogr.* 61(1): 53-73.
- Egler, F.E. (1954) Vegetation science concepts, I. Initial floristic composition - a factor in old-field vegetation development. *Vegetatio* 4: 412-417.
- Everham, E.M. and N.V.L. Brokaw (1996) Forest damage and recovery from catastrophic wind. *Bot. Rev.* 62: 113-185.
- Ewel, J., C. Berish, B. Brown, N. Price and J. Raich (1981) Slash and burn impacts on a Costa Rican wet forest site. *Ecology* 62: 816-829.
- FAO/Unesco/ISRIC (1988) *Revised legend of the FAO/Unesco soil map of the world*. FAO, Rome, Italy.

- Fenner, M. (1985) *Seed ecology*. Chapman and Hall, London, UK.
- Finegan, B. (1984) Forest succession. *Nature* 312: 109-114.
- Finegan, B. (1996) Pattern and process in neotropical secondary rain forest: the first 100 years of succession. *TREE* 11(3): 119-124.
- Fletcher, W.W. and R.C. Kirkwood (1979) The bracken fern (*Pteridium aquilinum* L. (Kuhn); its biology and control. Pp. 591-635. In: Dyer, A.F. (ed.) *The experimental biology of ferns*. Academic press, London, UK.
- Foster, S.A. (1986) On the adaptive value of large seeds for tropical moist forest trees: review and synthesis. *Bot. Rev.* 52: 260-299.
- Fredriksson, G.M. and M. de Kam (1999) *Strategic plan for the conservation of the Sungai Wain protection forest, East Kalimantan*. Pp.38. The International MOFEC – Tropenbos Kalimantan project, Wanariset Samboja. Balikpapan, Indonesia.
- Garwood, N.C. (1989) Tropical soil seed banks: a review. Pp. 149-209. In: Leck, M.A., V.T. Parker and R.L. Simpson (eds.) *Ecology of soil seed banks*. Academic Press. San Diego, California, USA.
- Gentry, A.H. and J. Terborgh (1990) Composition and dynamics of the Cocha Cashu "mature" floodplain forest. Pp. 542-572. In: Gentry, A.H. (ed.) *Four neotropical rainforests*. Yale University Press, New Haven, CT, USA.
- Gill, A.M. and D.H. Ashton (1968) The role of bark type in relative tolerance to fire of three central victorian eucalypts. *Aust. J. Bot.* 16: 491-498.
- Gillison, A.N. (1983) Tropical savannas of Australia and the Southwest Pacific. Pp. 183-243. In: Bourlière, F. (ed.) *Tropical savannas- Ecosystems of the world. Vol. 13*. Elsevier. Amsterdam, Netherlands.
- Gitay, H. I.R. Noble and J.H. Connell (1999) Deriving functional types for rain-forest trees. *J. Veg. Sci.* 10: 641-650.
- Glenn-Lewin, D.C. and E. van der Maarel (1992) Patterns and processes of vegetation dynamics. Pp. 11-59. In: Glenn-Lewin, D.C., R.K. Peet and T.T. Veblen (eds.) *Plant succession. Theory and prediction*. Pp.352. Chapman and Hall, London, UK.
- Glenn-Lewin, D.C., R.K. Peet and T.T. Veblen (eds.) (1992) *Plant succession. Theory and prediction*. Pp.352. Chapman and Hall, London, UK
- Goldammer, J.G. and B. Seibert (1989) Natural rain forest fires in eastern Borneo during the Pleistocene and Holocene. *Naturwissenschaften* 76(11): 518-520.
- Gómez-Pompa, A. and C. Vásquez-Yanes (1981) Successional studies of a rain forest in Mexico. Pp. 246-266. In: West, D.C., H.H. Shugart and D.B. Botkin (eds.) *Forest succession: Concepts and application*. Springer-Verlag, New York, USA.
- Grime, J.P. (1979) *Plant strategies and vegetation processes*. Pp. 222. John Wiley & Sons, Chichester, UK.
- Grime, J.P. and D.W. Jeffrey (1965) Seedling establishment in vertical gradients of sunlight. *J. Ecol.* 53: 621-642.
- Grubb, P.J. (1977) The maintenance of species-richness in plant communities: The importance of the regeneration niche. *Biol. Rev.* 52: 107-145.
- Guariguata, M.R. (1998) Response of forest tree saplings to experimental mechanical damage in lowland Panama. *For. Ecol. Manage.* 102: 103-111.
- Hacke, U.G., J.S. Sperry, W.T. Pockman, S.D. Davis and K.A. McCulloh (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126: 457-461.
- Hanes, T.L. (1971) Succession after fire in the chaparral of Southern California. *Ecol. Monogr.* 35: 213-235.
- Hartshorn, G.S. (1990) An overview of neotropical forest dynamics. Pp. 585-599. In: Gentry, A.H. (ed.) *Four neotropical rainforests*. Yale University Press, New Haven, CT, USA.
- Haskins, F.A. and H.J. Gorz (1975) Influence of plant size, planting depth, and companion crop on emergence and vigor of seedlings in sweetclover. *Agronomy J.* 67: 652-654.

