

**Plant diversity after rain-forest fires
in Borneo**

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Cover: Unburnt forest network in Sungai Wain. Two years after the fires of 1998.

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GENERAL INTRODUCTION

FIRE IN TROPICAL RAIN FORESTS

Up to a few decades ago, most ecologists regarded lowland tropical rain forests as stable ecosystems that were immune to fire (Goldammer et al., 1996; Uhl, 1998; Whitmore & Burslem, 1998), this in spite of the fact that ecologists had earlier stated the opposite (e.g. Van Steenis, 1937). However, this doctrine has been shattered, since there is now a large body of evidence that there is a long history of fire in rain forests throughout the tropics. Historical fires were first shown to be regular events in tropical rain forests by Sanford et al. (1985). By means of radiocarbon dating of soil charcoal, they were able to show that numerous fires had occurred in the north central Amazon Basin since the mid-Holocene. Later, fires were also shown to have occurred regularly in East Borneo since the late Pleistocene (Goldammer & Seibert, 1989), and to have occurred in the rain forests of Brazil, Venezuela, Ecuador, Panama, Guyana, Sabah, Brunei and Papua New Guinea (Goldammer et al., 1996; Hammond & Ter Steege, 1998; Turcq et al., 1999; Haberle & Ledru, 2001).

Ancient human activities, especially shifting cultivation, are likely to have been a major source of fires (Sanford et al., 1985; Richards, 1996; Turcq et al., 1999; Haberle & Ledru, 2001). Shifting cultivation includes the conversion of forest into agricultural land by cutting and burning the vegetation. After a short period, often only a year, the soil becomes depleted and the land will be left by the farmer, thereby giving the forest the opportunity to recover (Whitmore, 1984). However, many other fires seem to have occurred in the absence of human activities (Sanford et al., 1985; Hammond & Ter Steege, 1998). These natural fires were stimulated by climatic changes (Haberle & Ledru, 2001) and probably started by lightning, volcanic activity and permanently burning coal seams (Whitmore, 1984; Goldammer & Seibert, 1989; Mabblerley, 1992; Goldammer et al., 1996). In summary, many findings during the last two decades strongly suggest that fire is a natural part of tropical rain-forest ecology. The fact that there is today a well-developed, highly biodiverse rain forest present at most locations where abundant charcoal has been found in the soil, shows that tropical rain forests are to some extent adapted to fire.

FIRES AND TROPICAL DEFORESTATION

Tropical deforestation has become a major concern for the world community. Between 1990 and 1997, c. 5.8 million hectares (0.5%) of tropical rain forest were lost each year (Achard et al., 2002). Whole regions in South and Central America, Africa and Southeast Asia have already completely lost their forest or are expected to become deforested in the near future (see e.g. Laurance et al., 2001; Jepson et al., 2001). Apart from the economic, political, social and climatological problems arising from tropical deforestation, we are also facing severe ecological consequences. Deforestation

primarily leads to fragmentation and degradation of the remaining tropical rain forests (Skole & Tucker, 1993; Cochrane, 2003), this again leading to many processes negatively affecting populations of plants and animals. Among these processes are many ecological ones, such as the death of canopy trees due to edge effects (Laurance et al., 2000), recruitment failure resulting from overpredation of seeds (Curran et al., 1999), reduced seedling establishment and plant growth (Bruna et al., 2002; Bruna, 2003), local extinction of plants (Benitez-Malvido & Martinez-Ramos, 2003), butterflies (Cleary, 2002) and birds (Boulinier et al., 2001; Beier et al., 2002), and decreased pollination (Ashworth et al., 2004). Apart from ecological processes, harmful human activities like illegal logging and hunting also decrease the biodiversity of remaining forest fragments (Laurance, 1998; Hartshorn & Bynum, 2001; Curran et al., 2004). The final outcome may be catastrophic mass extinctions of species as has been recently documented for Singapore (Brook et al., 2003). Since tropical rain forests harbour most of the world's biodiversity, tropical deforestation has become the major cause of global species extinctions (Pimm & Raven, 2000).

Recent studies show that tropical deforestation is the result of a complex of social, political, economic, ecological and climatological interactions in which fires play a key role (Cochrane, 2003). This may seem to contradict the recent findings indicating that fire is a natural event in tropical rain forests and that these forests are able to recover from fire. The crux of tropical deforestation is, however, not so much the incidence of fire in these forests, but its frequency. Fires in tropical rain forests are much more abundant today, with intervals less than 15 years in most areas, compared with the past, when there were intervals of hundreds or even thousands of years (Cochrane & Schultze, 1998; Cochrane et al., 1999). This increase in frequency of forest fires is closely associated with increased human population density and increased accessibility to the forest by road construction (Laurance, 1998; Laurance et al., 2001; Nepstad et al., 2001; Peres, 2001).

Logging, including reduced-impact logging that is claimed to be sustainable, is often the starting point for a cascade of interactions leading to forest destruction (Laurance, 1998; Cochrane, 2003). Logging directly affects the forest by creating a more open canopy and generating fuel for potential fires in the form of logging debris (dead wood and other dead plant material on the forest floor). A more open canopy leads to increased evaporation and desiccation during dry periods, and to additional fuel by stimulating the development of a dense undergrowth of lianas, herbs and young trees (Cochrane & Schultze, 1998; Cochrane et al., 1999). The combination of increased desiccation during dry periods and the presence of abundant fuel in the undergrowth strongly increases the fire-susceptibility of forests. Apart from these direct effects, logging also leads to increased local human populations and to increased accessibility to the forest (Kartawinata et al., 1989), thereby stimulating additional destructive human activities such as illegal logging and slash-and-burn agriculture (Kartawinata et al., 1989; Laurance, 1998; Curran et al., 2004). Due to increased fire-susceptibility, fires ignited for shifting cultivation and for other activities easily get out of control in dry periods and often affect large areas of forest (Cochrane & Schultze, 1998, 1999; Nepstad et al., 1999; Siegert et al., 2001). These combined effects of logging and the subsequent developments explain why logged and other degraded areas are particularly prone to tropical forest fires (Goldammer et al., 1996; Siegert et al., 2001). However,

adjacent virgin forests are often also subject to these fires (Richards, 1996; Siegert et al., 2001).

Initial rain-forest fires are usually not more than a thin, slowly creeping ribbon of flames a few decimetres high (Cochrane & Schultze, 1998). They were thought not to be very harmful until recently it was shown that they are able to kill many trees (Cochrane & Schultze, 1999; Peres, 1999; Van Nieuwstadt, 2002) and to affect large areas of forest (Nepstad et al., 1999). Even more harmful than these direct effects are the subsequent developments. Initial fires are the starting point for several destructive processes in the form of positive feedbacks between forest fires and ecological, climatological and social factors (Cochrane, 2003). The positive feedback first perceived is that between forest fires and fire susceptibility (Cochrane et al., 1999). Once a forest has been burnt, it becomes very susceptible to subsequent fires, since the canopy layer is even more open than in logged forests and high loads of new fuel result from the defoliation of dying trees and the dense undergrowth that develops after the fire. A second feedback is related to the climatological effects of forest fires (Nepstad et al., 2001). Forest fires promote regional droughts by reducing the vegetation cover, thereby decreasing evaporation and increasing radiation, these again leading to increased seasonality and inhibition of rainfall (Shukla et al., 1990; Laurance, 1998; Berbet & Costa, 2003; Durieux et al., 2003). Several feedbacks have been noted between forest fires and human activities. For example, fires destroy agricultural and forestry systems, thereby discouraging landholders from making fire-sensitive investments that could replace their current slash-and-burn activities (Nepstad et al., 2001). Another example is that fires also lead to increased logging pressure on the canopy trees that survive the fires (Hoffmann et al., 1999; Van Nieuwstadt et al., 2001) and on the remaining unburnt forest fragments (Kartawinata et al., 1989; Laurance, 1998; Curran et al., 2004), thereby leading to further degradation and increased fire risk. All these feedbacks and other interactions between forest fires and ecological, climatological and sociological processes together make it very difficult to protect tropical rain forests and their biodiversity once they have become more readily accessible to people.

FIRES AND EL-NIÑO

El-Niño Southern Oscillation (ENSO) events occur irregularly but typically once every three to six years. They have major implications for the functioning of a wide range of ecosystems, including deserts, tropical rain forests and marine communities (Holmgren et al., 2001). While ENSO events often strongly increase rainfall and vegetation cover in arid regions, they lead to dramatic periods of drought and deforestation in tropical rain-forest areas. As drought is a strong promotor of fires, large areas of tropical rain forest are burnt during ENSO events. Correlations among charcoal records of fires in Latin America and Southeast Asia indicate that ENSO events induced pantropical fires during the past 16,000 years (Haberle & Ledru, 2001).

However, recent ENSO fires seem to be much more severe than their historic counterparts (Goldammer et al., 1996). The most destructive ENSO fires in human history were recorded in 1997–1998, when over 20 million hectares were burnt in Southeast Asia and Latin America (Cochrane, 2003). This dramatic increase of forest destruction by ENSO fires is mainly a result of the interaction between ENSO events and increasing

levels of forest degradation associated with increasing population pressures, accessibility, logging and other destructive activities, and thus fire susceptibility. Another part of the explanation for the fact that ENSO fires have become more extensive in recent times, however, is that ENSO events themselves have become stronger (Tudhope et al., 2001). Although it is still debated whether global warming is responsible for the fact that ENSO events have become stronger recently, certain climate models taking account of presumed global warming do predict a further increase of ENSO events in the near future (Timmermann et al., 1999). As tropical wildfires themselves contribute importantly to global warming by the emission of the greenhouse gas carbon dioxide (Goldammer et al., 1996; Laurance, 1998; Cochrane, 2003), there is a positive feedback between tropical forest fires and global warming as well.

FIRES IN EAST KALIMANTAN

As elsewhere in the tropics, fires have played an important role in the history of tropical rain forests in the Indonesian province of East Kalimantan. Goldammer & Seibert (1989) were the first to find evidence of ancient wildfires in this region. Charcoal records showed that numerous fires have occurred since the late Pleistocene (17,510 BP). Some of these fires were probably started by permanently burning coal seams, as Goldammer & Seibert (1989) found evidence that a coal seam burnt between c. 13,200 and c. 15,300 BP. In addition, in 1987 they observed the actual initiation of a forest fire by a burning coal seam in Bukit Soeharto National Park.

The oldest documented severe drought in Borneo dates back to 1877–1878, when about one third of the tree population in the forests of the Middle Mahakam Area died (Goldammer et al., 1996). During this dry period, large-scale forest fires are known to have occurred in both East and South Kalimantan. Several later large-scale forest fires have been documented in East Kalimantan (Goldammer et al., 1996), and such fires were considered to be regular events in the peat swamp forests of Borneo (Van Steenis, 1937). Most of these large-scale fires are likely to have been induced by ENSO events, as their occurrence is strongly correlated to droughts reported in Sandakan, Sabah (Goldammer et al., 1996). The meteorological information from Sandakan indicates two periods characterised by regular droughts, between 1879 and 1915 and since 1968, with a drought-free period between 1916 and 1967.

During the last three decades, pressure on the forests by mechanized logging and massive transmigration has strongly increased in East Kalimantan (Kartawinata & Vayda, 1984; Kartawinata et al., 1989; MacKinnon et al., 1996). Before 1970, human populations had little impact on the forest ecosystem. Shifting cultivation was practised around the villages but was still sustainable because population densities were small and technical equipment was insufficient for large-scale operations. This situation changed with the introduction of mechanized logging and the arrival of transmigrants from Sulawesi and Java in the late 1960s and 1970s. Forest destruction by human activities was no longer compensated for by forest recovery. Both the activities of logging companies and the immigration of people have been steadily increasing since then and resulted in a gradual degradation of the forests until the dramatic event of 1982–1983.

In 1982–1983, El-Niño caused an exceptional drought in East Kalimantan. At that time, mechanized logging and additional destructive activities had created large areas

of degraded rain forest that were highly susceptible to fire during dry periods. The result was a fire unprecedented in human history, in which 3.5 million hectares were burnt in East Kalimantan alone (Goldammer et al., 1996). Not only degraded forests were subject to the fires, 0.8 million hectares of adjacent primary forests were burnt as well. Logged-over forests accounted for 1.4 million ha, secondary forests for 0.75 million ha, and peat swamp forest for 0.55 million ha. The famous Kutai National Park was badly damaged with most of its forest severely damaged: 99% of the trees diameter at breast height (dbh) < 4 cm, 20–35% of the trees dbh > 25 cm, and virtually all lianas being killed in the burnt areas.

After some moderate ENSO events subsequently, the next exceptional ENSO drought occurred in 1997–1998. The resulting fires surpassed even those of 1982–1983, with 5.2 million ha of land, including 2.6 million ha of forest, burnt (Siegert et al., 2001). Lowland Dipterocarp forest accounted for 2.2 million ha (that is 40.5% of this vegetation type in East Kalimantan), secondary forest for 1.7 million ha (75.5%), peat swamp forest for 0.31 million ha (73%), and wetlands for 0.29 million ha (81%). Of the burnt forests, 76% had severe or total fire damage, meaning that at least half of the trees dbh > 20 cm were killed.

The lowland area of East Kalimantan was almost completely covered by tropical rain forest before the 1970s, and most of it was severely burnt in 1998. In this region, very few rain forests unaffected by the ENSO fires survive. In the Balikpapan–Samarinda area, the area with the highest population density in East Kalimantan, the last patch of a considerable size (approximately 5,000 ha) is in the Sungai Wain forest (Fredriksson & De Kam, 1999).

POST-FIRE RECOVERY

Although ENSO droughts and fires severely damaged most of the lowland rain forests in East Kalimantan, the burnt forest areas still show abundant regrowth at most locations (Hoffmann et al., 1999; Slik, 2001; Siegert et al., 2001; Dennis et al., 2001; Van Nieuwstadt, 2002; Cleary, 2002; this thesis). Pioneer trees and non-tree species regenerate abundantly from the soil seed bank after the fires (Van Nieuwstadt, 2002; this thesis), while the resprouting of burnt stems contributes importantly to the recovery of non-pioneer species (Goldammer et al., 1996; Van Nieuwstadt, 2002). Within this matrix of post-fire regrowth, forest remnants survive as scattered canopy trees not killed by the fires and as patches of unburnt forest on relatively wet soils along streams (Goldammer et al., 1996; Slik, 2001; Siegert et al., 2001; Dennis et al., 2001; Van Nieuwstadt, 2002; this thesis). Canopy trees have been shown to be important nuclei promoting forest regeneration at several sites in Neotropical forests (Guevarra et al., 1986, 1992; Guariguata & Ostertag, 2001), while nearby unburnt forest has been shown to promote forest regeneration as well (Saulei & Swaine, 1988; Guariguata & Ostertag, 2001).

Although these observations showed that ENSO fires have not yet caused permanent deforestation in most sites studied in East Kalimantan, any quantitative information on the affected ecosystems and their species diversity was lacking until 2000 (Siegert & Hoffmann, 2000). After the 1997–1998 fires, information on the biodiversity of burnt forests has become increasingly relevant for those concerned with species conserva-

tion. As it is expected that in Indonesia hardly any unburnt lowland rain forest will be left in the near future (Jepson et al., 2001), burnt and other degraded forests will soon become important for the protection of rain-forest biodiversity. For priority setting in the conservation of burnt forests, understanding the relationships between biodiversity and both the biotic and abiotic environment of such forests is a prerequisite.