- Hoffmann, A.A., A. Hinrichs, and F. Siegert (1999) Fire damage in East Kalimantan in 1997/98 related to land use and vegetation classes: satellite radar inventory results and proposal for further actions. *Integrated Forest Fire Management Project and Sustainable Forest Management Project. Report 1*. Samarinda, Indonesia.
- Holdsworth, A.R. and C. Uhl (1997) Fire in amazonian selectively logged rain forest and the potential for fire reduction. *Ecol. Appl.* 7(2): 713-725.
- Hope, G. (2001) Environmental change in the Late Pleistocene and later Holocene at Wanda site, Soroako, South Sulawesi, Indonesia. *Palaeo* 171(3-4): 129-145.
- Hopkins, B. (1992) Ecological processes at the forest-savanna boundary. Pp. 21-33. In: Furley, P.A., J. Proctor & J.A. Ratter (eds.) *Nature and dynamics of forest-savanna boundaries*. Chapman & Hall, London, UK.
- Hopkins, M.S. (1981) Disturbance and change in rainforests and the resulting problems of functional classification. Pp. 42-52. In: Gillison, A.N. and D.J. Anderson (eds.) *Vegetation classification in Australia*. CSIRO/ANU press, Canberra, Australia.
- Hopkins, M.S. and A.W. Graham (1983) The species composition of soil seed banks beneath lowland tropical rainforests in North Queensland, Australia. *Biotropica* 15(2): 90-99.
- Hopkins, M.S. and A.W. Graham (1984) The role of soil seed banks in regeneration in canopy gaps in Australian tropical lowland rainforest – Preliminary field experiments. *Malay. For.* 47(2): 146-158.
- Horn, H.H. (1976) Succession. Pp. 187-204. In: May, R.M. (ed.) *Theoretical ecology: Principles and applications*. Blackwell, Oxford.
- Howe, H.F., and J. Smallwood (1982) Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201-228.
- Hubbell, S.P. (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203: 1299-1309.
- Hubbell, S.P. (1980) Seed predation and the coexistence of tree species in tropical forests. *Oikos* 35: 214-229.
- Hubbell, S.P. (1998) The maintenance of diversity in a neotropical tree community: conceptual issues, current evidence, and challenges ahead. Pp. 17-44. In: Dallmeier, F. & J.A. Comiskey (eds.) *Forest biodiversity, research, monitoring and modelling. Conceptual background and old world case studies. UNESCO Man and the biosphere series. Volume 20*. Parthenon publishing group inc., USA.
- Hubbell, S.P. and R.B. Foster (1986 a) Biology, chance, and history and the structure of tropical rain forest tree communities. Pp. 314-329. In: Diamond, J. and T.J. Case (eds.) *Community ecology*. Harper and Row, New York, USA.
- Hubbell, S.P. and R.B. Foster (1986 b) Canopy gaps and the dynamics of a Neotropical forest. Pp. 77-96. In: Crawley, M.J. (ed.) *Plant Biology*. Blackwell Scientific Publications, London, UK.
- Hubbell, S.P. and R.B. Foster (1990) Structure, dynamics, and equilibrium status of old-growth forest on Barro Colorado Island. Pp. 522-541. In: Gentry, A.H. (ed.) *Four neotropical rainforests*. Yale University Press, New Haven, CT, USA.
- Hubbell, S.P. et al. (1990) Presence and absence of density-dependence in a neotropical tree community. *Phil. Trans. Roy. Soc. Lond.* B330: 269-281.
- Humphrey, J. and M.D. Swaine (1997) Factors affecting the natural regeneration of *Quercus* in Scottish oakwoods. I. Competition from *Pteridium aquilinum*. *J. Appl. Ecol.* 34: 577-584.
- Huston, M. (1979) A general hypothesis of species diversity. *Am. Nat.* 113: 81-101.
- Huston, M.A. (1994) *Biological diversity. The coexistence of species on changing landscapes*. Pp. 681. Cambridge University Press, Cambridge, New York, USA.
- Huston, M. and T. Smith (1987) Plant succession: Life history and competition. *Am. Nat.* 130(2): 168-198.
- Iwasa, Y. (2000) Dynamic optimization of plant growth. *Evol. Ecol. Res.* 2: 437-455.
- Iwasa, Y. and T. Kubo (1997) Optimal size of storage for recovery after unpredictable disturbances. *Evol. Ecol.* 11: 41-65.

- Janzen, D.H. (1974) Tropical blackwater rivers, animals, and mast-fruiting by the Dipterocarpaceae. *Biotropica* 6: 69-103.
- Jobidon, R. (1997) Stump height effects on sprouting of Mountain Maple, Paper Birch and Pin Cherry - 10 year results. *Forestry Chronicle* 73(5): 590-595.
- Jongeman, R.H.G., C.J.F. ter Braak and O.F.R. van Tongeren (1995) *Data analysis in community and landscape ecology*. (2nd edition). Pp. 299. Cambridge University Press, Cambridge, UK.
- Kammesheidt, L. (1998) The role of tree sprouts in the restoration of stand structure and species diversity in tropical moist forest after slash-and-burn agriculture in Eastern Paraguay. *Plant Ecol.* 139(2): 155-165.
- Kammesheidt, L. (1999) Forest recovery by root suckers and above-ground sprouts after slash-and-burn agriculture, fire and logging in Paraguay and Venezuela. *J. Trop. Ecol.* 15: 143-157.
- Kartawinata, K. (1993) A wider view of the fire hazard. Pp. 261-266. In: Brookfield, H. and Y. Byron (eds.) *South-east Asia's environmental future: The search for sustainability*. United Nations University Press, Tokyo, Japan.
- Kauffman, J.B. (1991) Survival by sprouting following fire in tropical forests of the eastern Amazon. *Biotropica* 23(3): 219-224.
- Kennard, D.K. and H.L. Gholz (2001) Effects of high- and low-intensity fires on soil properties and plant growth in a Bolivian dry forest. *Plant Soil* 234(1): 119-129.
- Ketterings, Q.M. and J.M. Bigham (2000) Soil color as an indicator of slash-and-burn fire severity and soil fertility in Sumatra, Indonesia. *Soil Sci. Soc. Am.* 64(5): 1826-1833.
- Ketterings, Q.M., J.M. Bigham and V. Laperche (2000) Changes in soil mineralogy and texture caused by slash-and-burn fires in Sumatra, Indonesia. *Soil Sci. Soc. Am.* 64(3): 1108-1117.
- King, D.A. (1990) Allometry of saplings and understorey trees of a panamanian forest. *Funct. Ecol.* 4: 27-32.
- Kinnaird, M.F. and T.G. O'Brien (1998) Ecological effects of wildfire on lowland rainforest in Sumatra. *Cons. Biol.* 12(5): 954-956.
- Klugmann, K. and A. Roloff (1999) Twig abscission (cladoptosis) and its ecophysiological significance for decline symptoms in *Quercus robur* L. *Forstwissenschaftliches Centralblatt* 118(4): 271-286.
- Kobayashi, S., M. Sutisna, A. Delmy and T. Toma (1999) Initial phase of secondary succession at the burnt logged-over forest in Bukit Soeharto, East Kalimantan, Indonesia - Which vegetation types are facilitation or competition process? Pp. 324-335. In: Suhartoyo, H. and T. Toma (eds.) *Pusrebut special publication 8. Proceedings of the 3rd international symposium on Asia tropical forest management*. Tropical Forest Research Center Mulawarman University & JICA, Samarinda, Indonesia.
- Kohyama, T. and M. Hotta (1990) Significance of allometry in tropical saplings. *Funct. Ecol.* 4: 515-521.
- Leighton, M. (1984) *The El Niño-Southern Oscillation event in Southeast Asia: Effects of drought and fire in tropical forest in eastern Borneo*. WWF report.
- Leighton, M. and N. Wirawan (1986) Catastrophic drought and fire in Borneo tropical rain forest associated with the 1982-1983 El Niño Southern Oscillation event. Pp. 75-102. In: G.T. Prance (ed.) *Tropical rain forest and the world atmosphere, AAAS Selected Symposium 101*. Washington DC: Amer. Assoc. for the Advancem. of Sc., USA.
- Lennertz, R. and K.F. Panzer (1984) *Preliminary assessment of the drought and forest fire damage in Kalimantan Timur*. Report by DFS German Forest Inventory Service for Gesellschaft für Technische Zusammenarbeit (GTZ). Pp. 45 + annexes. Germany.
- Lieberman, D. and M. Lieberman (1987) Forest tree growth and dynamics at La Selva, Costa Rica (1969-1982). *J. Trop. Ecol.* 3: 347-358.
- Loehle, C. (2000) Strategy space and the disturbance spectrum: a life history model for tree species coexistence. *Am. Nat.* 156(1): 14-33.

- Louda, S. (1989) Predation in the dynamics of seed regeneration. Pp. 25-52. In: Leck, M.A., V.T. Parker and R.L. Simpson (eds.) *Ecology of soil seed banks*. Academic press. San Diego, California, USA.
- Lucas, P.W., H.T.W. Tan and P.Y. Cheng (1997) The toughness of secondary cell wall and woody tissue. *Phil. Trans. Roy. Soc. Lond. Series B*. 352(1351): 341-352.
- MacKinnon, K., G. Hatta, H. Halim and A. Mangalik (1996) *The ecology of Kalimantan. The ecology of Indonesia series*. Vol. 3. Pp. 802. Periplus editions, Singapore.
- MacMahon, J.A. (1981) Successional processes: Comparisons among biomes with special reference to probable roles of and influences on animals. Pp. 275-304. In: West, D.C., H.H. Shugart and D.B. Botkin (eds.) *Forest succession. Concepts and application*. Pp. 517. Springer-Verlag, NY, USA.
- Makihara, H., H. Kinuura, K. Yahiro and C. Soeyamto (2001) The effects of droughts and fires on Colepteran insects in lowland dipterocarp forests in Bukit Soeharto, East Kalimantan. Pp. 153-166. In: Guhardja, E. et al. (eds.) *Rainforest ecosystems of East Kalimantan. El Niño, drought, fire and human impacts*. Springer, Tokyo, Japan.
- Malanson, G.P. (1984) Intensity as a third factor of disturbance regime and its effect on species diversity. *Oikos* (43): 411-413.
- Manokaran, N. and K.M. Kochummen (1987) Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. *J. Trop. Ecol.* 3: 315-330.
- Martin, R.E. and C.T. Cushwa (1966) Effects of heat and moisture on leguminous seed. *Proceedings of the tall timbers fire ecology conference* 5: 159-175.
- Matius, P., T. Toma and M. Sutisna (2001) Tree species composition of a burned lowland dipterocarp forest in Bukit Soeharto, East Kalimantan. Pp. 99-104. In: Guhardja, E. et al. (eds.) *Rainforest ecosystems of East Kalimantan. El Niño, drought, fire and human impacts*. Springer, Tokyo, Japan.
- Metcalfe, D.J. and P.J. Grubb (1995) Seed weights and light requirements for regeneration in South-east Asian rain forest. *Can. J. Bot.* 73: 817-826.
- Metcalfe D.J., P.J. Grubb and I.M. Turner (1998) The ecology of very small-seeded shade-tolerant trees and shrubs in lowland rain forest in Singapore. *Plant Ecol.* 134(2): 131-149.
- Metcalfe, D.J. and I.M. Turner (1998) Soil seed bank from lowland rain forest in Singapore: Canopy-gap and litter-gap demanders. *J. Trop. Ecol.* 14: 103-108.
- Miller, T.E. (1982) Community diversity and interactions between the size and frequency of disturbance. *Am. Nat.* 120: 533-536.
- Miyagi, Y., H. Tagawa, E. Suzuki, N. Wirawan and N. Oka (1988) Phytosociological study of the vegetation of Kutai national park, East Kalimantan, Indonesia. Pp. 51-62. In: Tagawa, H. and N. Wirawan (eds.) *A research on the process of earlier recovery of tropical rain forest after a large scale fire in Kalimantan Timur, Indonesia. Occasional papers no. 14*. Pp. 136. Kagoshima Univ. Research Center for the South Pacific, Japan.
- Molofsky, J. and C.K. Augspurger (1992) The effect of litter on early seedling establishment in a tropical forest. *Ecology* 73: 68-77.
- Moreno, J.M. and W.C. Oechel (1989) A simple method for estimating fire intensity after a burn in California chaparral. *Acta Oecol.* 10(1): 57-68.
- Mori, T. (2001) Effects of droughts and forest fires on dipterocarp forest in East Kalimantan. Pp. 29-48. In: Guhardja, E. et al. (eds.) *Rainforest ecosystems of East Kalimantan. El Niño, drought, fire and human impacts*. Springer, Tokyo, Japan.
- Nakagawa, M. et al. (2000) Impact of severe drought associated with the 1997-1998 El Niño in a tropical forest in Sarawak. *J. Trop. Ecol.* 16: 355-367.
- Negreiros-Castillo, P. and R.B. Hall (2000) Sprouting capability of 17 tropical tree species after overstory removal in Quintana Roo, Mexico. *For. Ecol. Manage.* 126: 399-403.
- Ng, F.S.P. (1991) Manual of forest fruits, seeds and seedlings (2 vol.). Vol 1: Pp. 1-400. Vol. 2: Pp. 401-997. *Malayan forest records 34*. Forest Research Institute Malaysia. Kepong, Malaysia.
- Niklas, K.J. (1992) *Plant biomechanics*. University of Chicago Press, Chicago, USA.