BASIC RESEARCH QUESTIONS

In order to contribute to a better understanding of the relationships between biodiversity and the biotic and abiotic environment of burnt forests in East Kalimantan and elsewhere, I will address two basic questions in this thesis:

- 1) What is the effect of ENSO fires on plant diversity in the lowland rain forests of East Kalimantan?
- 2) How is plant diversity spatially distributed within the burnt lowland rain forests of East Kalimantan?

Since 2000, some aspects of these two questions have already been addressed in other research projects. Slik et al. (2002) studied the species diversity of tall trees (dbh > 10 cm) in once-burnt forests and concluded that diversity was still quite high in comparison to primary forests (respectively 50 and 80 species per 0.3 ha). However, they also found signs that tree species richness had not yet recovered in forests that were burnt 15 years before and they suggested that it might be permanently altered by the fires.

Van Nieuwstadt (2002) found that species richness of tall trees (dbh > 10 cm) per 0.4 ha was only 30% of pre-ENSO values of the Sungai Wain forest. This strong decrease in tree diversity seems to conflict with the results of Slik and co-workers but was largely explained by the fact that tall trees were more affected by the ENSO drought than by the ENSO fires, thereby resulting in a high tree mortality in both burnt and unburnt forests. The number of species per number of trees was nearly identical between unburnt and once-burnt forest, meaning that the reduction in diversity was mainly the result of a reduction in density.

In contrast to the tall trees, small trees were almost completely removed from the forest by the fires. Cleary (2002) estimated that 97.5% of the smaller trees (dbh < 8 cm) were killed by fires in the Sungai Wain forest. After the fires, seedling and sapling densities remained much lower in once-burnt than in unburnt forest and species composition remained very different during the first three years of regeneration. While species richness increased in seedlings of both forest types, it decreased in saplings of the once-burnt forest.

Van Nieuwstadt (2002) also showed that resprouting, together with the survival of tall trees (dbh > 10 cm), contributed greatly to the post-fire diversity in non-pioneer species, whereas seed rain appeared to be much less important than expected. The average density of new shoots was 22 per 100 m² and species numbers per stem numbers in new shoots were as high as in trees in the unburnt forest. In contrast, pioneer trees mainly regenerated from seeds, apparently coming from both the soil seed bank and the seed rain.

Together with J.W.F. Slik (Slik & Eichhorn, 2003), I studied all trees taller than 130 cm in unburnt, once-burnt and twice-burnt forests at several locations in the Balikpapan–Samarinda area. We showed that the negative relation between fire mortality and stem diameter only resulted in disproportionate mortality and local extinction of small tree species after repeated fires. We also studied how tree diversity was spatially distributed in the burnt forests. Both tree densities and species richness were related to topography, as climax tree species were most common in swamps, river valleys and on lower slopes. This indicates that apart from stem diameter, topographic position of trees also affects the fire survival chances of trees.

Although the above-mentioned studies generated information that greatly contributed to our understanding of fire-effects and patterns of regeneration in rain forests of East Kalimantan and elsewhere in the tropics, many aspects of my two basic questions still remain unanswered. With respect to the first question, previous studies mainly focused on the effects of fires on the tree community, and especially on tall trees (dbh > 10 cm). In contrast, effects on lianas and smaller growth forms have only been studied at the level of community abundance, while effects on individual species, species composition and species diversity remain unknown. With respect to the second question, only the spatial relationships between topography, tree diameter and fire survival of trees have been studied. Of the many other possible relationships between topography, unburnt remnant forest, tall remnant trees that survived the fires, post-fire regeneration of trees, palms, lianas and smaller growth forms like ferns, grasses, gingers, bamboos etc., none has been quantitatively studied.

OUTLINE OF THIS THESIS

The aim of this study is to increase our knowledge of fire effects on plant diversity in the tropical rain forests of Borneo, and in particular of spatial patterns in the post-fire diversity of burnt areas. **Chapter 2** describes a study of plant diversity in the largest remaining patch of unburnt rain forest in the lowland part of the Balikpapan–Samarinda area: the fire-protected area in the Sungai Wain forest. Comparison of my Sungai Wain data with those of other inventories in rather undisturbed (often called primary) forests in East Kalimantan reveals that it is most similar to the nearby forests of Bukit Bankirai and Wanariset before the latter was destroyed by the ENSO fires. The plant community of this forest is apparently typical of unburnt forests in this area and serves as a reference for subsequent studies in the burnt forests. Within this unburnt forest, several significant relationships between topography, canopy gaps and plant community structure, composition and diversity were observed, but little local variation was explained by these relationships. In addition, several plant species were shown to be pioneer species (*sensu* Swaine & Whitmore, 1988), i.e. species dependent on canopy gaps for their regeneration in primary forest.

Chapter 3 focuses on the first basic question of this thesis: What is the effect of the ENSO fires on plant diversity in the rain forests of East Kalimantan? As mentioned above, only indications of fire-effects could be derived from the applied plot design. However, as there are no other studies executed on the fire-response of species composition and species diversity in non-tree plant communities, such indications may still

provide an important contribution to our understanding of the impact of fire. We found indications that a few local and invasive pioneer species have increased after the fires, while the great majority of species is strongly reduced in abundance. Nevertheless, overall plant diversity is still remarkably high after the fires, even in the twice-burnt forest. Our study at the landscape-scale (450 ha) strongly suggests that the majority of plant species is still present in the forest, though in much lower densities than before the fires.

Chapter 4 focuses on the second question of this thesis: How is plant diversity spatially distributed within the burnt forests of East Kalimantan? In both burnt forests, a network of unburnt remnant forest was seen along streams in the valleys. A comparison of this network with the surrounding burnt matrix showed that most of the tree and liana diversity in burnt forests was located in this network. However, this does not provide reliable information on the fire-effects themselves, as forest remnants are a non-random subset of the original plant community. In the burnt matrix surrounding the network, variation in the structure, composition and diversity of the tree and liana community was also determined by topographic variation, as well as by remnant canopy trees.

Chapter 5 provides a synthesis of the previous chapters in the context of both the current fire crisis in East Kalimantan and the recent observations made by remote sensing. This thesis shows that plant diversity can remain high in burnt forests as long as the network of unburnt remnant forest is conserved. SAR-photographs showed that such unburnt networks are present in many other burnt forests of East Kalimantan, indicating that most of the plant diversity is still conserved in this region. These findings highlight the urgent need to put a halt to the destructive activities that are currently taking place in the burnt forests. Finally, I discuss some unanswered questions and offer suggestions for future research.

STUDY SITES

The field study was carried out from January to May 2000 in two forest reserves north of Balikpapan, in the Indonesian province of East Kalimantan (Fig. 1.1). The reserves are considered to be very similar with respect to their pre-fire vegetation, topographic characteristics, soil type and rainfall (Van Nieuwstadt, 2002). Before the fires, they were covered with Mixed Dipterocarp Forest (MDF), which is the most common type of lowland rain forest in Kalimantan (MacKinnon et al., 1996). The topography of the reserves is characterised by gentle to steep hills intersected by many small rivers. The soil type comprises mainly Alisols, very deep, acid and infertile soils with a high fraction of loam and clay (Van Bremen et al., 1990). Rainfall is about 2472 mm per year and relatively aseasonal. In 1982–1983 and 1997–1998, two exceptionally long droughts occurred as a result of ENSO events, with some shorter droughts in between. These droughts were accompanied by large-scale fires, which severely damaged the studied reserves. In addition to disturbance by fire and drought, small-scale illegal logging is executed in both sites (Fredriksson & De Kam, 1999; Van Nieuwstadt, 2002).

The Sungai Wain forest (116.49 E, 1.06 S) is a water catchment area for the city of Balikpapan (Fredriksson & De Kam, 1999), and originally comprised c. 10,000 ha of MDF. About half of the total area was burnt during the first half of 1998, while a central core area was protected from fire by the establishment of firebreaks. In this reserve,

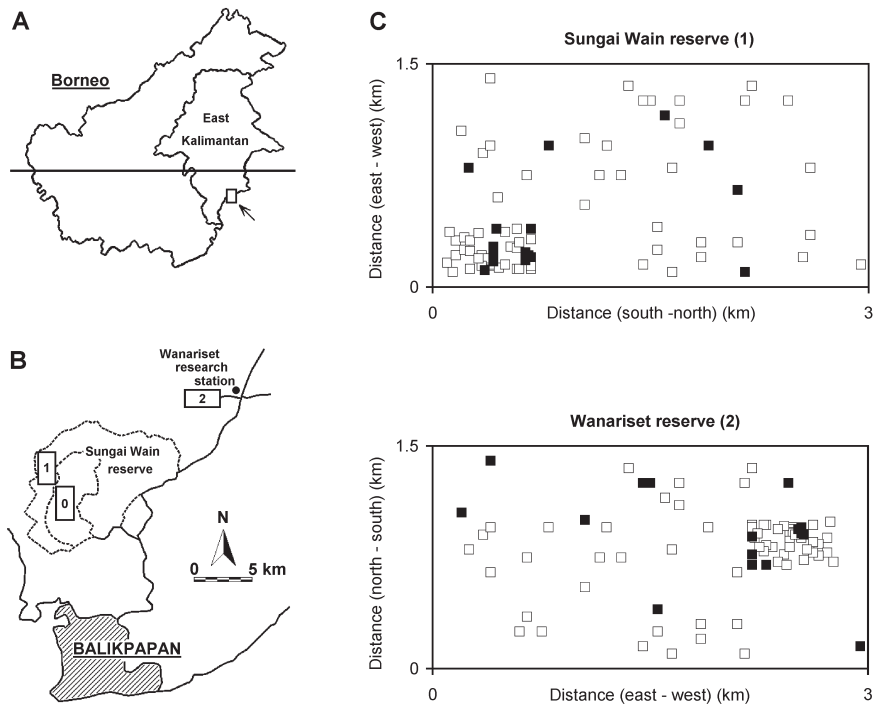


Fig. 1.1. Maps of the research area and plot design. — A. Position of the Balikpapan area in Borneo. — B. Positions of the 450 ha plots in the Balikpapan area. Numbers in the plots correspond to the number of fires that occurred in it. — C. Positions of the two sets of 40 random subplots in the 18 ha and 450 ha plots in the burnt forests studied. Subplots (10 × 20 m) not on scale, white subplots were entirely burnt, black subplots contained unburnt remnant forest. The unburnt forest was sampled using the same design.

plant diversity was studied in unburnt and once-burnt forest. The unburnt forest site was located in the central core area and had a very similar tree composition as other MDF in this region (Chapter 2; Van Nieuwstadt, 2002; Slik et al., 2003). The once-burnt forest site is in the north-western part of the reserve. It was heavily damaged by the fires over most of its area, as could be concluded from the very few stems that survived the fires (Van Nieuwstadt et al., 2001). It should therefore be classified as having total fire damage, the most severely affected category of forests (Siegert et al., 2001). After the fires, it became dominated by a thick layer of ferns and scattered bushes of pioneer trees, particularly *Macaranga trichocarpa* and *M. gigantea* (Euphorbiaceae), *Vernonia arborea* (Compositae) and *Dillenia borneensis* (Dilleniaceae) (Fig. 5.1A, see p. 86).

The Wanariset forest (116.57 E, 0.59 S) originally comprised c. 500 ha of MDF and was severely burnt both in 1982–1983 and in 1998. Here we studied twice-burnt forest that was mainly surrounded by agricultural land. This reserve also includes Wartono Kadri, a small area (c. 50 ha) of MDF that was saved by the establishment of firebreaks. Although the Wanariset forest was as heavily damaged by the fires as the Sungai Wain

forest, the post-fire vegetation was very different as a dense secondary forest developed afterwards (Fig. 5.1B, see p. 86). At the time of field inventory (two years after the last fires), many pioneer species were abundant in the forest. The largest pioneer trees belonged to the genera *Trema* (Ulmaceae s.l.) and *Mallotus* (Euphorbiaceae) and already approached 10 cm dbh. Scattered liana tangles were nested within these dense stands of pioneer trees.

PLOT DESIGN

Answering the two basic questions of this thesis requires differences in plot design of the field study. Ideally, fire effects (question 1) are studied by quantifying plant diversity in several forest plots and then burning half of them after random selection, while using the others as control plots. However, very few studies have used this approach in tropical rain forest (but see Uhl et al., 1981), as it would lead to further destruction of this already threatened ecosystem. Therefore, nearly all studies on fire effects have been executed by comparing already burnt forest plots with unburnt forest plots, thus without pre-treatment assessments of the plots and without randomly assigning the treatments. All recent studies in East Kalimantan are examples of this approach and the field study of this thesis is no exception. However, such a study requires several burnt and unburnt forest patches to serve as replicates, these patches being arranged in a spatial design that avoids statistical spatial dependence of the treatment as much as possible. As the ENSO fires in East Kalimantan affected large areas, a proper sample design to assess their impact can consequently only be realised by recording plots at widely spaced localities. In practice, finding suitable forest patches for plot establishment requires much time and only a few burnt and unburnt forest plots can be compared in a single field study (e.g. Slik et al., 2002).

A study of the spatial distribution of plant diversity (question 2) can be executed within a single burnt forest, but requires the establishment of several inventory plots within each study site. The combination of sampling several forests and sampling several plots within each forest would have been impossible within the limited time span of this field study (less than one year). I therefore decided to choose as many plots as possible within three forest types (unburnt, once-burnt and twice-burnt forest) for sampling, while having no replication for each of these forest types. The consequence of this approach is that the question concerning the spatial distribution of plant diversity in burnt forest (2) could be answered in more detail than in any previous study, but that only indications were obtained concerning the question on fire-effects (1). As previous studies in the burnt forests of East Kalimantan focused more on fire effects than on the spatial distribution of plant diversity, the study of this thesis particularly provides new understanding of the second question.

All three forest types were sampled with the same basic design (Fig. 1.1C). Two sets of 40 subplots (10 × 20 m) were randomly located in plots of 18 ha and 450 ha. The exact position of subplots was determined by assigning them at random to grid cells on maps. Since two subplots would have been located in a small part of the Wanariset forest that was actively protected by fire breaks (Wartono Kadri), these subplots were considered to be not representative for the twice-burnt treatment and were transferred to new random positions.

GROWTH FORMS

Throughout this thesis, each plant species is referred to one of the following three growth forms:

- 1) *Trees* (including tall shrubs and treelets) defined as non-climbing woody species of which the mature individuals were on average more than two metres tall.
- 2) *Lianas* defined as climbing woody species of which the mature individuals had a stem diameter of more than 0.5 cm on average.
- 3) *Small plants* defined as all herbaceous species, non-climbing woody species of which the mature individuals were on average less than two metres tall (i.e. small shrubs), and climbing woody species of which the mature individuals had a stem diameter of less than 0.5 cm on average.

This classification was largely based on reproductive individuals observed in the study site. When too few individuals were available for reliable classification, information from labels on herbarium collections at the Wanariset Research Station was also used. Climbing species were defined as species of which the mature individuals need external support for their height growth. Plant height was defined as the vertical distance from the highest growth bud to the ground, similar to the system used by Raunkiaer (1934). By definition, trees comprised also a few woody plants that are often described as treelets, such as large non-climbing bamboos and palms, while lianas also included climbing bamboos and rattans.

DATA COLLECTION IN THE FIELD

All plants taller than 1.3 m were sampled and measured for their dbh in each subplot of 10 × 20 m. Small plant species were additionally sampled in quadrats of 2 × 4 m within these subplots and their cover was estimated using five cover classes: 0–10, 10–30, 30–70, 70–90 and 90–100 %. All plant samples were identified to the lowest possible taxonomic level by staff at the Herbarium Wanariset, Samboja, at the Leiden branch of the National Herbarium of the Netherlands, or by taxonomic specialists elsewhere. Taxonomic classification and nomenclature according to Mabberley (1997), except for a few adjustments based on recently changed taxonomic views (D.J. Mabberley 2005, pers. com.).