- Noble, I.R. and R.O. Slatyer (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43: 5-21.
- Nykvist, N. (1996) Regrowth of secondary vegetation after the "Borneo fire" of 1982-1983. *J. Trop. Ecol.* 12: 307-312.
- Pacala, S.W., C.D. Canham, J. Saponara, J.A. Silander, R.K. Kobe and E. Ribbens (1996) Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecol. Monogr.* 66(1): 1-43.
- Paciorek, C.J., R. Condit, S.P. Hubbell and R.B. Foster (2000) The demographics of resprouting in tree and shrub species of a moist tropical forest. *J. Ecol.* 88(5): 765-777.
- Pate, J.S., R.H. Froend, B.J. Bowen, A. Hansen and J. Kuo (1990) Seedling growth and storage characteristics of seeder and resprouter species of Mediterranean-type ecosystems of S.W. Australia. *Ann. Bot.* 65: 585-601.
- Pedersen, B.S. (1998) The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. *Ecology* 79(1): 79-93.
- Peña-Claros, M. (2001) Secondary forest succession. Processes affecting the regeneration of Bolivian tree species. Pp. 170. Ph.D. Thesis. *Promab scientific series 3*. Riberalta, Bolivia.
- Pianka, E.R. (1970) On r- and K-selection. *Am. Nat.* 104: 592-597.
- Pickett, S.T.A., S.L. Collins and J.J. Armesto (1987) Models, mechanisms and pathways of succession. *Bot. Rev.* 53: 335-371.
- Pinard, M.A. and J. Huffman (1997) Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *J. Trop. Ecol.* 13: 727-740.
- Pinard, M.A. and F.E. Putz and J.C. Licona (1999) Tree mortality and vine proliferation following a wildfire in a subhumid tropical forest in eastern Bolivia. *For. Ecol. Manage.* 116: 247-252.
- Pons, T. (1992) Seed responses to light. Pp. 259-284. In: Fenner, M. (ed.) *Seeds. The ecology of regeneration in plant communities*. C.A.B. International, Willington, UK.
- Pons, T.L. (2000) Seed responses to light. Pp. 237-260. In: Fenner, M. (ed.) *Seeds. The ecology of regeneration in plant communities*. Second edition. CABI Publishing, Wallingford, UK.
- Priadjati, A. (1999) The impacts of forest fires on seedlings and saplings structure in Sungai Wain protection forest, East Kalimantan, Indonesia. Pp. 310-319. In: Suhartoyo, H. and T. Toma (eds.) *Impacts of fire and human activities on forest ecosystems in the tropics. Proceedings of the 3rd international symposium on Asia tropical forest management. Pusrehut special publication 8*. Tropical Forest Research Center Mulawarman University & JICA, Samarinda, Indonesia.
- Probert, R.J. (1992) The role of temperature in germination ecophysiology. Pp. 285-325. In: Fenner, M. (ed.) *Seeds. The ecology of regeneration in plant communities*. C.A.B. International, Willington, UK.
- Probert, R.J. (2000) The role of temperature in the regulation of seed dormancy and germination. Pp. 261-292. In: Fenner, M. (ed.) *Seeds. The ecology of regeneration in plant communities*. Second edition. CABI Publishing, Wallingford, UK.
- Putz, F.E. and N.V.L. Brokaw (1989) Sprouting of broken trees on Barro Colorado Island, Panama. *Ecology* 70(2): 508-512.
- Raich J.W. and W.K. Gong (1990) Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. *J. Trop. Ecol.* 6: 203-217.
- Rankin-de-Merona, J.M., R.W. Hutchins and T.E. Lovejoy (1990) Tree mortality and recruitment over a five-year period in undisturbed upland rain forest of the Central Amazon. Pp. 573-584. In: Gentry, A.H. (ed.) *Four neotropical rainforests*. Yale University Press, New Haven, CT. USA.
- Richards, P.W. (1996) *The tropical rain forest*. Second edition. Pp. 575. University Press, Cambridge, UK.
- Rijks M.H., E.J. Malta and R.J. Zagt (1998) Regeneration through sprout formation in *Chlorocardium rodiei* (Lauraceae) in Guyana. *J. Trop. Ecol.* 14(4): 463-475.
- Riswan, S. and K. Kartawinata (1988) A lowland dipterocarp forest 35 years after pepper plantation in East Kalimantan, Indonesia. Pp. 1-40. In: Soemodihardjo, S. (ed.) *Some ecological aspects*

- of tropical forest of East Kalimantan: A collection of research reports.* MAB Indonesia Contribution no. 48, Jakarta: Man and the Biosphere Programme.
- Riswan, S. and K. Kartawinata (1989) Regeneration after disturbance in a lowland mixed dipterocarp forest in East Kalimantan, Indonesia. *Ekologi Indonesia* 1: 9-28.
- Riswan, S. and K. Kartawinata (1991 a) Regeneration after disturbance in a lowland mixed dipterocarp forest in East Kalimantan, Indonesia. Pp. 295-301. In: Gomez-Pompa, A., T.C. Whitmore & M. Hadley (eds.) *Rain forest regeneration and management.* Man and the biosphere series.
- Riswan, S. and K. Kartawinata (1991 b) Species strategy in early stage of secondary succession associated with soil properties status in a lowland mixed dipterocarp forest and kerangas forest in East Kalimantan. *Tropics* 1: 13-34.
- Riswan, S. and R. Yusuf (1986) Effects of forest fires on trees in the lowland dipterocarp forest of East Kalimantan, Indonesia. Pp. 155-163. In: *Proc. of the Symp. on Forest Regeneration in South-east Asia, Bogor, Indonesia, 9-11 May 1984. BIOTROP spec. publ. no. 25.* Bogor, Indonesia.
- Riswan, S. et al. (1985) The estimation of temporal processes in tropical rain forest: a study of primary mixed dipterocarp forest in Indonesia. *J. Trop. Ecol.* 1: 171-182.
- Roberts, E.H. (1972) Storage environment and the control of viability. In: Roberts, E.H. (ed.) *Viability of seeds.* pp. 15-57. Chapman and Hall, London, UK.
- Roberts, E.H. and F.H. Abdalla (1968) The influence of temperature, moisture, and oxygen on period of seed viability in Barley, Broad beans, and Peas. *Ann. Bot.* 32: 97-117.
- Ropelewski, C.F. and M.S. Halpert (1996) Quantifying Southern Oscillation - precipitation relationships. *J. Climate* 9: 1043-1059.
- Rose, S.A. (2000) *Seeds, seedlings and gaps - size matters. A study in the tropical rain forest of Guyana.* Pp. 175. Ph.D. thesis, Tropenbos Guyana Programme, Georgetown, Guyana.
- Rosenberg, N.J. (1974) *Microclimate: The biological environment.* Pp. 315. J. Wiley and sons, New York, USA.
- Runkle, J.R. (1985) Disturbance regimes in temperate forests. Pp. 17-34. In: Pickett, S.T.A. and P.S. White (eds.) *The ecology of natural disturbance and patch dynamics.* Academic Press, Orlando, Florida, USA.
- Saldarriaga, J.G. and D.C. West (1986) Holocene fires in the northern Amazon basin. *Quat. Res.* 26: 358-366.
- Saulei, S.M. and M.D. Swaine (1988) Rain forest seed dynamics during succession at Gogol, Papua New Guinea. *J. Ecol.* 76: 1133-1152.
- Sawyer, R. and E.J. Dixon (1968) The automatic determination of original gravity of beer. Part I. Introduction and determination of reducing sugar after hydrolysis. *Analyst* 93: 669-679.
- Schier, G.A. and J.C. Zasada (1973) Role of carbohydrate reserves in the development of root suckers in *Populus tremuloides*. *Can. J. For. Res.* 3: 243-250.
- Sheil, D. (1995) A critique of permanent plot methods and analysis with examples from Budongo forest, Uganda. *For. Ecol. Manage.* 77: 11-34.
- Sheil, D. (1999) Tropical forest diversity, environmental change and species augmentation: After the intermediate disturbance hypothesis. *J. Veg. Sci.* 10: 851-860.
- Sheil, D., D.F.R.P. Burslem and D. Alder (1995) The interpretation and misinterpretation of mortality rate measures. *J. Ecol.* 83: 331-333.
- Shimokawa, E. (1988) Effect of fire of a tropical rain forest on soil erosion. Pp. 2-11. In: Tagawa, H. and N. Wirawan (eds.) *A research on the process of earlier recovery of tropical rain forest after a large scale fire in Kalimantan Timur, Indonesia, Occasional paper no. 14,* Research Center for the South Pacific, Japan.
- Sidiyasa, K. Arbainsyah and P.J.A. Kessler (1999) *List of collections stored at the Wanariset herbarium, East Kalimantan, Indonesia.* The International MOFEC-Tropenbos Kalimantan project, Samboja, Indonesia. Pp. 252.
- Siegert, F., G. Ruecker, A. Hinrichs and A.A. Hoffmann (2001) Increased damage from fires in logged forests during droughts caused by el Niño. *Nature* 414: 437-440.

- Slik, J.W.F., P.J.A. Kessler and P.C. van Welzen (2001) *Macaranga* and *Mallotus* species (Euphorbiaceae) as indicators for disturbance in the mixed lowland dipterocarp forest of East Kalimantan (Indonesia). Pp. 21-36. In: J.W.F. Slik. *Macaranga* and *Mallotus* (Euphorbiaceae) as indicators for disturbance in the lowland dipterocarp forests of East Kalimantan, Indonesia. Ph.D. thesis. *Tropenbos-Kalimantan series 4*. Balikpapan, Indonesia.
- Sokal, R.R. and F.J. Rohlf (1981) *Biometry*. 2nd edition. Pp.859. Freeman and Company, New York, USA.
- Sousa, W.P. (1985) Disturbance and patch dynamics on rocky intertidal shores. Pp. 101-124. In: Pickett, S.T.A. and P.S. White (eds.) *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Florida, USA.
- Steiniger, M.K. (2000) Secondary forest structure and biomass following short and extended land-use in central and southern Amazonia. *J. Trop. Ecol.* 16(5): 689-708.
- Stocker, G.C. (1981) Regeneration of a North Queensland rain forest following felling and burning. *Biotropica* 13(2): 86-92.
- Suparan, P., R.A.C. Dam, S. van der Kaars and T.E. Wong (2001) Late Quaternary tropical lowland environments on Halmahera, Indonesia. *Palaeo* 171(3-4): 229-258.
- Suzuki, E. (1988) The socio-ecological study of Orangutans and the forest conditions after the big forest fires and drought, 1983, in Kutai national park, Indonesia. Pp. 117-136. In: Tagawa, H. and N. Wirawan (eds.) *A research on the process of earlier recovery of tropical rain forest after a large scale fire in Kalimantan Timur, Indonesia, Occasional paper no. 14*, Research Center for the South Pacific, Japan.
- Suzuki, E. (1999) Diversity in specific gravity and water content of wood among Bornean tropical rainforest trees. *Ecol. Res.* 14(3): 211-224.
- Swaine, M.D., V.K. Agyeman, B. Kyereh et al. (1997) Ecology of forest trees in Ghana. Overseas Development Agency. *Forestry series 7*. UK.
- Swaine, M.D. and T.C. Whitmore (1988) On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81-86.
- Symington, C.F. (1933) The study of secondary growth on rain forest sites in Malaya. *Malay. For.* 2: 107-117.
- Tanner, E.J.V., V. Kapos and J.R.H. Healey (1991) Hurricane effects on forest ecosystems in the Caribbean. *Biotropica* 23: 513-521.
- ter Steege, H. (1996) Winphot 5.0: A programme to analyze vegetation indices, light and light quality from hemispherical photographs. *Tropenbos Guyana report 95-2*. Tropenbos Guyana Programme, Georgetown, Guyana.
- ter Steege, H. and D.S. Hammond (2001) Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology* 82(11): 3197-3212.
- TerHeerdt G.N.J., G.L. Verweij, R.M. Bekker and J.P. Bakker (1996) An improved method for seed-bank analysis: Seedling emergence after removing the soil by sieving. *Funct. Ecol.* 10(1): 144-151.
- Thomas, S.C. (1996) Relative size at onset of maturity in rain forest trees: A comparative analysis of 37 Malaysian species. *Oikos* 76(1): 145-154.
- Tilman, D. (1982) *Resource competition and community structure*. Princeton University Press, Princeton, N.J., USA.
- Tilman, D. (1988) *Plant strategies and the dynamics and structure of plant communities*. Pp. 360. Princeton University Press, Princeton, N.J., USA.
- Tolhurst, K.G. and N.D. Turvey (1992) Effects of bracken (*Pteridium esculentum* (Forst. f. Cockayne)) on eucalypt regeneration in west-central Victoria. *For. Ecol. Manage.* 54: 45-67.
- Toma, T. (1999) Effects of selective logging and forest fire on microclimate of lowland dipterocarp forest in Bukit Soeharto, East Kalimantan. *Proc. 3rd Intern. Symp. Asean Trop. For. Manage.*
- Toma, T., et al. (1998) Floristic composition and stand dynamics in logged-over and burnt lowland dipterocarp forests in Bukit Soeharto, East Kalimantan. *Pusrehut special publication*. Samarinda, Indonesia.