In addition to the plant data, specific environmental data were collected systematically in each subplot. The inclination (°) of all subplots was measured from corner pole to corner pole with a clinometer, and calculated as the plane defined by the average vectors of each pair of parallel sites of the subplot. The elevation (m a.s.l.) was calculated as the average of the four corner poles and derived from clinometer data on paths connecting them with positions of known elevation on maps. Remnant forest was still easily recognizable in the burnt forest sites. From the strong contrast in the vegetation structure and the absence of burnt wood fragments, limits could usually be mapped in the subplots to within 1 m.

THE PLANT COMMUNITY OF SUNGAI WAIN, EAST KALIMANTAN, INDONESIA: PHYTOGEOGRAPHICAL STATUS AND LOCAL VARIATION¹

SUMMARY

In the Balikpapan–Samarinda area of East Kalimantan, the Sungai Wain forest contains one of the last lowland tropical rain forests not severely disturbed by logging or fire. We studied its plant community by assessing three features: forest structure, composition and species richness. We evaluated its phytogeographical status by comparing its tall tree community to those of other rain forests that have been studied in East Kalimantan. At the local scale, we related its internal variation to two environmental factors that were expected to be important modifiers of the plant community: topography and canopy gaps. For this local study, we also included small trees, lianas and herbaceous growth forms.

In Sungai Wain, tree densities were generally intermediate in comparison to other rain forests in East Kalimantan. Sungai Wain was most similar in family and genus composition to the nearby forests of Bukit Bankirai and Wanariset. Although the similarity between Sungai Wain and the other forests is negatively related to spatial distance, we also found deviations from this relationship: the family and genus composition of Sungai Wain is more similar to that of Berau than to that of ITCI and Kutai, while Berau is located at the largest distance. Tree diversity is slightly lower in Sungai Wain than the average in these forests.

At the local scale, topographic variation was found to affect the plant community of Sungai Wain in some growth forms and some community characteristics, but most correlations were not significant. Moreover, nearly all significant correlations explained little variation in the plant community data and Detrended Correspondence Analyses (DCA) revealed only weak patterns in the species composition of the forest. In contrast, large gaps were found to affect species composition strongly and several species were found to have gap preferences. However, large gaps were rare in Sungai Wain making it unlikely that they accounted for much local variation in the plant community. Finally, we discuss the phenomenon that in tropical rain forests usually little floristic variation is explained by environmental variables.

INTRODUCTION

Plant community – environment relationships and spatial scale

Various studies in tropical rain forests have demonstrated relationships between plant community characteristics (i.e. forest structure, composition and diversity) and environmental variation. Among the best studied abiotic factors are mean annual rainfall (e.g. Gentry, 1988; Ter Steege et al., 2003; Slik et al., 2003), soil factors (e.g. Ashton, 1976; Potts et al., 2002), hydrology (e.g. Svenning, 1999; Harms et al., 2001), light climate (e.g. Davies et al., 1998; Webb & Peart, 2000); and spatial distance (e.g. Terborgh & Andresen, 1998; Pyke et al., 2001; Potts et al., 2002; Slik et al., 2003). However, a large amount of variation in the plant community usually remains unex-

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plained by the factors that were studied. This has led to theoretical models explaining the coexistence of species as a result of chance processes and limitations of dispersal (e.g. Hubbell, 2001; Chave & Leigh, 2002) rather than as a result of competition and niche differentiation related to variation in the abiotic environment.

During the past ten years, ecologists have become increasingly aware of the importance of spatial scale in studying relationships between biodiversity and the environment (e.g. Condit et al., 1996; Hamer & Hill, 2000). Field studies in tropical rain forests generally focus on environmental variation at two levels of spatial scale: phytogeographical and local variation. However, environmental factors affecting biodiversity were often shown to operate at very different spatial scales (Crawley & Harrel, 2001; Willis & Whittaker, 2002), which means that factors affecting a plant community at the phytogeographical scale do not necessarily cause variation at the local scale and vice versa.

Phytogeographical variation

At the phytogeographical scale, variation in the plant community of tropical rain forests is usually studied by comparing various sites within a specific region (e.g. Terborgh & Andresen, 1998; Ter Steege et al., 2000, 2003). In Borneo, phytogeographical variation was recently studied by Slik et al. (2003). Based on similarity in tree composition between lowland tropical rain forests at 28 localities, they distinguished five main floristic regions for this island. They considered rainfall and spatial distance to be the major determinants of the observed differences between the plant communities of these forests. Slik et al. (2003), however, mainly focused on variation in tree composition and diversity for the whole island. At smaller spatial scales, phytogeographical studies have been limited to certain areas in northern Borneo (Ashton, 1976; Baillie et al., 1987; Newbery, 1991; Potts et al., 2002). For the Indonesian province of East Kalimantan, little is known about the variation in plant community characteristics between forests, especially with regard to the forest structure and tree diversity at the species level.

Local variation

At the local scale, variation in the plant community of tropical rain forests is usually studied by comparing recording units (either plots or subplots) within a single forest (e.g. Condit et al., 1996; Svenning, 1999; Webb & Peart, 2000). In several local studies, topographic variables most strongly affected the plant community of the measured variables (e.g. Clark et al., 1999; Svenning, 1999). The relatively high impact of topography on the plant community is probably a result of the fact that it indirectly affects the vegetation in various different ways, since it is closely related to several soil factors such as texture (Davies et al., 1998; Clark et al., 1999; Webb & Peart, 2000), nutrient status (Baillie et al., 1987), and hydrology (Svenning, 1999; Harms et al., 2001). These soil factors themselves more directly affect growth conditions for plants as well as interactions between plants such as competition for resources, thereby finally leading to variation in forest structure, composition and diversity.

Canopy gaps, these being usually created by tree falls, also greatly influence the plant community of tropical rain forests (Brokaw, 1985, 1987; Denslow, 1987; Rose,

2000). In gaps, light intensity at lower strata is much higher than in the surrounding areas of closed canopy (Schultz, 1960; Whitmore et al., 1993). Due to a light climate being more favourable for the growth of plants, the vegetation soon becomes much denser at these strata after the creation of a canopy gap (Brokaw, 1985; Schnitzer et al., 2000). The vegetation structure of a canopy gap is therefore not only characterised by a more open canopy layer, but, soon after its creation, also by lower vegetation layers being more dense than in the understorey of closed canopy. Pioneer species (*sensu* Swaine & Whitmore, 1988) are plants that are specialised on canopy gaps. They have fast growth rates at high light intensities while being intolerant of shade (Whitmore, 1984; Brokaw, 1985; Denslow, 1987; Mabblerley, 1992). As these species are usually abundant in canopy gaps and relatively rare outside these patches, canopy gaps do have a different species composition from the surrounding forest. Forest diversity is enhanced by canopy gaps since pioneer species would have been absent in a forest without such gaps, as they are unable to establish below a closed canopy (Whitmore, 1984; Mabblerley, 1992).

Research questions

The core area in the forest of Sungai Wain is one of the last rain forests areas in the Balikpapan–Samarinda region of East Kalimantan not severely affected by fire, logging or other human influences (Fredriksson & De Kam, 1999). A better knowledge of its biodiversity may greatly support the protection of this valuable forest reserve. We studied its plant community both at a phytogeographical and a local scale. At the phytogeographical scale, we compared the plant community of Sungai Wain to other rain forests in East Kalimantan. At the local scale, we related the variation within the forest of Sungai Wain to topography and canopy gaps. Finally, we discussed our own observations in the context of ecological relationships demonstrated in previous studies.

We address three questions:

- 1) What are the plant community characteristics (i.e. tree structure, composition and diversity) of the Sungai Wain forest?
- 2) How do other rain forests in East Kalimantan compare to Sungai Wain in terms of plant community characteristics?
- 3) What part of the local variation in the plant community characteristics of the Sungai Wain forest is determined by environmental factors (in particular topography and canopy gaps)?

METHODS

Data collection

Within the Sungai Wain forest, three groups of plants (trees, lianas and small plants) and two topographic variables (elevation and inclination) were systematically recorded in two sets of 40 subplots (10 × 20 m) that were randomly located in plots of 18 ha and 450 ha (see Chapter 1 for details). In addition to these random subplots, 25 subplots (also 10 × 20 m) were established in the centre of canopy gaps that were scattered throughout the 450 ha plot. Canopy gaps were defined as openings in the

Table 2.1. General data of the forest inventories included in the phytogeographical study. Site = site name; Position = latitude and longitude position; Distance = distance in km between this site and Sungai Wain 1; Elevation = position in metres above sea level; Rainfall = mean annual rainfall at closest weather station in mm year⁻¹; Area = sampled area in ha; Trees = number of trees with dbh > 10 cm observed; Species = number of species observed.

No	Site	Position	Distance	Elevation	Rainfall	Area	Trees	Species	Reference
1.	Apo Kayan	115.00 E, 1.40 N	379	800	4152	1.12	750	264	Van Valkenburg (1997)
2.	Berau 1	117.15 E, 1.59 N	356	50	2329	3.00	2116	358	Slik (unpubl. data)
3.	Berau 2	117.08 E, 1.54 N	345	100	2329	0.30	186	96	Slik (unpubl. data)
4.	Berau 3	117.14 E, 2.02 N	362	85	2329	12.00	6302	478	Strek (unpubl. data)
5.	Bukit Bankirai	116.52 E, 1.02 S	10	80	2695	0.30	150	79	Slik (unpubl. data)
6.	ITCI 1	116.20 E, 0.49 S	64	120	2493	0.90	291	122	Slik (unpubl. data)
7.	ITCI 2	116.34 E, 0.54 S	39	440	2493	0.60	246	118	Slik (unpubl. data)
8.	ITCI 3	116.37 E, 0.56 S	30	140	2493	0.30	114	74	Slik (unpubl. data)
9.	ITCI 4	116.34 E, 0.61 S	30	300	2493	1.14	509	168	Eyk-Bos (unpubl. data)
10.	ITCI 5	116.34 E, 0.62 S	30	400	2493	2.00	771	242	Eyk-Bos (unpubl. data)
11.	ITCI 6	116.34 E, 0.59 S	32	400	2493	1.25	659	150	Eyk-Bos (unpubl. data)
12.	ITCI 7	116.34 E, 0.55 S	35	400	2493	1.65	574	150	Eyk-Bos (unpubl. data)
13.	Kutai NP.	117.25 E, 0.20 N	178	190	2108	0.80	337	82	Miyagi et al. (1988)
14.	Sungai Wain 1	116.49 E, 1.06 S	0	60	2472	1.60	753	193	This study
15.	Sungai Wain 2	116.49 E, 1.05 S	2	90	2472	3.60	1691	267	Van Nieuwstadt (unpubl. data)
16.	Wanariset Samboja 1	116.57 E, 0.59 S	20	80	2411	1.80	834	273	Slik (unpubl. data)
17.	Wanariset Samboja 2	116.58 E, 0.59 S	22	50	2411	10.50	5401	545	Kartawinata et al. (1981)
18.	Wanariset Samboja 3	116.58 E, 0.60 S	21	30	2411	0.51	264	117	Van Valkenburg (1997)

forest extending down through all foliage levels to a height of 5 m above ground. This is in accordance with the most commonly applied definition by Brokaw (1982), except that gaps were openings extending down to 2 m above ground in Brokaw's original definition. Our adjustment permits the inclusion of somewhat older gaps where tree regeneration is already well-developed. For canopy gaps, species were only recorded in a particular subplot when they were present with at least five stems taller than 1.3 m in that subplot. Exclusion of the less abundant species enabled us to study many more gaps in the same time span than would have been possible if all the present species had been included. Nearly all recorded species could then be identified in the field and plant collection and identification at the herbarium was reduced to a minimum amount of work.

Data from other inventories

In order to study the phytogeographical status of Sungai Wain, we compared our dataset (Sungai Wain 1) with those of 17 other rain-forest inventories in East Kalimantan (Table 2.1, Fig. 2.1), including seven inventories executed in the unlogged forests of the PT ITCI concession, a logging concession west of Balikpapan. The datasets included in this study had four characteristics in common:

- 1) an area of known size was recorded for the inventory;
- 2) all trees within the recorded area were included in the inventory;
- 3) each individual tree was assigned to a species, either identified or not; and
- 4) the diameter at breast height was measured for each individual tree.

Apart from these common characteristics, plot numbers, sizes and shapes often varied considerably between studies.

Data analysis

Three plant community characteristics were used to compare Sungai Wain 1 with the other forest inventories: tree structure, tree composition and tree diversity. Tree structure was studied by comparing tree densities in seven dbh classes: > 0 cm, > 1 cm, > 5 cm, > 10 cm, > 20 cm, > 40 cm and > 80 cm. These dbh classes correspond to the classes most commonly used in earlier studies.

Tree composition was studied by comparing the relative abundance of tree families and genera expressed as the percentage of all stems with dbh > 10 cm. The similarity in tree genus composition was studied between forest records by calculating percentage similarity (PS) in random samples of 200 trees using the Sørensen similarity index for quantitative data (Jongman et al., 1995):

$$PS_{ij} = 200 \sum_k \min(y_{ki}, y_{kj}) / (\sum_k y_{ki} + \sum_k y_{kj})$$

Tree diversity was studied by relating the number of species to the sampled area and to the number of stems in the forest record.

Local patterns in the plant community composition were studied by means of Detrended Correspondence Analysis (DCA), an indirect gradient analysis technique that detects gradients from species abundance data (Hill & Gauch, 1980; Jongman et al., 1995). DCA was performed using CANOCO software for Windows, version 4.02

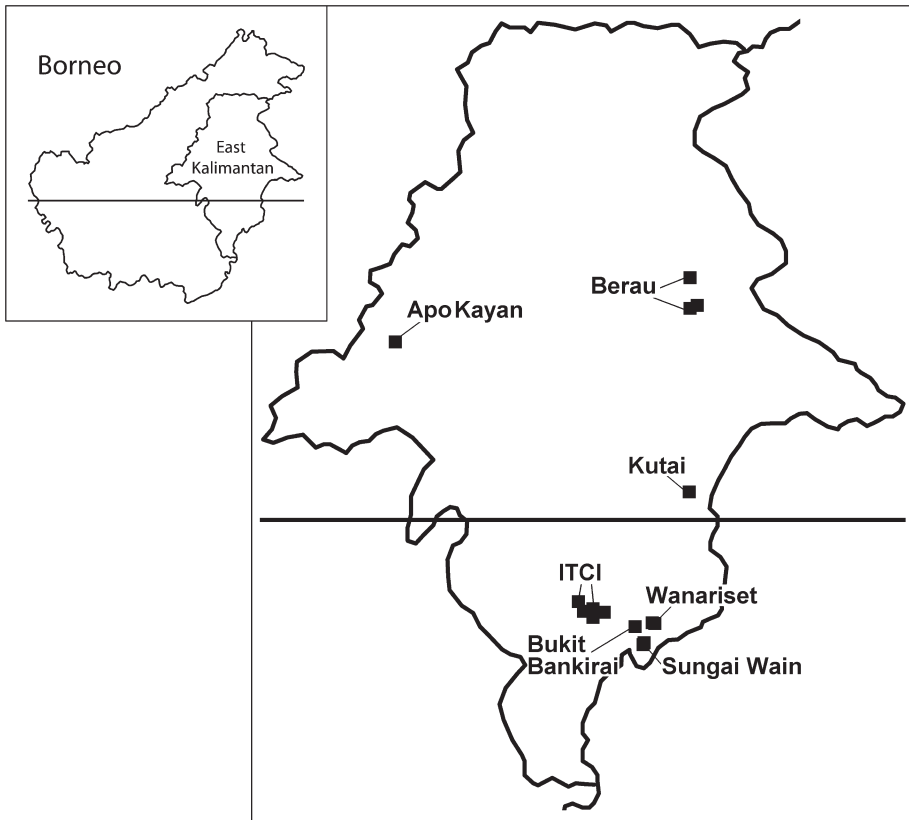


Fig. 2.1. Map of East Kalimantan showing the positions of all forest inventories included in the phytogeographical study. Names refer to the sites where these forest inventories were executed. See Table 2.1 for details of these inventories.

(Ter Braak, 1988; Ter Braak & Smilauer, 1998). All species with five or more recorded stems in the dataset (density > 3.1 stems ha^{-1}) were included in the DCA. Data were used untransformed and detrending was carried out by segments. Statistical analyses of the plant community structure and diversity were based on all recorded species.

The relationships between plant community characteristics and topographic variation were studied using continuous topographic variables (elevation and inclination), as well as by assigning the subplots to discrete topographic classes (ridge, slope and valley). As the latter method did not generate additional relationships between plant community and topography, only the results for the continuous topographic variables are shown. The continuous variables were preferred since they were calculated directly from the parameters that were actually measured in the field, while for topographic classes it was necessary to set additional limits based on arbitrary criteria. The relationships with continuous topographic variables were analysed by performing linear regression

analysis using SPSS 10.0 software for Windows. Bonferroni correction was used to compensate for multiple tests when several diameter classes were related to elevation and inclination and when several DCA-axes were related to these variables.

In order to study the species composition of gaps and gap preferences of species, the gap-plots were compared to the random subplots. As mentioned above, species were only recorded in the gap-plots when they were present with at least five stems taller than 1.3 m, while all species were recorded in the random subplots. In order to make both datasets comparable, species were eliminated from the record of a random subplot if they had less than five stems taller than 1.3 m in that subplot. Differences in the species composition were again studied using DCA, while species having preferences for canopy gaps were determined by means of the non-parametric Mann-Whitney test. Following previous species-environment studies executed in tropical rain forest and including many species (e.g. Svenning, 1999; Webb & Peart, 2000; Harms et al., 2001), no statistical correction was applied to compensate for the number of species tested.

RESULTS

Phytogeographical variation in forest structure

The forest structure of Sungai Wain 1 (this study) was studied by comparing tree densities of seven diameter classes with those of other forest inventories in East Kalimantan (Table 2.2). Most of these inventories included only trees with dbh > 10 cm but data on the stem diameters were not always available. As a result, thirteen forest records were available for comparison in the larger diameter classes, while only five records were available in the smaller diameter classes.

The forest structure of Sungai Wain 1 is rather typical of rain forests in East Kalimantan (Table 2.2). The density of trees with dbh > 10 cm varied between 323 stems ha⁻¹ in ITCI 1 and 722 stems ha⁻¹ in Berau 1. With 486 stems ha⁻¹, Sungai Wain 1 was not among the highest nor among the lowest values recorded. Forest records with similar values to Sungai Wain 1 were Bukit Bankirai (500 stems ha⁻¹), ITCI 4 (509), ITCI 5 (477), ITCI 7 (473), Sungai Wain 2 (470) and Wanariset 1 (463).

In Sungai Wain 1, tree densities in the higher diameter classes were also intermediate, both in absolute densities and in percentages of all trees with dbh > 10 cm (Table 2.2). Tree densities were highly variable between records in the largest diameter class (dbh > 80 cm), with Bukit Bankirai and Berau 1 having very low densities (3 or 4 stems ha⁻¹ and 0.6% of all stems with dbh > 10 cm), and ITCI 3 having very high densities (23 stems ha⁻¹ and 6.1% of all stems with dbh > 10 cm).

Tree densities were usually also intermediate in the smaller diameter classes of Sungai Wain 1 (Table 2.2). Here tree densities of Sungai Wain 1 were never the highest of the five forests records studied and were only the lowest in the smallest diameter class (dbh > 0 cm) when taken as a percentage of all trees with dbh > 10 cm (15.7%), while absolute tree densities in this diameter class were lowest in ITCI 3 (6907 stems ha⁻¹).

Table 2.2. Tree densities (stems ha⁻¹) for seven dbh classes at various sites. Densities relative to the dbh > 10 cm class between parentheses.

No.	Site	dbh > 0 cm	dbh > 1 cm	dbh > 5 cm	dbh > 10 cm	dbh > 20 cm	dbh > 40 cm	dbh > 80 cm
1.	Apo Kayan				670			
2.	Berau 1				722	224 (31.0%)	55 (7.6%)	4 (0.6%)
3.	Berau 2	13933 (22.5)	8683 (14.0)	1433 (2.3)	620	260 (41.9%)	97 (15.7%)	10 (1.6%)
4.	Berau 3				525	192 (36.6%)	53 (10.1%)	8 (1.5%)
5.	Bukit Bankirai	11070 (22.1)	6403 (12.8)	1153 (2.3)	500	163 (32.6%)	33 (6.6%)	3 (0.6%)
6.	ITCI 1				323	122 (37.8%)	39 (12.1%)	10 (3.1%)
7.	ITCI 2				410	167 (40.7%)	62 (15.1%)	13 (3.2%)
8.	ITCI 3	6907 (18.2)	4407 (11.6)	1073 (2.8)	380	153 (40.3%)	53 (14.0%)	23 (6.1%)
9.	ITCI 4				509	175 (30.4%)	51 (10.0%)	9 (1.8%)
10.	ITCI 5				386	134 (34.7%)	40 (10.4%)	8 (2.1%)
11.	ITCI 6				527	198 (37.6%)	65 (12.3%)	15 (2.8%)
12.	ITCI 7				348	118 (33.9%)	44 (12.6%)	8 (2.3%)
13.	Kutai NP				421			
14.	Sungai Wain 1	7606 (15.7)	6044 (12.4)	1310 (2.7)	486	176 (36.2%)	44 (9.1%)	10 (2.1%)
15.	Sungai Wain 2				470			
16.	Wanariset Samboja 1	10640 (23.0)	5807 (12.5)	1223 (2.6)	463	156 (33.6%)	39 (8.5%)	6 (1.3%)
17.	Wanariset Samboja 2				514			
18.	Wanariset Samboja 3				518			

Phytogeographical variation in tree composition

The tree composition of Sungai Wain 1 was studied by comparing the relative abundance of the ten most abundant families and genera with those of other inventories. The dominant tree family in Sungai Wain 1 was Sapotaceae, comprising 17.2% of all recorded stems (Table 2.3). *Madhuca kingiana* alone accounted for most of the dominance of Sapotaceae, as it was by far the most abundant tree species. It comprised 9.1% of all stems, while the second most abundant species was *Macaranga lowii* (Euphorbiaceae) comprising 5.8%. Bukit Bankirai was the only other forest record having Sapotaceae as the largest family. Other forest records, including Sungai Wain 2, always had Euphorbiaceae or Dipterocarpaceae as their largest tree family. In Sungai Wain 1 these two families were ranking second and third, respectively. While Euphorbiaceae and Dipterocarpaceae were always among the major tree families, Sapotaceae were often ranking the 10th to the 20th position in the other forest records. Other members of the ten most abundant families of Sungai Wain 1, e.g. Annonaceae, Burseraceae, Lauraceae, Leguminosae, Myristicaceae and Myrtaceae, were usually also among the ten most important families in other forest records. Only Ulmaceae s.l., this family comprising mainly trees of *Gironniera nervosa* in Sungai Wain, were never abundant in the forest records outside Sungai Wain.

At the genus level (Table 2.4), the results resembled those at the family level. *Madhuca* (Sapotaceae) was the dominant tree genus in Sungai Wain and in Bukit Bankirai, while it was usually much less abundant in other forests. *Shorea* (Dipterocarpaceae) was the dominant tree genus in most other inventories. Percentage similarity between Sungai Wain 1 and other forest records was calculated using the Sørensen similarity index for quantitative data (Fig. 2.2). Bukit Bankirai was the forest record being most

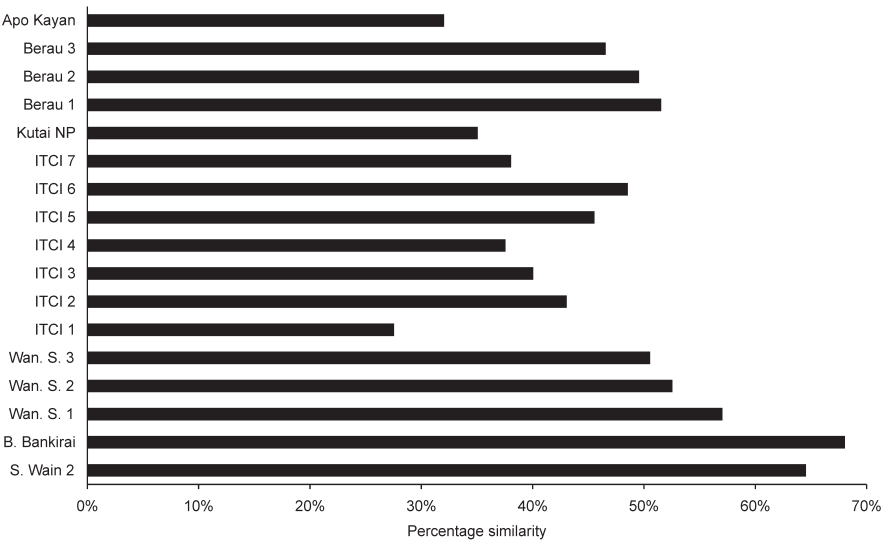


Fig. 2.2. Percentage similarity in tree genus composition between Sungai Wain 1 (this study) and 17 other forest inventories in East Kalimantan.

Table 2.3. Relative abundance of the ten most common families in Sungai Wain 1 (this study) at 18 sites. Relative abundance expressed as the percentage of all trees recorded during the inventory (and their rank, indicated with – if higher than 10).

Family	S. Wain 1	S. Wain 2	B. Bankirai	Wan. S. 1	Wan. S. 2	Wan. S. 3	ITCI 1	ITCI 2	ITCI 3
Annonaceae	3.1 (8)	1.6 (–)	3.4 (8)	2.5 (–)	6.5 (6)	3.8 (9)	2.1 (10)	3.0 (8)	5.4 (6)
Burseraceae	4.0 (7)	4.3 (7)	3.0 (9)	4.9 (7)	2.6 (–)	7.2 (6)	3.5 (6)	3.1 (7)	1.4 (–)
Dipterocarpaceae	12.8 (3)	11.8 (3)	13.9 (2)	14.0 (1)	8.4 (2)	8.4 (4)	24.2 (1)	13.2 (2)	18.2 (1)
Euphorbiaceae	16.9 (2)	14.8 (1)	10.2 (3)	14.0 (1)	14.4 (1)	11.0 (1)	16.5 (2)	16.7 (1)	14.4 (2)
Lauraceae	2.8 (10)	5.2 (5)	5.4 (6)	6.4 (5)	5.3 (8)	8.4 (4)	11.2 (3)	3.0 (8)	13.5 (3)
Leguminosae	2.9 (9)	4.5 (6)	4.0 (7)	3.2 (8)	3.7 (10)	4.9 (8)	0.7 (–)	1.4 (–)	1.4 (–)
Myristicaceae	4.9 (5)	6.5 (4)	5.7 (5)	7.0 (4)	7.3 (3)	5.7 (7)	2.5 (8)	3.7 (6)	2.1 (10)
Myrtaceae	5.9 (4)	3.3 (10)	6.3 (4)	5.8 (6)	6.7 (5)	8.7 (3)	2.1 (10)	10.8 (4)	2.8 (7)
Sapotaceae	17.2 (1)	13.0 (2)	19.5 (1)	8.3 (3)	7.1 (4)	9.1 (2)	1.4 (–)	11.2 (3)	6.4 (4)
Ulmaceae s.l.	4.8 (6)	4.0 (8)	2.2 (–)	1.1 (–)	1.1 (–)	1.5 (–)	0.7 (–)	0.4 (–)	0.7 (–)
Family	ITCI 4	ITCI 5	ITCI 6	ITCI 7	Kutai NP.	Berau 1	Berau 2	Berau 3	Apo Kayan
Annonaceae	3.3 (7)	3.8 (7)	2.7 (8)	5.4 (4)	9.1 (4)	1.4 (–)	0.8 (–)	2.4 (–)	4.7 (6)
Burseraceae	3.5 (6)	1.6 (–)	4.5 (5)	1.4 (–)	1.6 (9)	2.7 (9)	5.1 (6)	5.3 (5)	6.4 (3)
Dipterocarpaceae	29.4 (1)	19.3 (1)	37.3 (1)	29.9 (1)	22.5 (2)	26.8 (1)	34.1 (1)	26.3 (1)	18.0 (2)
Euphorbiaceae	16.5 (2)	16.8 (2)	14.7 (2)	17.6 (2)	27.2 (1)	8.2 (3)	5.3 (4)	14.4 (2)	20.6 (1)
Lauraceae	10.8 (3)	14.1 (3)	1.5 (–)	9.6 (3)	12.2 (3)	2.0 (–)	2.9 (8)	3.0 (10)	5.6 (5)
Leguminosae	1.4 (–)	0.8 (–)	2.4 (9)	0.2 (–)	4.4 (6)	3.3 (6)	2.3 (9)	3.0 (9)	2.1 (–)
Myristicaceae	2.0 (10)	4.1 (5)	2.9 (7)	2.1 (10)	2.2 (8)	2.8 (7)	5.3 (4)	5.7 (4)	1.3 (–)
Myrtaceae	1.6 (–)	4.0 (6)	4.7 (4)	2.3 (9)	1.3 (10)	4.2 (5)	6.8 (3)	4.3 (7)	6.0 (4)
Sapotaceae	6.3 (4)	6.9 (4)	8.6 (3)	3.7 (5)	0.3 (–)	14.5 (2)	8.9 (2)	7.1 (3)	1.7 (–)
Ulmaceae s.l.	0.2 (–)	0.4 (–)	0.0 (–)	0.5 (–)	0.6 (–)	2.2 (–)	2.2 (–)	0.4 (–)	0.0 (–)

Table 2.4. Relative abundance of the ten most common genera in Sungai Wain 1 (this study) at 18 sites. Relative abundance expressed as the percentage of all trees recorded during the inventory (and their rank, indicated with – if higher than 10).