- Toma, T., P. Matius and M. Sutisna (1999) Fire and human impacts on aboveground biomass of lowland dipterocarp forests in East Kalimantan. Pp. 297-305. In: Suhartoyo, H. and T. Toma (eds.) *Pusrehut special publication 8. Proceedings of the 3rd international symposium on Asia*
- Toma, T., Marjenah and Hastaniah (2001 a) Climate in Bukit Soeharto, East Kalimantan. Pp. 13-25. In: Guhardja, E. et al. (eds.) *Rainforest ecosystems of East Kalimantan. El Niño, drought, fire and human impacts*. Springer, Tokyo, Japan.
- tropical forest management*. Tropical Forest Research Center Mulawarman University & JICA, Samarinda, Indonesia.
- Toma, T., P. Matius, Hastaniah, et al. (2001 b) Dynamics of burned lowland Dipterocarp forest stands in Bukit Soeharto, East Kalimantan. Pp. 107-120. In: Guhardja, E. et al. (eds.) *Rainforest ecosystems of East Kalimantan. El Niño, drought, fire and human impacts*. Springer, Tokyo, Japan.
- Turner M.G., W.H. Romme, R.H. Gardner and W.W. Hargrove (1997) Effects of fire size and pattern on early succession in Yellowstone national park. *Ecol. Monogr.* 67(4): 411-433.
- Tyree M.T., S. Patiño and P. Becker (1998) Vulnerability to drought-induced embolism of Bornean heath and dipterocarp forest trees. *Tree Physiol.* 18: 583-588.
- Uhl, C. (1987) Factors controlling succession following slash-and-burn agriculture in Amazonia. *J. Ecol.* 75: 377-407.
- Uhl, C., R. Buschbacher and E.A.S. Serrao (1988 b) Abandoned pastures in Eastern Amazon. I. Patterns of plant succession. *J. Ecol.* 76: 663-668.
- Uhl, C., H. Clark, K. Clark and P. Maquirino (1982) Successional patterns associated with slash-and-burn agriculture in the Upper Rio Negro region of the Amazon basin. *Biotropica* 14(4): 249-254.
- Uhl, C., K. Clark, H. Clark and P. Murphy (1981) Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon basin. *J. Ecol.* 69: 631-649.
- Uhl, C., K. Clark, N. Dezzeo and P. Maquirino (1988 c) Vegetation Dynamics in Amazonian Treefall Gaps. *Ecology* 69(3): 751-763.
- Uhl, C. and C.F. Jordan (1984) Succession and nutrient dynamics following forest cutting and burning in Amazonia. *Ecology* 65(5): 1476-1490.
- Uhl, C. and J.B. Kauffman (1990) Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* 71(2): 437-449.
- Uhl, C., J.B. Kauffman and D.L. Cummings (1988 a) Fire in the Venezuelan Amazon 2: Environmental conditions necessary for forest fires in the evergreen rainforest of Venezuela. *Oikos* 53: 176-184.
- Ulbricht, R., A. Hinrichs, and Y. Ruslim (1999) Technical guideline for salvage felling in rehabilitation areas after forest fires. *Sustainable Forest Management Project. Report 1*. Samarinda, Indonesia.
- Urban, D.L. and H.H. Shugart (1992) Individual-based models of forest succession. Pp. 249-292. In: Glenn-Lewin, D.C., R.K. Peet and T.T. Veblen (eds.) *Plant succession. Theory and prediction*. Pp.352. Chapman and Hall, London, UK.
- van Dam, O. (2001) Forest filled with gaps. Effects of gap size on water and nutrient cycling in tropical rain forest. A study in Guyana. Ph.D. thesis. *Tropenbos-Guyana series 10*. Georgetown, Guyana. Pp. 208.
- van Eijk-Bos, C., and R.B. de Kock (1996) Tree species composition and increment of dipterocarp forest in permanent plots in East Kalimantan. *Wanariset technical report 1996-1*. International MOF Tropenbos-Kalimantan project. Balikpapan, Indonesia.
- van Nieuwstadt, M.G.L., D. Sheil and K. Kartawinata (2001) The ecological consequences of logging in the burned forests of East Kalimantan, Indonesia. *Cons. Biol.* 15(4): 1183-1186.
- van Valkenburg, J.L.C.H. (1997) Non-timber forest products of East Kalimantan - Potentials for sustainable forest use. *Tropenbos series 16*. Backhuys Publ. Leiden, Netherlands.

- Vázquez-Yanes, C. and A. Orozco-Segovia (1982) Seed germination of a tropical rain forest tree *Heliocarpus donell-smithii* in response to diurnal fluctuations of temperature. *Physiol. Plant.* 56: 295-298.
- Vázquez-Yanes, C. and A. Orozco-Segovia (1993) Patterns of seed longevity and germination in the tropical rainforest. *Annu. Rev. Ecol. Syst.* 24: 69-87.
- Veblen, T.T. (1992) Regeneration dynamics. Pp. 152-187. In: Glenn-Lewin, D.C., R.K. Peet and T.T. Veblen (eds.) *Plant succession. Theory and prediction*. Pp.352. Chapman and Hall, London, UK.
- Vines, R.G. (1968) Heat transfer through bark, and the resistance of trees to fire. *Aust. J. Bot.* 16: 499-514.
- Vleeshouwers, L.M. (1997) Modelling the effects of temperature, soil penetration resistance, burial depth and seed weight on pre-emergence growth of weeds. *Ann. Bot.* 79: 553-563.
- Vose, R.S., R.L. Schmoyer, P.M. Steurer, T.C. Peterson, R. Heim, T.R. Karl, and J.K. Eischeid (1992) *The global historical climatology network: Long-term monthly temperature, precipitation, sea level pressure, and station pressure data*. Carbon Dioxide Information Analysis Center. Oak Ridge, TN. Available from <ftp://cdiac.esd.ornl.gov/pub/ndp041/> (accessed 8 November 2000).
- Walsh, R.P.D. (1996 a) Climate. Pp. 159-236. In: Richards, P.W. *The Tropical Rain Forest* (2nd edition). Cambridge University Press, Cambridge, UK.
- Walsh, R.P.D. (1996 b) Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. *J. Trop. Ecol.* 12: 385-407.
- Walsh, R.P.D. and D.M. Newbery (1999) The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. *Phil. Trans. R. Soc. Lond. B* 354: 1869-1883.
- Werger, M.J.A. (1983) Tropical grasslands, savannas, woodlands: natural and manmade. Pp. 107-137. In: Holzner, W., M.J.A. Werger and I. Ikisima (eds.) *Man's impact on vegetation. Geobotany 5*. Dr. W. Junk Publ., The Hague, Netherlands.
- Wesson, G. and P.F. Wareing (1969) The role of light in the germination of naturally occurring populations of buried weed seeds. *J. Exp. Bot.* 20(63): 402-413.
- West, D.C., H.H. Shugart and D.B. Botkin (1981) *Forest succession: concepts and application*. Pp. 517. Springer-Verlag, New York, USA.
- Whelan, R.J. (1995) *The ecology of fire*. Pp. 346. Cambridge University Press, Cambridge, USA.
- White, P.S. (1979) Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* 45: 229-299.
- White, P.S. and S.T.A. Pickett (1985) Natural disturbance and patch dynamics: An introduction. Pp. 3-13. In: Pickett, S.T.A. and P.S. White (eds.) *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, US.
- Whitmore, T.C. (1984) *Tropical rain forests of the Far East*. Pp. 352. Clarendon Press, Oxford, UK.
- Whitmore, T.C. and D.F.R.P. Burslem (1998) Major disturbances in tropical rainforests. Pp. 549-566. In: Newbery, D.M., H.H.T. Prins and N. Brown (eds.) *Dynamics of tropical communities. 37th symposium of the British Ecological Society*. Blackwell Science, Oxford, UK.
- Whittaker, R.J., M.B. Bush and K. Richards (1989) Plant Recolonization and Vegetation Succession on the Krakatau Islands, Indonesia. *Ecol. Monogr.* 59(2): 59-123.
- Whitten, A.J., S.J. Damanik, S.J. Anwar and H. Nazaruddin (1987) *The ecology of Sumatra*. Gadjah Mada University Press, Yogyakarta, Indonesia.
- Wich, S.A. and C.P. van Schaik (2000) The impact of el Niño on mast fruiting in Sumatra and elsewhere in Malesia. *J. Trop. Ecol.* 16(4): 563-578.
- Wiens, J.A. and K.R. Parker (1995) Analyzing the effects of accidental environmental impacts: Approaches and assumptions. *Ecol. Appl.* 5(4): 1069-1083.
- Williamson, G.B. et al. (2000) Amazonian tree mortality during the 1997 el Niño drought. *Cons. Biol.* 14(5): 1538-1542.
- Wilson, B.F. (2000) Apical control of branch growth and angle in woody plants. *Am. J. Bot.* 87(5): 601.