Genus	S. Wain 1	S. Wain 2	B. Bankirai	Wan. S. 1	Wan. S. 2	Wan. S. 3	ITCI 1	ITCI 2	ITCI 3
<i>Cleistanthus</i>	2.5 (10)	2.8 (9)	2.1 (10)	0.0 (–)	0.1 (–)	0.4 (–)	0.0 (–)	13.8 (1)	0.2 (–)
<i>Dacryodes</i>	2.8 (9)	2.5 (10)	1.7 (–)	4.1 (5)	1.6 (–)	4.6 (3)	1.4 (–)	1.8 (8)	0.9 (–)
<i>Dipterocarpus</i>	3.6 (6)	3.9 (4)	1.6 (–)	1.9 (–)	0.9 (–)	1.1 (–)	0.4 (–)	0.0 (–)	0.7 (–)
<i>Drypetes</i>	3.6 (6)	2.0 (–)	1.7 (–)	4.3 (4)	2.3 (9)	2.7 (–)	0.4 (–)	0.0 (–)	1.7 (–)
<i>Gironniera</i>	4.8 (4)	4.0 (3)	2.2 (7)	1.1 (–)	1.1 (–)	1.5 (–)	0.7 (–)	0.4 (–)	0.7 (–)
<i>Knema</i>	3.1 (8)	2.9 (7)	3.0 (5)	3.5 (6)	3.2 (8)	4.6 (3)	1.8 (–)	1.6 (10)	1.9 (–)
<i>Macaranga</i>	4.5 (5)	3.7 (5)	1.5 (–)	3.5 (6)	0.8 (–)	1.1 (–)	0.4 (–)	0.0 (–)	2.4 (9)
<i>Madhuca</i>	16.0 (1)	9.2 (1)	17.4 (1)	4.4 (3)	5.1 (4)	4.6 (3)	0.4 (–)	9.6 (4)	3.5 (4)
<i>Shorea</i>	7.1 (2)	7.2 (2)	8.1 (2)	9.1 (1)	5.0 (5)	5.7 (2)	21.4 (1)	9.4 (5)	12.3 (1)
<i>Syzygium</i>	5.5 (3)	2.9 (8)	5.8 (3)	5.1 (2)	6.4 (1)	8.0 (1)	2.1 (9)	10.8 (2)	2.6 (7)

Genus	ITCI 4	ITCI 5	ITCI 6	ITCI 7	Kutai NP.	Berau 1	Berau 2	Berau 3	Apo Kayan
<i>Cleistanthus</i>	0.2 (–)	0.1 (–)	7.4 (2)	0.0 (–)	0.0 (–)	1.1 (–)	0.1 (–)	0.7 (–)	0.0 (–)
<i>Dacryodes</i>	1.8 (–)	0.9 (–)	2.9 (8)	0.5 (–)	0.6 (–)	1.3 (–)	2.9 (7)	3.2 (8)	3.9 (5)
<i>Dipterocarpus</i>	0.8 (–)	0.0 (–)	0.0 (–)	16.3 (1)	0.3 (–)	7.0 (4)	3.9 (6)	6.1 (2)	0.0 (–)
<i>Drypetes</i>	0.6 (–)	0.3 (–)	1.8 (–)	0.0 (–)	3.8 (9)	1.3 (–)	1.2 (–)	1.4 (–)	0.4 (–)
<i>Gironniera</i>	0.2 (–)	0.4 (–)	0.0 (–)	0.5 (–)	0.6 (–)	2.2 (10)	2.2 (9)	0.4 (–)	0.0 (–)
<i>Knema</i>	1.2 (–)	2.8 (6)	2.6 (9)	1.2 (–)	1.3 (–)	0.6 (–)	0.4 (–)	4.1 (6)	0.0 (–)
<i>Macaranga</i>	1.6 (–)	6.0 (2)	0.3 (–)	4.0 (5)	9.7 (4)	0.3 (–)	0.4 (–)	1.5 (–)	0.4 (–)
<i>Madhuca</i>	4.7 (3)	5.7 (2)	6.2 (4)	2.3 (8)	0.0 (–)	8.1 (2)	7.1 (3)	5.4 (3)	0.0 (–)
<i>Shorea</i>	22.7 (1)	14.0 (1)	25.1 (1)	12.0 (2)	10.3 (3)	12.8 (1)	7.9 (2)	12.5 (1)	3.9 (5)
<i>Syzygium</i>	1.6 (–)	4.0 (5)	4.7 (6)	2.3 (8)	1.3 (–)	3.8 (6)	6.8 (4)	4.2 (5)	5.6 (3)

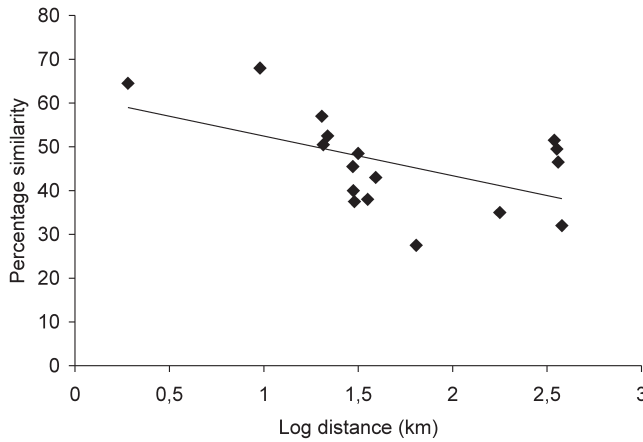


Fig. 2.3. Relation between percentage similarity in tree genus composition and log-transformed geographic distance between Sungai Wain 1 (this study) and 17 other forest inventories in East Kalimantan.

similar to Sungai Wain 1. It was even more similar than Sungai Wain 2. Generally, similarity was still high in the records of Wanariset, slightly lower in the Berau records, and even lower in the ITCI records. Forest records of very low similarity with Sungai Wain were those of Apo Kayan, Kutai National Park and ITCI 1. Similarity between Sungai Wain 1 and other forest inventories was generally decreasing with increasing log-transformed distance (Fig. 2.3). The distance was studied log-transformed because it has been shown that log-transformed distance reflects the decline of similarity between locations much better than untransformed distance (Condit et al., 2002).

Phytogeographical variation in tree species richness

The records in East Kalimantan forest studied were obtained from plots of very different size and shape and the sampled areas varied between 0.3 and 12 ha. Consequently, tree numbers in the records varied strongly with values ranging between 114 trees in ITCI 3 and 6302 trees in Berau 3. As species numbers increase with both increasing plot sizes and tree numbers (e.g. Condit et al., 1996), species-area and species-individual curves were used to compare species numbers of the forest records (Fig. 2.4).

Both the species-area and the species-individual curve indicate that tree species richness (i.e. species number) in Sungai Wain is slightly lower than the average of the forest records. Regression analysis showed that explained variation was higher when species richness was related to tree number ($r^2 = 0.87$) than when related to plot size ($r^2 = 0.76$), i.e. tree number was a better predictor for species richness than was plot size. In both the species-area and the species-individual curve, there were no outliers with a clearly higher or lower species diversity than average.

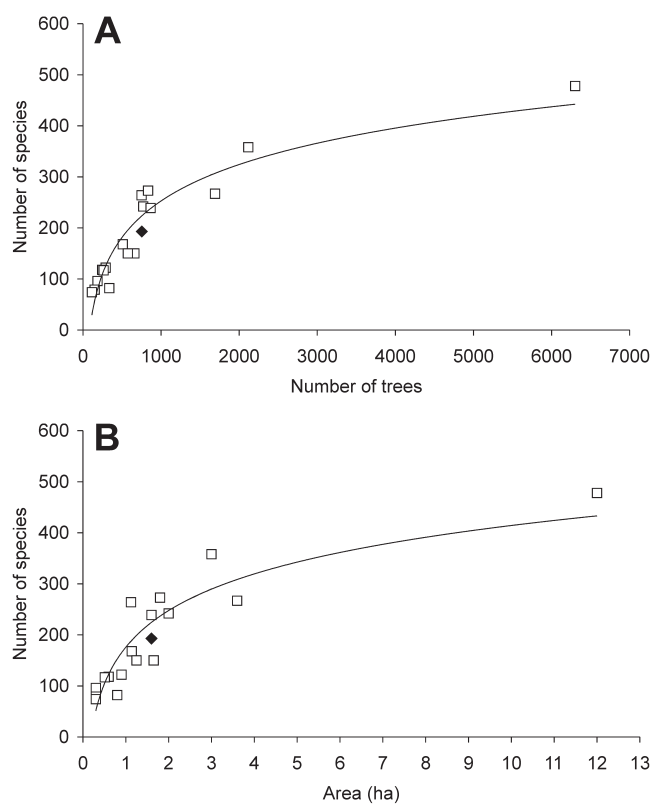


Fig. 2.4. Number of tree species related to the number of trees (dbh < 10 cm) (A) and to the recorded area (B) in forest inventories of East Kalimantan. ◆: Sungai Wain 1 (this study).

Local variation and topography

Two topographic variables were determined for all 80 subplots individually: elevation and inclination. The elevation of the subplots varied between 34 and 101 m a.s.l. with an average of 56.5 ± 13.0 m a.s.l. and the inclination varied between 0° and 26° with an average of $9.8^\circ \pm 6.5^\circ$. Local variation in the plant community structure, composition and diversity were then related to these variables. Forest structure was expressed as stem densities of lianas and various tree diameter classes and as the percentage ground cover of small plants. None of these parameters was significantly related to inclination, while only the cover of small plants was related to elevation ($y = -0.61x + 61.6$, $p < 0.005$, $r^2 = 0.173$). Thus, variation in the forest structure was apparently not explained by topography in Sungai Wain, except that small plants were more abundant at higher elevations.

Local variation in species composition was studied by Detrended Correspondence Analysis (DCA) of trees, lianas and small plants separately (Table 2.5). In trees, the first DCA-axis was negatively related to both elevation and inclination, showing that

Table 2.5. Linear regression analysis of the relation between species composition and topography. Species composition analysed for three growth forms separately using Detrended Correspondence Analysis (DCA) and then related to two topographic variables: elevation and inclination. Only the first four DCA-axes are shown with their percentage of explained variation. *) $p < 0.05$, ***) $p < 0.005$, NS not significant at $p < 0.05$.

	DCA-axis	Explained	Elevation	Inclination
Trees	DCA 1	6.1	$y = -0.057x + 6.21^{***}$	$y = -0.055x + 3.52^*$
	DCA 2	4.3	NS	$y = 0.049x + 1.58^*$
	DCA 3	3.0	NS	NS
	DCA 4	2.4	NS	NS
Lianas	DCA 1	9.1	NS	NS
	DCA 2	4.2	NS	NS
	DCA 3	3.7	NS	NS
	DCA 4	2.6	NS	NS
Small plants	DCA 1	8.7	$y = 0.050x - 2.60^{***}$	NS
	DCA 2	6.3	NS	NS
	DCA 3	4.4	NS	$y = 0.066x + 1.80^*$
	DCA 4	3.2	NS	NS

tree species composition changes towards higher elevations and towards steeper areas. Tree species like *Crudia reticulata* (Leguminosae), *Pentace laxiflora* (Malvaceae) and *Rinorea sp. 1* (Violaceae) were particularly abundant in flat areas at low elevations, while for example *Shorea laevis*, *Dipterocarpus confertus* (both Dipterocarpaceae) and *Macaranga lowii* (Euphorbiaceae) increased in abundance towards steeper areas and higher elevations. The second DCA-axis only showed a significant relation to inclination, while the next two DCA-axes were not at all related to the topographic variables.

In lianas no significant relations were found at all between DCA-axes and topography (Table 2.5). In small plants, the first DCA-axis was positively related to elevation, while the third DCA-axis was positively related to inclination (Table 2.5). This shows that species composition in small plants changed with both elevation and inclination, but different species assemblages accounted for these changes. Species composition changed towards higher elevations due to an increased abundance of *Ixora sp. 4* (Rubiaceae) and Zingiberaceae sp. 9, and changed towards steeper areas due to an increased abundance of *Scleria terrestris* (Cyperaceae) and *Hedyotis congesta* (Rubiaceae).

Local variation in species diversity was studied by relating species richness, i.e. the number of species per subplot, to elevation and inclination for trees, lianas and small plants separately (Fig. 2.5). Tree species richness was negatively related to elevation and not related to inclination. As with liana composition, no relations were found at all between liana diversity and topography. In small plants, species richness was negatively related to elevation and positively related to inclination. In summary, species richness in trees and small plants was higher towards lower elevations, while species richness in small plants was also higher towards steeper areas.

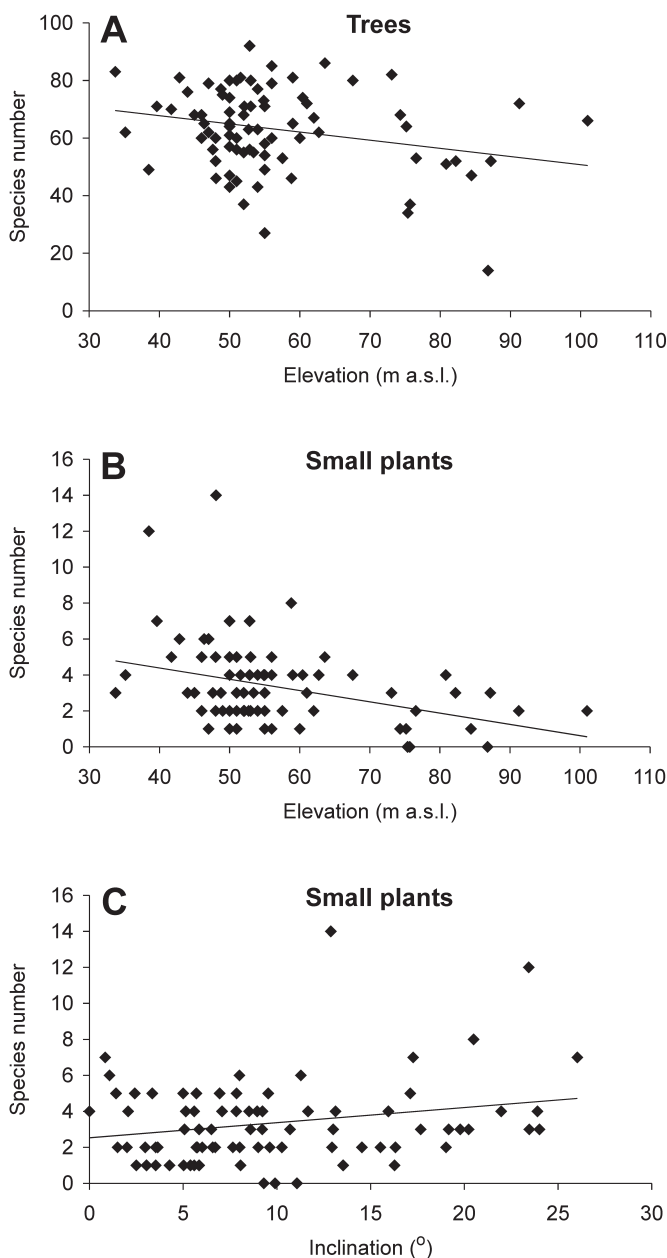


Fig. 2.5. Linear regression analysis of the relation between species richness in trees, lianas and small plants and two topographic variables: elevation and inclination. — A. Trees and elevation ($y = -0.284x + 79.1$, $p < 0.05$, $r^2 = 0.063$). — B. Small plants and elevation ($y = -0.063x + 6.89$, $p < 0.005$, $r^2 = 0.121$). — C. Small plants and inclination ($y = 0.084x + 2.53$, $p < 0.05$, $r^2 = 0.054$). The relations between trees and inclination, lianas and elevation, and lianas and inclination were not significant at $p < 0.05$ (data not shown).

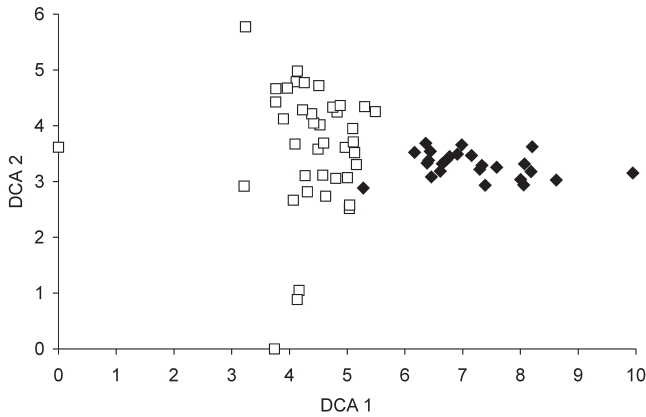


Fig. 2.6. Detrended Correspondence Analysis (DCA) of the species composition in 25 gap-plots (◆) and in 40 random subplots (□). DCA 2 (explained variation 3.7%) plotted against DCA 1 (5.0%).

Table 2.6. List of species that were significantly more often present in canopy gaps when compared to the random subplots (Mann-Whitney tests for $p < 0.05$, 58 species tested). Behind each species name the number of gap-plots (Gap, $n = 25$) and random subplots (Random, $n = 40$) having more than five stems exceeding 1.3 m in height of this species.

		Gap	Random
Trees	<i>Dillenia borneensis</i> (Dilleniaceae)	3	0
	<i>Macaranga bancana</i> (Euphorbiaceae)	6	0
	<i>Macaranga confiera</i> (Euphorbiaceae)	8	0
	<i>Macaranga gigantea</i> (Euphorbiaceae)	10	0
	<i>Macaranga hypoleuca</i> (Euphorbiaceae)	3	0
	<i>Macaranga trichocarpa</i> (Euphorbiaceae)	5	0
	<i>Vernonia arborea</i> (Compositae)	6	1
Lianas	<i>Ampelocissus winkleri</i> (Vitaceae)	4	0
	<i>Dissochaeta gracilis</i> (Melastomataceae)	4	0
	<i>Embelia</i> sp. 2 (Myrsinaceae)	3	0
	<i>Embelia</i> sp. 3 (Myrsinaceae)	4	0
	<i>Maesa ramentacea</i> (Myrsinaceae)	5	0
	<i>Spatholobus ferrugineus</i> (Leguminosae)	3	0
	<i>Tetracera scandens</i> (Dilleniaceae)	4	0
	<i>Uncaria barbata</i> (Rubiaceae)	9	0
	<i>Uncaria borneensis</i> (Rubiaceae)	3	0
	<i>Uncaria cordata</i> (Rubiaceae)	5	0
	<i>Uncaria kunstleri</i> (Rubiaceae)	3	0
Small plants	<i>Hedyotis congesta</i> (Rubiaceae)	8	1
	<i>Scleria terrestris</i> (Cyperaceae)	8	3

Local variation in species composition and canopy gaps

Within the 450 ha plot, species composition of the 25 gap-plots and the 40 random subplots was studied using DCA. Species composition in the gaps clearly differed from the random subplots (Fig. 2.6). Subplot scores on the first DCA-axis were always higher for gaps when compared to the random subplots, with the exception of one gap that had a much lower value than the other gaps. This shows that 24 gaps had a species composition being very different from non-gap areas, while only one gap had a species composition more or less typical of non-gap areas. On the other hand, none of the 40 random subplots had a species composition typical of gaps.

Pioneer species (*sensu* Swaine & Whitmore, 1988) are typically more abundant in canopy gaps than in the surrounding areas of closed canopy. In order to verify which species in the dataset are pioneers, the frequency of species in the gap-plots was compared to their frequency in the random subplots. In total, 20 out of 58 (34%) species were significantly more often present in canopy gaps and could be regarded as pioneer species (Table 2.6). Seven out of 29 (24%) tree species were found to be pioneer species in this way, including five species of the genus *Macaranga* (Euphorbiaceae) and two other species: *Vernonia arborea* (Compositae) and *Dillenia borneensis* (Dilleniaceae). Eleven out of 25 (44%) liana species were pioneer species, of which four belonged to the genus *Uncaria* (Rubiaceae) and two to the family Myrsinaceae. Finally, two species of small plants were significantly more often present in canopy gaps: *Hedyotis congesta* (Rubiaceae) and *Scleria terrestris* (Cyperaceae). As only four small plant species were included in the analysis, the percentage of pioneer species was still higher in this growth form (50%) than in trees.

DISCUSSION

Phytogeographical status of Sungai Wain

The forest structure of Sungai Wain seems to be typical of rain forests in East Kalimantan. In nearly all diameter classes, tree densities in Sungai Wain were not among the highest nor among the lowest densities in the studied forest records, even when considering the tallest diameter class (dbh > 80 cm) (Table 2.2). Fredriksson & De Kam (1999) and Van Nieuwstadt (2002) reported small-scale illegal logging in Sungai Wain. So far, the observed tree densities in the taller diameter classes indicate that these practices did not affect Sungai Wain more than other forests in East Kalimantan. The forest structure seems to be more strongly affected by logging in Bukit Bankirai and Berau I, where tall trees have much lower densities.

The tree family composition of Sungai Wain is also rather typical of forests in East Kalimantan, although relatively high numbers of Sapotaceae and Ulmaceae s.l. were observed (Table 2.3). Tree inventory data from 28 lowland rain forests throughout Borneo (see Slik et al., 2003, for details) suggest that the large proportion of Sapotaceae is a feature that is shared with several other forests in East Kalimantan and seems to be typical of rain forests in this part of Borneo. However, Sungai Wain and Bukit Bankirai were the only two forests where Sapotaceae reach a dominant position among the tree families. These two forests therefore seem to be the most characteristic examples of the Sapotaceae-rich forests in East Kalimantan. *Madhuca kingiana* is very abundant

in these two forests, while other species of *Madhuca* and some *Palaquium* species are dominant in the forests elsewhere in East Kalimantan. The relatively high abundance of *Ulmaceae* s.l. in Sungai Wain apparently does not reflect a phytogeographical pattern. It was the result of a single species (*Gironiera nervosa*) that was only very abundant in the Sungai Wain forest.

Bukit Bankirai is the forest being most similar to Sungai Wain (Fig. 2.2). This result is partly explained by the shared dominance of *Madhuca kingiana*, but still holds even if this species is excluded from the analysis. Bukit Bankirai is also the locality at the shortest distance from Sungai Wain (c. 10 km). Wanariset Samboja is the second most similar forest (Fig. 2.2; Slik et al., 2003) and is also second closest to Sungai Wain (c. 20 km). These results obviously reflect the close relationship between geographical distance and similarity in tree composition that was often observed before (e.g. Terborgh & Andresen, 1998; Pyke et al., 2001; Potts et al., 2002; Slik et al., 2003). However, we also found a clear deviation from this relationship: the forest records of Berau were generally more similar to Sungai Wain than those from ITCI and Kutai (Fig. 2.2), but are at a much larger distance (Table 2.1). Moreover, this seems to contradict the proposed floristic regions by Slik et al. (2003). They assigned the Berau area to a floristic region different from that with Sungai Wain, ITCI and Kutai, although they stated that the forest community in Berau was in fact almost intermediate between both floristic regions. The altitudinal position of the forest records might explain this deviation from the relation between distance and floristic similarity. Both the forests of Sungai Wain and Berau are located at 100 m a.s.l. or at lower altitudes, while those of ITCI and Kutai are located at higher altitudes (Table 2.1). Altitude has often been shown to affect the tree community in tropical rain forests (e.g. Kitayama, 1992). Additional research on the floristic composition of these forests in relation to their altitudinal position (not topographic position) is therefore necessary to fully understand the complex phytogeographical relationships between these areas.

In contrast to other phytogeographical studies (e.g. Slik et al., 2003), we did not have sufficient data to study the relation between tree similarity and mean annual rainfall. The forest at Apo Kayan has a much higher rainfall than the other forests studied in East Kalimantan (Table 2.1) and is also among the forests being most dissimilar to Sungai Wain. However, this high dissimilarity can equally well be explained by the fact that it was recorded at the highest altitude or by the fact that it was at the largest distance from Sungai Wain. Too little variation was present in the other forest records to study the impact of rainfall on tree composition separately from other environmental factors.

Tree species richness in Sungai Wain seems to be slightly lower than average for forests in East Kalimantan (Fig. 2.4). This was also observed for tree diversity at the genus and family level by Slik et al. (2003). An obvious explanation could be that the strong dominance of *Madhuca kingiana* decreases overall tree diversity. However, this species was even more dominant in Bukit Bankirai, though species richness is slightly higher than average in this forest. Slik et al. (2003) also report very different values for tree diversity in forests that were near to each other. In order to understand the underlying mechanisms that explain this phenomenon, future research should combine diversity studies at the phytogeographical scale with local diversity studies.

Local variation and topography

The observed topographic variation within the Sungai Wain forest was expected to affect the plant community characteristics, since local variation in topography was often found to be related to soil factors that directly affect plants (see Introduction). However, rather few close relationships between plant community characteristics and topographic variables were actually found in this study (Table 2.5, Fig. 2.5). In lianas, none of the studied relationships was found to be statistically significant. Several relationships were statistically significant in trees and small plants, but the total amount of variation explained by these relations was generally low (12% or less). An exception to this was the negative correlation between the ground cover of small plants and elevation, where 17% of all variation in cover was explained by elevation alone. Generally, relations between individual species distributions and topographic position are also rather weak in tropical rain forests (Pitman et al., 1999; Clark et al., 1999; Svenning, 1999; Webb & Peart, 2000; Harms et al., 2001), in spite of the fact that several authors considered topography to be the most important abiotic factor (e.g. Clark et al., 1999; Svenning, 1999).

Apparently, patterns in the species composition are rather weak as well in Sungai Wain. The DCA-axes never explained more than 9.1% of the variation in species composition in our study (Table 2.5). Similarly, Webb & Peart (2000) never found more than 9.4% of the variation explained by Principal Component Analyses (PCA) on rain-forest trees and seedlings in West Kalimantan, in spite of the fact that PCA-axes principally explain more variation than do DCA-axes (Jongman et al., 1995). Although patterns in species composition were rather weak, we nevertheless found these patterns to be related to elevation and inclination in both trees and small plants (Table 2.5). Similar relations between species composition and topography have also been observed in previous studies (Clark et al., 1999; Svenning, 1999; Webb & Peart, 2000).

Local variation and canopy gaps

In the Sungai Wain forest, canopy gaps generally have a very different species composition from that of the surrounding areas of closed canopy (Fig. 2.6). However, few gaps larger than 400 m² were present in this forest and most of them were sampled during our gap-plot study. None of the 80 random subplots was located in such a gap. It is therefore unlikely that large gaps explain much local variation in the plant community.

Pioneer species (*sensu* Swaine & Whitmore, 1988) are restricted to (former) canopy gaps since they are unable to establish themselves below a closed canopy. The degree to which canopy gaps have a different species composition compared to other parts of the forest will therefore be strongly dependent on the number of pioneer species present in the forest. One of the gaps in our study had a species composition that was very similar to those of random subplots below closed canopy (Fig. 2.6). Apparently, this was explained by the fact that this was a very recent gap and pioneers species were not yet established. However, the fact that the other 24 studied canopy gaps had a very different species composition from those of the random subplots indicates that Sungai Wain harbours relatively many pioneer species.

Within Sungai Wain, 20 plant species were shown to occur more frequently in canopy gaps (Table 2.6). This was 34% of all species recorded in canopy gaps. Of the recorded tree species 24% were shown to be pioneers. For tree seedlings in the understorey of a rain forest in northern Borneo, the abundance of 18% of the species was shown to be positively related to high light intensities (Webb & Peart, 2000). However, the lower proportion of trees with pioneer characteristics observed in the latter study may well result from the different method applied, as the two species that were included in both studies, *Xanthophyllum stipitatum* (Polygalaceae) and *Neoscortechinia kingii* (Euphorbiaceae), were found to be positively related to high light intensities in northern Borneo, but were not found to have gap preferences in Sungai Wain. This supports the hypothesis that more species in Sungai Wain are positively related to high light intensities than the 20 species that were found to be pioneers according to the definition of Swaine & Whitmore (1988).

Macaranga (Euphorbiaceae) was clearly the most important pioneer genus among trees, while *Uncaria* (Rubiaceae) was equally important among pioneer lianas (Table 2.6). *Macaranga* is considered to be the most important pioneer genus in Southeast Asia (e.g. Whitmore, 1984) and was therefore often used for ecological studies on pioneer trees (e.g. Primack & Lee, 1991; Davies et al., 1998; Slik, 2001). In contrast, *Uncaria* received little attention but seems to be an equally suitable genus for studying pioneer lianas. There were about 12 *Uncaria* species present in the area and they were all relatively abundant in the seed bank, in disturbed forests, as well as in canopy gaps (see Chapter 3).

Unexplained local variation

In this study, both topography and canopy gaps were shown to affect the plant community in Sungai Wain. In addition, both factors were often considered to be among the most important environmental variables structuring plant communities in tropical rain forests in previous publications (e.g. Brokaw, 1985, 1987; Clark et al., 1999; Svenning, 1999; Web & Peart, 2000). Topography indirectly affects the vegetation by controlling soil factors like hydrology, nutrients, toxic elements and texture (Webb & Peart, 2000; Harms et al., 2001). Canopy gaps indirectly affect the vegetation by controlling light intensity and quality, soil and air temperature, and relative humidity (e.g. Schultz, 1960; Denslow, 1987; Whitmore et al., 1993).

In addition to topography, canopy gaps and the above-mentioned abiotic factors related to them, several other environmental factors have been shown to affect plant communities of tropical rain forests. At a local scale, interactions with animals such as predation, pollination and dispersal (Harms et al., 2000) have been shown to affect plant community characteristics within rain forests. At a phytogeographical scale, rainfall (Gentry, 1988; Ter Steege et al., 2000; Slik et al., 2003), Pleistocene climatic fluctuations (Haffer, 1969; Prance, 1982), isolation and habitat size (Ter Steege et al., 2000; Slik et al., 2003) have all been considered to account for variation among tropical rain forests. Moreover, spatial distance between inventories often accounts for a rather large part of the remaining unexplained variation, both at the local scale (Tuomisto et al., 1995; Svenning, 1999) and at the phytogeographical scale (Terborgh & Andresen, 1998; Pyke et al., 2001; Potts et al., 2002; Slik et al., 2003; Fig. 2.3). Perhaps these

additional factors are all active controllers of the plant community in Sungai Wain: further local and phytogeographical studies should throw light on this.

In spite of the fact that we showed several significant relationships between the plant community and environmental factors (topography and canopy gaps), by far the greatest variation in the plant community remains unexplained in our study. Two hypotheses can be proposed for this:

- 1) other environmental variables that we did not study (like the above-mentioned ones) are more important factors controlling the plant community variation; or
- 2) most of the variation is random with respect to the environment.

The second hypothesis is supported by studies that were including other environmental factors, both at the local scale (e.g. Pitman et al., 1999; Webb & Peart, 2000; Harms et al., 2001) and at the phytogeographical scale (e.g. Ter Steege et al., 2000). All these studies report a high proportion of unexplained variation, suggesting that most of the variation in plant communities of tropical rain forests will be random with respect to the environment. Several recent theoretical models have therefore attempted to explain plant diversity by random processes and dispersal limitation in tropical rain forests (e.g. Hubbell, 2001; Chave & Leigh, 2002). However, it should be realised that field studies never capture the full floristic and environmental variation that is actually present in the forest (see Clark et al., 1999, for a detailed discussion). It is therefore likely that in reality environmental variation accounts for more floristic variation than is reflected in our correlations.

STRUCTURE, COMPOSITION AND DIVERSITY OF PLANT COMMUNITIES IN BURNT AND UNBURNT RAIN FOREST¹

SUMMARY

The impact of El-Niño fires on plant communities was studied in once-burnt, twice-burnt, and unburnt rain forest in the Balikpapan region of East Kalimantan, Indonesia. Two sets of 40 randomly located subplots within areas of 18 ha and 450 ha were sampled for all terrestrial vascular plant species, their soil seed bank and topographic position. Structure, composition and diversity of the vegetation were assessed using plant types that can be readily applied in the field. As floristic similarity between unburnt forests in the study sites was shown to be very high when compared to other unburnt forests in Kalimantan, the impact of fire is likely to be the single most important factor determining the differences between the plant communities of the three forests.