- Woods, P. (1989) Effects of logging drought and fire on structure and composition of tropical forests in Sabah Malaysia. *Biotropica* 21(4): 290-298.
- Wooley, J.T. and E.W. Stoller (1978) Light penetration and light-induced seed germination in soil. *Plant Physiol.* 61: 579-600.
- Wright, S.J. (1992) Seasonal drought, soil fertility and the species diversity of tropical forest plant communities. *TREE* 7: 260-263.
- Wright, S.J. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130: 1-14.
- Yajima, T. (1988) Change in the terrestrial invertebrate community structure in relation to large fires at the Kutai national park, East Kalimantan (Borneo), Indonesia. Pp. 63-81. In: Tagawa, H. and N. Wirawan (eds.) *A research on the process of earlier recovery of tropical rain forest after a large scale fire in Kalimantan Timur, Indonesia, Occasional paper no. 14*, Research Center for the South Pacific, Japan.
- Yang, S.D. and M.T. Tyree (1993) Hydraulic resistance in *Acer-Saccharum* shoots and its influence on leaf water potential and transpiration. *Tree Physiol.* 12(3): 231-242.
- Yeaton, R.I. (1988) Porcupines, fires and the dynamics of the tree layer of the *Burkea africana* savanna. *J. Ecol.* 76: 1017-1029.
- Young, K.R., J.J. Ewel and B.J. Brown (1987) Seed dynamics during forest succession in Costa Rica. *Vegetatio* 71: 157-173.
- Zagt, R.J. (1997) Tree demography in the tropical rain forest of Guyana. PhD thesis. *Tropenbos-Guyana series 3*. Georgetown, Guyana.
- Zagt, R.J. and M.J.A. Werger (1998) Community structure and the demography of primary species in tropical rainforest. Pp. 193-220. In: Newbery, D.M., H.H.T. Prins and N. Brown (eds.) *Dynamics of tropical communities. 37th symposium of the British Ecological Society*. Blackwell Science, Oxford, UK.
- Zedler, P.H. (1981) Vegetation change in chaparral and desert communities in San Diego County, California. Pp. 406-430. In: West, D.C., H.H. Shugart and D.B. Botkin (eds.) *Forest Succession*. Springer-Verlag, New York, USA.



Field camp in the Sungai Wain research forest.

Acknowledgements

Originally focussing on the effects of forest fragmentation, I did not wish for a catastrophe to engulf my research plots in East Kalimantan. Nevertheless, that event and my presence at that place and time put me in a unique position, allowing me to study the effects of a rare large-scale event from the very moment that it occurred.

However, it would have been virtually impossible to find a suitable study site if not for Gabriella Fredriksson, who fought the fires and protected the Sungai Wain forest reserve. Building upon her dedication and determination, she and people from Sungai Wain village managed to save the core of this forest. They cleaned the forest floor from litter by using palm leaves as broomsticks, thus creating a kilometres-long firebreak, which they patrolled for weeks on end. My debt therefore goes to Gabriella, who moreover proved to be a pleasant companion with whom to share a research camp. My hope and faith are that she will succeed in making an important contribution to the conservation of some of the threatened pieces of nature on this earth.

If an unexpected fire and a fire break of unlikely narrowness enabled me to start this research, the consistent involvement of many people was indispensable to bring the project to a successful ending. I am greatly indebted to my promotor Marinus Werger for his counsel throughout the whole endeavour, and for the freedom that I was given to develop the project according to my own views. My other promotor, Jeff Sayer, impressed me by the promptness at which he spotted my face and arranged a meeting as soon as I dropped in at CIFOR, notwithstanding the myriad of directorial duties on his agenda. I will always remember how, on one of his visits to Sungai Wain, a tremendous rainstorm surprised us in the middle of the forest. This, however, was of no concern to Jeff, who declined the umbrella offered to him, informing us that he was testing a new pair of trousers which supposedly would dry up very quickly.

Probably the most indispensable contributions to the project were made by my two "day-to-day supervisors", Wim Dijkman in the Netherlands and Douglas Sheil in Indonesia. Wim solved many logistic issues and provided a listening ear whenever disappointments threatened to accumulate beyond what I could cope with. Discussions with Doug were crucial in structuring the research, and several of his ideas were to occupy key positions in the design and execution of my experiments.

At different stages, also Heinjo During, Meine van Noordwijk, Herman Wijnne and Roderick Zagt provided very valuable technical advice. Tim Boyle, Andy Gillison, Anja Hoffmann, Paul Keßler, John Poulsen, Feike Schieving, Frank Sterck, Hans ter Steege, Wim Tolcamp and Rene Verburg acted as excellent sounding boards in diverse discussions.

Working in Indonesia was often logistically challenging. I have been very fortunate that the CIFOR support staff were willing to deal with many bureaucratic issues and to assist in countless other ways. Above all I would like to express my gratitude to Inna Bangun, Rosita Go, Norman MacDonald, Ismed Mahmud, Ramsey Omar, Murniati Sono, Kustiani Suharsono, Indah Susilanasari and Meilinda Wan for their helpfulness and efficiency.

Also innumerable staff members at the International Ministry of Forestry (MOFEC)-Tropenbos Kalimantan Research Station (*aku* Wanariset Samboja) provided much appreciated assistance and scientific co-operation. I would especially like to thank Agustin, Arsad Anom, Riskan Efendi, Bas van Helvoort, Tinus de Kam, Mulyana Omon, Aldrianto Priadjati and Adi Susilo for their logistic involvement.

Setting up a network of 18 permanent sample plots was an endeavour too large for a single person. Two research units from the Wanariset Samboja, namely the forest management unit and the herbarium, were heavily involved. I thank the staff of the forest management unit, particularly Marten Buntu, Antonius Kari Pakala, Yance Pitoy, and

Herry Prajitno for planting some 1900 reference poles in the forest, and for making topographic maps of the permanent plots. Having little knowledge of the local flora when I arrived, the taxonomic expertise of the herbarium staff proved invaluable. I thank Kade Sidiyasa, Ambriansyah, Arbainsyah, Zainal Arifin and Yan for the identification of several thousand trees. I thank Rien Beukema, Karl Eichhorn, Ferry Slik, Saskia Bodegom and Pieter Pelser for deploying their specialised expertise in the identification of rogue specimens. Staff from the greenhouse nursery unit, in particular Hamdansyah, meticulously maintained my seed germination experiments at the research station while I was in the forest. Panjul, Manis, Scizo, an aged Bearded Pig and an anonymous python are thanked for the unanticipated (and sometimes scary) encounters in the forest, which provided me with a wealth of stories to entertain my children in the future.