Strong differences in the species composition of the three forests were found, and the abundance of most plant types differed significantly between forests. Young trees in the twice-burnt forest were as abundant as in the unburnt forest, while they were considerably less abundant in the once-burnt forest. In the twice-burnt forest, the second fire apparently stimulated the regeneration of a limited set of pioneer species thereby compensating for a reduction in the regeneration of the majority of the tree species after the first fire.

The impact of fire on plant diversity was strongly dependent on the spatial scale at which it was assessed. Differences in species richness at the subplot-scale reflected differences in abundance rather than true species richness. Only species richness at the landscape-scale was therefore used as a criterion for assessing plant diversity. Overall plant diversity was somewhat lower in the burnt forests, though only trees accounted for this difference. There was no difference in liana diversity between forests, while small plants such as herbs and shrubs were more abundant and species-rich in the burnt forests.

Our results show that the burnt forests still have a high regenerative power. This indicates that as long as fires are infrequent events, rain forests are able to conserve most of their plant diversity. However, since fires occur at high frequencies nowadays due to interaction with human activities and positive feedback, subsequent high-frequency wildfires rather than El-Niño fires alone have the potential to cause permanent deforestation and loss of biodiversity.

INTRODUCTION

Although the processes that cause tropical deforestation by fire are largely known (see Chapter 1), it is still not clear to what extent the ENSO fires actually caused deforestation and loss of biodiversity. Recent studies report abundant regeneration in the burnt forests (e.g. Siegert et al., 2001; Dennis et al., 2001) but do not provide information on species composition and diversity. Subsequent studies on diversity and composition mainly focused on the effects on tall trees of dbh > 10 cm (e.g. Slik et al., 2002; Van Nieuwstadt, 2002). But trees are not the only plants present in the tropical rain-forest ecosystem. Other growth forms like herbs, shrubs and lianas generally constitute a large component of the total plant diversity. The impact of fire on these plants has nevertheless

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received little attention. The frequency of lianas has been quantified in burnt forests of the Amazon region but without information on species diversity (Cochrane & Schultze, 1998, 1999). In addition, development of the ground layer has been quantified after the 1982–1983 fires in Borneo (Nykvist, 1996). These studies showed that growth forms other than trees strongly increased in abundance but did not provide information on the responses of individual species. This information is essential for understanding fire effects on plant diversity, as an increase in overall abundance does not mean that all species benefit from fires. It may well be accompanied by a change in species composition and loss of many species characteristic of the original forest.

Here we present the results of a first detailed inventory of burnt and unburnt rain forests in the Indonesian province of East Kalimantan, including all terrestrial vascular plants. Tree regeneration was also studied. We compared forests that were burnt, once (1998) and twice (1982–1983 and 1998) by ENSO fires, with one of the last areas of unburnt lowland rain forest left in this region. We analysed the structure and composition of these forests by assigning species to plant types that can be readily applied in the field. We assessed the impact of fires at the landscape scale to ensure that our plant diversity assessments were representative for the large-scale at which disturbance itself took place. Finally, we discuss the most relevant phenomena that arise from our results in order to answer the following questions:

- 1) To what extent may factors other than fire have contributed to differences in the plant community between the three forests?
- 2) To what extent is the forest structure (permanently) affected by the fires?
- 3) To what extent is the impact of the fires on plant diversity related to scale of assessment?
- 4) To what extent were the two burnt forests able to maintain their high plant diversity?

METHODS

Plant types

In order to provide a detailed description of the structure and composition of the terrestrial vascular plant community in the three forests, all species were assigned to plant types based on growth form and taxonomic criteria (Table 3.1). The criteria used were chosen in such a way that they provided maximum information about the forest structure and composition while still being easy to apply for non-specialists in comparative studies in East Kalimantan and elsewhere in the tropics. To enhance compatibility with growth forms that were used in similar studies in the past, species were first assigned to three major plant groups: trees, lianas and small plants (see Chapter 1 for details on this classification). Several plant types were distinguished within these three major groups, based on taxonomic criteria and growth form. Taxonomic criteria were chosen in such a way that the resulting plant types are easy to recognize in the field by non-taxonomists. Trees and lianas were subdivided using only taxonomic criteria, but small plants were also subdivided according to their growth form:

- 1) Small climbers: species that need external support for their height growth at maturity (average stem diameter of mature individuals less than 0.5 cm).

Table 3.1. List of the plant types used in this study and the taxa, growth form and size class they are representing.

Plant type	Taxa	Growth form and size
Trees (woody non-climbers > 2 m tall)		
Palms – trees	Palmae	woody non-climbers, height > 2 m
Bamboos – non-climbers	Gramineae–Bambusoidae	woody non-climbers, height > 2 m
Monocots – treelets	Other Monocotyledonae	woody non-climbers, height > 2 m
Dicots – trees	Dicotyledonae	woody non-climbers, height > 2 m
Gymnosperms – trees	Gnetopsida + Pinopsida	woody non-climbers, height > 2 m
Ferns – trees	Filicopsida	woody non-climbers, height > 2 m
Lianas (climbers with stem diameter > 0.5 cm)		
Palms – lianas (rattans)	Palmae	climbers with stem diam. > 0.5 cm
Bamboos – lianas	Gramineae–Bambusoidae	climbers with stem diam. > 0.5 cm
Monocots – lianas	Other Monocotyledonae	climbers with stem diam. > 0.5 cm
Dicots – lianas	Dicotyledonae	climbers with stem diam. > 0.5 cm
Gymnosperms – lianas	Gnetopsida	climbers with stem diam. > 0.5 cm
Ferns – lianas	Filicopsida	climbers with stem diam. > 0.5 cm
Small plants (herbs, woody climbers with stem diameter < 0.5 cm, woody non-climbers < 2 m tall)		
Palms – palmlets	Palmae	woody non-climbers, height < 2 m
Monocots – grass-like	Gramineae + Cyperaceae	herbaceous, leaves linear
Monocots – other herbs	Monocotyledonae	herbaceous non-climbers
Dicots – small climbers	Dicotyledonae	climbers with stem diam. < 0.5 cm
Dicots – small shrubs	Dicotyledonae	woody non-climbers, height < 2 m
Dicots – herbs	Dicotyledonae	herbaceous non-climbers
Ferns – small climbers	Filicopsida	climbers with stem diam. < 0.5 cm
Ferns – treelets	Filicopsida	woody non-climbers, height < 2 m
Ferns – herbs	Filicopsida + Lycopsida	herbaceous non-climbers

- 2) Small shrubs and treelets: non-climbing species having woody stems at maturity (average height of mature individuals less than 2 m).
- 3) Grass-like herbs: non-climbing herbaceous species of Gramineae and Cyperaceae having linear leaves (lamina length/width ratio < 0.2).
- 4) Herbs: other non-climbing species having herbaceous stems.

Seed bank analysis

All plant types and two topographic variables (elevation and inclination) were systematically recorded in two sets of 40 subplots (10 × 20 m) that were randomly located in plots of 18 ha and 450 ha (see Chapter 1 for details). In addition, soil samples (12 × 12 × 3 cm) from the corners of each subplot in the 450 ha plots were collected in April 2000 and plated on trays in a stratified random design at the nursery of the Wanariset Station. Twelve control trays received soil that was sterilized by heating. The trays received water once or twice a day depending on the weather. To avoid excessive transpiration of seedlings, all trays were shaded by nets that reduced the relative light intensity to 30–40%. Newly germinated seedlings were identified every two weeks

until no new seedlings germinated anymore (13 weeks). Unfortunately, we did not have the opportunity to check for ungerminated seeds at the end of our experiment. We did not include ferns and lycopods as they have very small spores that germinated throughout the nursery.

Data analysis

Data analysis was largely executed with the use of SPSS 10.0 software. Comparisons and statistical tests between sites were executed with the notion that the principal treatment was the spatial variable site itself, not fire disturbance history. The role of fire disturbance history and factors other than fire in the explanation of the observed differences between sites are therefore further elaborated in the discussion section. When statistical tests between sites were executed for several plant groups, alpha was corrected using Bonferroni correction.

Estimations of total species richness were based both on the Incidence-based Coverage Estimator (ICE) and Fisher's alpha. These indices are rather different in the way total species richness is estimated for a given area, but both methods have often been used in previous studies. The non-parametric ICE-index provides estimations of total species richness based on presence-absence data of species in samples (see Lee & Chao, 1994; Chazdon et al., 1996, for details). The total number of species is estimated by:

$$S_{ice} = S_{freq} + S_{infr}/C_{ice} + Q_1/C_{ice} * \gamma_{ice}^2$$

S_{ice} = ICE-estimated total number of species
 S_{freq} = number of frequent species (each found in more than 10 quadrats)
 S_{infr} = number of infrequent species (each found in 10 or fewer quadrats)
 Q_1 = number of species that occur in exactly 1 quadrat
 $C_{ice} = 1 - Q_1/N_{infr}$
 N_{infr} = total number of individuals in infrequent species
 $\gamma_{ice}^2 = \max \{S_{infr}/C_{ice} * m_{infr} / (m_{infr} - 1) * 10 \sum_{j=1}^{m_{infr}-1} (j-1) Q_j / N_{infr}^2 * -1, 0\}$
 m_{infr} = number of quadrats that have at least one infrequent species

The ICE-index is an adapted version of the Chao 2-index that was used in several earlier biodiversity studies. It was shown to be the best non-parametric estimator of species richness in the regeneration of tropical primary and secondary rain forests (Chazdon et al., 1996).

Fisher's alpha index is based on the assumption that the abundances of species fit a log-series distribution (Fisher et al., 1943; Rosenzweig, 1995). It is defined by:

$$s = \alpha * \ln(1+n/\alpha) \quad (1)$$

α = Fisher's alpha
 n = number of individuals
 s = number of species

Fisher's alpha can be calculated for each of our three study areas by equation (1) using n as the average number of individuals per subplot and s as the average number of spe-

cies per subplot. In non-contiguous plots of three primary rain forests, Fisher’s alpha has been shown to be independent of tree numbers when at least 1000 individuals were used for its calculation (Condit et al., 1996). Assuming that Fisher’s alpha is constant with increasing individual numbers, we estimated the total number of species in each study area using equation (1) by substituting the estimated total number of individuals per study area (N) for n and by calculating α from the subplots in the study area under consideration.

As the subplots were allocated randomly with respect to stem densities (stems per ha) within the three study areas, it was very likely that stem densities of the total areas were close to the average of all subplots in those areas. Consequently, the number of individuals in the total study area N could be estimated by equation (2).

$$N = n * (A / a) \tag{2}$$

a = subplot size (0.02 ha)

n = average number of individuals per subplot

A = size of study area (450 ha)

N = total number of individuals in the entire study area

The estimations of the ICE- and Fisher’s alpha index as well as the species accumulation curves were performed using EstimateS version 6.0.b1, a program that can be downloaded together with a manual free of charge from the internet at <http://viceroy.eeb.uconn.edu/estimates>. Calculations of both indices were based on 500 randomisations with default settings. Further details about the procedures are explained in the manual and in Colwell & Coddington (1994).

RESULTS

Topography and unburnt patches in the three forests

Small, though significant, differences were found in elevation and inclination (Table 3.2). The subplots in the once-burnt forest were located on average 24 m higher above sea level than those in the unburnt and twice-burnt forest. In addition, slopes were significantly steeper in the twice-burnt forest than in the other two forests. The cover by unburnt forest patches was not significantly different between the two burnt forests.

Table 3.2. Topographic variation and fire damage (average \pm standard deviation) per forest type and the results of a Mann-Whitney test between forest types ($p < 0.05$).

Variable	Unburnt forest (0)	Once-burnt forest (1)	Twice-burnt forest (2)	Mann-Whitney test
Elevation (m a.s.l.)	56.5 \pm 13.0	80.6 \pm 16.8	56.6 \pm 17.2	1 > 0 = 2
Inclination (°)	9.8 \pm 6.5	10.3 \pm 7.0	15.4 \pm 7.1	2 > 0 = 1
Unburnt (% cover)	0.0 \pm 0.0	11.6 \pm 27.4	8.1 \pm 22.8	0 > 1 = 2

Table 3.3. Abundance and species richness (average \pm standard deviation) at two spatial scales for all large plant types and forest types. Abundance expressed as densities of stems exceeding 1.3 m in height. Species richness at the subplot scale expressed as species numbers per subplot and at the landscape scale as the total observed species numbers in all subplots together and as the Fisher's alpha estimated total per forest type for trees and lianas (between parentheses, see text for explanation). **Bold** averages for the burnt forest types differ significantly from those of the unburnt forest (Mann-Whitney tested with Bonferroni correction for multiple tests).

Large growth forms	Abundance (stems ha ⁻¹)			Species per subplot (10 × 20 m)			Total species number			
	Once-burnt		Twice-burnt	Once-burnt		Twice-burnt	Unburnt		Once-burnt	Twice-burnt
	Unburnt	Once-burnt	Twice-burnt	Unburnt	Once-burnt	Twice-burnt	Unburnt	Once-burnt	Twice-burnt	
Plant types										
Palms – trees	20 ± 53	19 ± 45	15 ± 28	0.28 ± 0.57	0.21 ± 0.41	0.26 ± 0.47	6	2	5	
Bamboos – non-climbers	0.6 ± 5.6	3.8 ± 33.5	41 ± 273	0.01 ± 0.11	0.01 ± 0.11	0.04 ± 0.19	1	1	1	
Monocots – treelets	1.9 ± 9.6	0.6 ± 5.6	3.1 ± 16.6	0.04 ± 0.19	0.01 ± 0.11	0.04 ± 0.19	1	1	2	
Dicots – trees	7578 ± 2256	2368 ± 1490	7263 ± 4063	62.7 ± 14.6	20.7 ± 10.6	31.4 ± 16.2	500	322	414	
Gymnosperms – trees	5.0 ± 17.1	1.3 ± 7.9	0.6 ± 5.6	0.09 ± 0.28	0.03 ± 0.16	0.01 ± 0.11	2	1	1	
Ferns – trees	0.0 ± 0.0	0.6 ± 5.6	0.0 ± 0.0	0.00 ± 0.00	0.01 ± 0.11	0.00 ± 0.00	0	1	0	
Palms – lianas (rattans)	216 ± 283	98 ± 192	88 ± 349	1.51 ± 1.27	0.50 ± 0.81	0.53 ± 1.17	31	8	13	
Bamboos – lianas	0.0 ± 0.0	0.0 ± 0.0	880 ± 3486	0.00 ± 0.00	0.00 ± 0.00	0.59 ± 0.50	0	0	1	
Monocots – lianas	39 ± 54	16 ± 46	41 ± 65	0.61 ± 0.77	0.31 ± 0.85	0.58 ± 0.84	11	12	12	
Dicots – lianas	1083 ± 724	957 ± 641	1006 ± 1136	11.7 ± 6.4	10.0 ± 5.5	10.6 ± 8.2	139	124	156	
Gymnosperms – lianas	0.0 ± 0.0	1.9 ± 16.8	8.8 ± 46.9	0.00 ± 0.00	0.03 ± 0.22	0.10 ± 0.41	0	2	6	
Ferns – lianas	1.3 ± 7.9	113 ± 143	104 ± 169	0.03 ± 0.16	0.71 ± 0.48	0.58 ± 0.52	1	2	2	
Growth forms										
Trees	7606 ± 2250	2394 ± 1504	7323 ± 4089	63.1 ± 14.6	21.0 ± 10.9	31.8 ± 16.4	510 (1118)	328 (812)	423 (908)	
Lianas	1339 ± 818	1186 ± 803	2128 ± 3668	13.9 ± 7.5	11.6 ± 6.5	13.0 ± 10.1	182 (450)	148 (360)	190 (435)	
Taxa										
Monocots	278 ± 289	138 ± 237	1068 ± 3579	2.45 ± 1.79	1.05 ± 1.53	2.03 ± 2.03	50	24	34	
Dicots	8661 ± 2438	3325 ± 1799	8269 ± 4041	74.4 ± 17.4	30.7 ± 15.1	42.0 ± 23.5	639	446	570	
Gymnosperms	5.0 ± 17.1	3.1 ± 18.4	9.4 ± 52.2	0.09 ± 0.28	0.05 ± 0.27	0.11 ± 0.50	2	3	7	
Ferns	1.3 ± 7.9	113 ± 143	104 ± 169	0.03 ± 0.16	0.73 ± 0.50	0.58 ± 0.52	1	3	2	
Total	8945 ± 2541	3579 ± 1965	9451 ± 5181	77.0 ± 18.3	32.6 ± 16.3	44.7 ± 25.3	692 (1568)	476 (1172)	613 (1343)	

Table 3.4. Abundance and observed species richness (average \pm standard deviation) at two spatial scales for all small plant types and forest types. Abundance expressed as the percentage ground cover. Species richness at the subplot scale expressed as species numbers per subplot and at the landscape scale as the total observed species numbers in all subplots together and as the ICE-estimated total per forest type for trees and lianas (between parentheses, see text for explanation). **Bold** averages for the burnt forest types differ significantly from those of the unburnt forest (Mann-Whitney tested with Bonferroni correction for multiple tests).