Special thanks go to my field assistants Nurdin Syah and Fathar Udin, who accompanied me most of my time in the forest, lightening the atmosphere with a continuous flow of cheerful stories and jokes. They did most of the practical handiwork that forms the foundations of this thesis, and they were always prepared to commit themselves to yet another labour-intensive experiment. Much appreciated field assistance was also provided by Jake Paul, who unfortunately had to leave before he could see his hard work go up in smoke, and Janneke Helleman and Claudia Vissers, who saw their research plans turned upside-down by the burnings before they had even got into the field. Syahrudin Laysa Putra helped me out when I was a pair of hands short in the final months of my fieldwork.

Being required for my studies to stay on three different islands, I met hospitable people everywhere. In Bogor, Tina, Siti Nadiroh, and the other staff members made one always feel at home in the CIFOR guesthouse. Gus Hellier and Nell Wilson let me share their house with them, and taught me to appreciate the potion that is called “gin ‘n’ tonic”. Jeff and Mireille, Meine and Kurniatun, Doug and Miriam, Rien and Fred, and Carmen made me feel at home in the *expat* community of Bogor. Ratna and co. provided housing during my stay in Sumatra, and in East Kalimantan, I found the front door of the house of Tinus de Kam always open for more or less expected visits.

Back in the Netherlands, a long period of data analysis and writing laid ahead of me. Fortunately, I encountered a lively group of enthusiastic Ph.D. colleagues, post-docs, and permanent staff who had created a pleasant working atmosphere. Thank you long-time roommates Zeng Bo and Marielos Peña Claros, and corridormates Niels Anten, Eric Arets, Roel Brienen, Wim Dijkman, Marjet Elemans, Gerrit Heil, Shirrinka Goubitz, Tessa Pronk, Jacaranda van Rheenen, Simone Rose, Feike Schieving, Merel Soons, Marja van Staalduinen, Hans ter Steege, Frank Sterck, Bert van Ulft, Rene Verburg, Marinus Werger, Jo Willems and Roderick Zagt for the small talk during coffee breaks and the discussions over lunch. I reserve a special word of gratitude for Pieter Zuidema, who actually wrote the initial research proposal that allowed me to do research in Indonesia. Among others, Leonard Bik, Bertus Ebbenhorst, and Hans de Nooijer provided logistic support in the Netherlands.

Tot slot wil ik mijn familie en vrienden bedanken: Mijn vader en moeder voor de liefde die ze me hebben bijgebracht voor het buitenleven en de natuur, waarin vermoedelijk de basis is terug te vinden voor mijn voorkeur te verdwalen op onhandig geplande expedities in het oerwoud. Mijn vader, moeder en Anneke voor hun liefde als oppas-opa en oma's. Michiel, Suzanne, Joris, Mira en Jeroen voor de emails, brieven en pakjes die hun weg vonden naar mijn hutje in het bos. En Judith, die altijd met engelengeduld wachtte tot ik weer terugkwam naar Nederland, die vasthoudend iedere nieuwe onderzoeksplek bezocht die ik had uitgekozen, en die de moed er in wist te houden bij de verschillende kleine en grotere rampen die in de loop der tijd passeerden. Zonder haar ondersteuning zou ik er lang geleden de brui aan hebben gegeven. Bovenal prijs ik mij gelukkig omdat Judith, Simone en sinds kort Hajo een welkomscomitee vormen waar ik na iedere werkdag weer naar uitkijk!

Curriculum vitae

Mark van Nieuwstadt was born in Breda, the Netherlands on the 29th of June, 1970. He received his secondary education at the Onze Lieve Vrouwe Lyceum in Breda. After obtaining his high school degree in 1988, he studied Biology at Utrecht University, specialising in plant ecology and animal ecology. He investigated long-term vegetation dynamics of calcareous grasslands in Southern Limburg, and did research on the foraging behaviour of tropical bees in Costa Rica (Central America). Both studies resulted in publications in international scientific journals. He graduated *cum laude* in 1993.

After graduating, Mark took up a post as associate expert in the Proyecto Regional de Apicultura y Meliponicultura (PRAM) at the Universidad Nacional (UNA) in Costa Rica. He assisted in the development of research programs on pollination and the foraging behaviour of bees. Responsibilities included the supervision of M.Sc. students from throughout the region, and the development of a methodology for palynological analysis of honey and pollen samples. Based on these activities several papers were published.

In August 1996 he accepted a Ph.D. position at Utrecht University in a cooperation program with the Center for International Forestry Research (CIFOR) in Indonesia. The research was done at the Wanariset Samboja research station in East Kalimantan, which is managed by Tropenbos International and the Indonesian Ministry of Forestry (MOF). During the first 1.5 years, his research focussed on the effects of forest fragmentation on populations dynamics of shade tolerant trees. The continuation of this research was impeded by extensive fires in March 1998, which burned the largest part of the forest in the research area. Adjusting his research to the new circumstances, he studied vegetation dynamics after forest fire in the four years that followed.

Publications

- Biesmeijer, J.C., M.G.L. van Nieuwstadt, S. Lukács and M.J. Sommeijer (1998) The role of internal and external information in foraging decisions of *Melipona* workers (Hymenoptera: Meliponinae). *Behav. Ecol. Sociobiol.* 42: 107-116.
- van Nieuwstadt, M.G.L. and J.F. Ramirez (1994) Uso de colmenas para la polinización de cultivos: plaguicidas y el uso de un contrato. In: van Veen, J.W., H.G. Arce & A. Ortiz (eds.) *Apicultura: estrategias para el manejo adecuado de las colmenas, Memorias del tercer congreso nacional de apicultura, Costa Rica* (In Spanish).
- van Nieuwstadt, M.G.L. and C.E. Ruano Iraheta (1997) Relation between size and foraging range in stingless bees (Apidae, Meliponinae). *Apidologie* 27: 219-228.
- van Nieuwstadt, M.G.L., L.A. Sanchez C., J.C. Biesmeijer, H.G. Arce A. & M.J. Sommeijer (1997) Foraging behaviour of stingless bees: are their diets really so diverse? In: Mardan, M. et al. (eds.) *Tropical bees and the environment. Proceedings of the Conference on tropical bees and the environment*, Malaysia 1995. Beenet Asia, Universiti Pertanian Malaysia, Southbound.
- van Nieuwstadt, M.G.L., D. Sheil and K. Kartawinata (2001) The ecological consequences of logging in the burned forests of East Kalimantan, Indonesia. *Cons. Biol.* 15(4): 1183-1186.
- Willems, J.H. and M.G.L. van Nieuwstadt (1996) Long-term after effects of fertilization on above-ground phytomass and species diversity in calcareous grassland. *Journal of Vegetation Science* 7: 177-184.