Small growth forms	Abundance (% Cover)			Species per subplot (2 × 4 m)			Total species number		
	Unburnt	Once-burnt	Twice-burnt	Unburnt	Once-burnt	Twice-burnt	Unburnt	Once-burnt	Twice-burnt
Plant type									
Palms – palmlets	6.0 ± 11.2	0.4 ± 2.4	0.9 ± 6.0	0.45 ± 0.57	0.05 ± 0.22	0.04 ± 0.19	2	1	1
Monocots – grass-like	5.1 ± 5.8	11.0 ± 13.8	7.0 ± 5.8	0.89 ± 0.81	1.35 ± 0.90	1.24 ± 0.86	6	10	13
Monocots – other herbs	14.6 ± 18.0	19.0 ± 17.9	24.7 ± 17.5	1.11 ± 0.89	1.80 ± 1.59	3.91 ± 2.21	18	25	39
Dicots – small climbers	0.0 ± 0.0	5.1 ± 10.1	6.9 ± 15.4	0.00 ± 0.00	0.35 ± 0.48	0.55 ± 0.50	0	1	1
Dicots – small shrubs	0.7 ± 1.9	0.4 ± 1.4	4.0 ± 5.0	0.14 ± 0.38	0.09 ± 0.28	0.61 ± 0.58	7	4	4
Dicots – herbs	1.7 ± 2.8	1.5 ± 2.9	6.0 ± 5.2	0.35 ± 0.58	0.31 ± 0.59	1.15 ± 0.96	5	3	8
Ferns – small climbers	0.2 ± 1.0	3.4 ± 4.4	4.1 ± 2.9	0.04 ± 0.19	0.56 ± 0.59	0.83 ± 0.59	2	2	3
Ferns – treelets	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.6	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.11	0	0	1
Ferns – herbs	1.8 ± 4.2	46.2 ± 24.1	15.5 ± 14.4	0.38 ± 0.89	2.43 ± 0.74	2.29 ± 1.02	19	15	17
Growth forms									
Small climbers	0.2 ± 1.0	8.4 ± 10.3	10.7 ± 15.2	0.04 ± 0.19	0.91 ± 0.75	1.38 ± 0.82	2	3	4
Small shrubs	6.6 ± 11.3	0.9 ± 2.7	5.0 ± 7.6	0.59 ± 0.65	0.14 ± 0.35	0.66 ± 0.64	9	5	6
Herbs	21.7 ± 18.3	62.9 ± 18.7	45.0 ± 16.5	2.73 ± 2.29	5.89 ± 2.41	8.59 ± 3.30	48	53	77
Taxa									
Monocots	24.0 ± 18.7	28.4 ± 19.9	30.6 ± 17.8	2.45 ± 1.45	3.20 ± 1.98	5.19 ± 2.53	26	36	53
Dicots	2.4 ± 3.3	7.0 ± 10.6	15.8 ± 16.1	0.49 ± 0.67	0.75 ± 0.88	2.31 ± 1.45	12	8	13
Ferns	2.0 ± 4.2	47.9 ± 24.0	18.9 ± 14.5	0.41 ± 0.90	2.99 ± 1.06	3.13 ± 1.42	21	17	21
Total	27.1 ± 19.1	66.1 ± 18.1	53.6 ± 17.1	3.35 ± 2.34	6.94 ± 2.73	10.63 ± 3.97	59 (101)	61 (100)	87 (139)

Abundance and composition in three major groups of species

Differences in plant composition and abundance between three forest types (unburnt, once-burnt and twice-burnt forest) were studied by dividing all species into three major groups (trees, lianas and small plants, see Chapter 1) that were further subdivided in plant types (Table 3.1). Considerable differences were observed between plant types with respect to their abundance in the three forests.

Trees density was equally high in the unburnt and in the twice-burnt forest, but was three times lower in the once-burnt forest (Table 3.3). Dicot trees were clearly the dominant tree type, as they accounted for c. 99% of the stems in all three forest types. Palm trees and non-climbing bamboos still exceeded densities of more than 10 stems ha^{-1} in at least one of the three forest types, while monocot treelets, gymnosperm trees and tree ferns were always rare.

Lianas were in general equally abundant in all three forests, but due to a single species, the climbing bamboo *Dinochloa scandens*, the total number of climbing stems in the twice-burnt forest was almost twice as high as in the other two forests (Table 3.3). When this species was excluded from the analysis, stem densities in the twice-burnt forest were 1248 stems ha^{-1} , which is intermediate between the unburnt and once-burnt forest that had respectively 1339 and 1186 stems ha^{-1} .

Dicot lianas were the most common type of liana in all three forest types though they were less dominant than dicot trees were among the trees. They accounted for c. 80% of all stems in the unburnt and once-burnt forest and for c. 50% in the twice-burnt forest. In the latter forest, the high abundance of *D. scandens* strongly reduced the dominance of dicot lianas. Rattans (climbing palms), other monocot lianas and fern lianas often also had considerable stem densities in the forests, while gymnosperm lianas (*Gnetum sp.*) were rare.

Small plants were significantly more abundant in the two burnt forests than in the unburnt forest (Table 3.4), where their ground cover was roughly twice as large as in the unburnt forest. Unlike among trees and lianas, there was no dominance of dicot plants. Monocot herbs were clearly the most abundant plant type in the unburnt forest, while monocot herbs and herbaceous ferns were both very abundant in the burnt forests. In all three forest types, several plant types made a considerable contribution to the total cover of small species, and only fern treelets were always rare or absent.

Abundance and composition in different types of trees

Dicot trees had significantly fewer stems ha^{-1} in the once-burnt forest when compared to the unburnt forest, but stem densities in the twice-burnt forest were similar to the unburnt forest (Table 3.3). In the unburnt forest, the dominant families were Euphorbiaceae, Dipterocarpaceae, Sapotaceae, Leguminosae and Myristicaceae (Table 3.5). Species that greatly contributed to the dominance of these families were *Macaranga lowii* (Euphorbiaceae), *Shorea laevis* and *Dipterocarpus confertus* (both Dipterocarpaceae), *Madhuca kingiana* (Sapotaceae), *Fordia splendidissima* (Leguminosae) and *Knema percoriacea* (Myristicaceae).

Due to the abundant regeneration of several species of *Macaranga*, Euphorbiaceae were even more dominant in the two burnt forests than in the unburnt forest, while other

Table 3.5. The ten most abundant families, genera and species of trees in the unburnt, once-burnt and twice-burnt forest. In columns after each taxon the corresponding abundance (Abun), expressed as the densities of stems exceeding 1.3 m in height, and the percentage of all stems of trees exceeding 1.3 m in height (%). Between parentheses behind families the numbers of observed genera and species and behind genera the corresponding family and the numbers of observed species.

Trees — Unburnt			Once-burnt			Twice-burnt		
Families	Abun	%	Abun	%	Abun	%	Abun	%
1. Euphorbiaceae (18, 49)	1341	17.3	1. Euporbiaceae (15, 41)	921	38.5	1. Euphorbiaceae (18, 54)	4342	59.3
2. Dipterocarpaceae (6, 22)	971	12.8	2. Compositae (2, 2)	204	8.5	2. Moraceae (2, 24)	556	7.6
3. Sapotaceae (4, 11)	749	9.8	3. Myrtaceae (3, 20)	148	6.2	3. Piperaceae (1, 1)	274	3.7
4. Leguminosae (7, 15)	417	5.5	4. Melastomataceae (2, 9)	142	5.9	4. Compositae (2, 2)	238	3.3
5. Myristicaceae (4, 27)	398	5.2	5. Dilleniaceae (1, 1)	105	4.4	5. Leguminosae (8, 10)	223	3.0
6. Myrtaceae (4, 27)	345	4.5	6. Moraceae (2, 14)	90	3.8	6. Melastomataceae (2, 7)	183	2.5
7. Burseraceae (4, 17)	317	4.2	7. Leguminosae (5, 12)	86	3.6	7. Rubiaceae (16, 22)	159	2.2
8. Meliaceae (8, 29)	280	3.7	8. Lauraceae (10, 27)	73	3.0	8. Labiatae (3, 6)	153	2.1
9. Rubiaceae (17, 23)	225	3.0	9. Dipterocarpaceae (4, 11)	65	2.7	9. Vitaceae (1, 1)	141	1.9
10. Lauraceae (42, 12)	224	2.9	10. Rubiaceae (11, 15)	59	2.5	10. Rutaceae (1, 1)	124	1.7
Genera								
1. <i>Madhuca</i> (Sapo, 4)	724	9.5	1. <i>Macaranga</i> (Euph, 10)	798	33.3	1. <i>Macaranga</i> (Euph, 12)	2686	36.7
2. <i>Shorea</i> (Dipt, 10)	513	6.7	2. <i>Vernonia</i> (Comp, 1)	174	7.3	2. <i>Homalanthus</i> (Euph, 1)	1221	16.7
3. <i>Macaranga</i> (Euph, 8)	458	6.0	3. <i>Syzgium</i> s.l. (Myrt, 16)	145	6.1	3. <i>Ficus</i> (Mora, 14)	526	7.2
4. <i>Syzgium</i> s.l. (Myrt, 19)	319	4.2	4. <i>Dillenia</i> (Dill, 1)	105	4.4	4. <i>Piper</i> (Pipe, 1)	274	3.7
5. <i>Knema</i> (Myri, 12)	299	3.9	5. <i>Pternandra</i> (Mela, 3)	73	3.0	5. <i>Mallotus</i> (Euph, 3)	274	3.7
6. <i>Aporosa</i> (Euph, 6)	297	3.9	6. <i>Ficus</i> (Mora, 9)	71	3.0	6. <i>Vernonia</i> (Comp, 1)	232	3.2
7. <i>Fordia</i> (Legu, 1)	256	3.4	7. <i>Melastoma</i> (Mela, 1)	61	2.5	7. <i>Fordia</i> (Legu, 1)	153	2.1
8. <i>Dacryodes</i> (Burs, 6)	251	3.3	8. <i>Fordia</i> (Legu, 1)	48	2.0	8. <i>Leea</i> (Vita, 1)	141	1.9
9. <i>Dipterocarpus</i> (Dipt, 3)	229	3.0	9. <i>Litsea</i> (Laur, 7)	36	1.5	9. <i>Melicope</i> (Ruta, 1)	124	1.7
10. <i>Aglaita</i> (Meli, 12)	211	2.8	10. <i>Knema</i> (Myri, 7)	33	1.4	10. <i>Melastoma</i> (Mela, 1)	116	1.6
Species								
1. <i>Madhuca kingiana</i>	692	9.1	1. <i>Macaranga trichocarpa</i>	421	17.6	1. <i>Macaranga trichocarpa</i>	1938	26.5
2. <i>Macaranga lowii</i>	439	5.8	2. <i>Macaranga gigantea</i>	262	10.9	2. <i>Homalanthus populneus</i>	1221	16.7
3. <i>Shorea laevis</i>	268	3.5	3. <i>Vernonia arborea</i>	174	7.3	3. <i>Macaranga gigantea</i>	378	5.2
4. <i>Fordia splendidissima</i>	256	3.4	4. <i>Dillenia borneensis</i>	105	4.4	4. <i>Piper anduncum</i>	274	3.7
5. <i>Dipterocarpus confertus</i>	217	2.9	5. <i>Pternandra coerulescens</i>	66	2.8	5. <i>Mallotus paniculatus</i>	255	3.5
6. <i>Dacryodes rostrata</i>	190	2.5	6. <i>Melastoma malabathricum</i>	61	2.5	6. <i>Vernonia arborea</i>	232	3.2
7. <i>Giomtiera nervosa</i>	151	2.0	7. <i>Fordia splendidissima</i>	48	2.0	7. <i>Ficus obscura</i>	230	3.1
8. <i>Vatica umbonata</i>	133	1.7	8. <i>Macaranga bancana</i>	43	1.8	8. <i>Fordia splendidissima</i>	153	2.1
9. <i>Knema percoriacea</i>	116	1.5	9. <i>Syzgium nigricans</i>	39	1.6	9. <i>Macaranga hypoleuca</i>	143	2.0
10. <i>Durio acutifolius</i>	114	1.5	10. <i>Macaranga lowii</i>	38	1.6	10. <i>Leea indica</i>	141	1.9

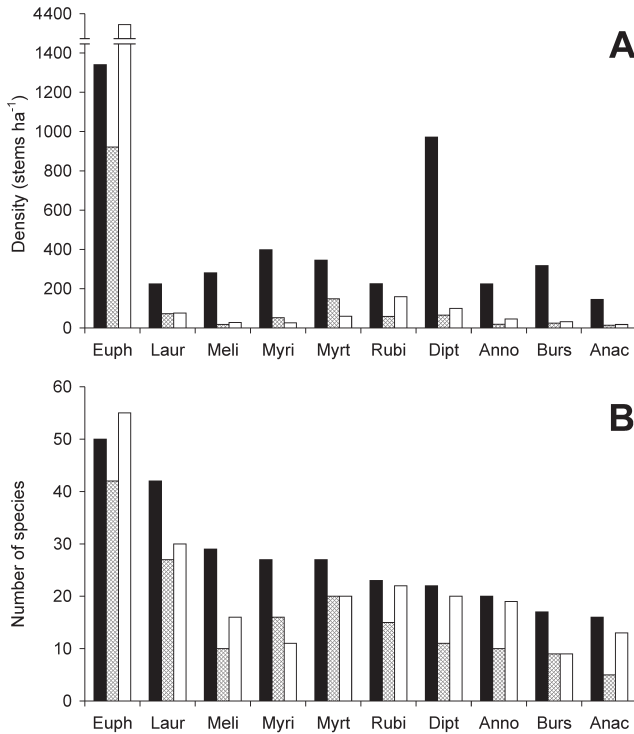


Fig. 3.1. Stem density (A) and total observed species number (B) in three forest types of the ten most species rich tree families of the unburnt forest in Sungai Wain. Solid bars: unburnt forest; cross-hatched bars: once-burnt forest; open bars: twice-burnt forest.

dominant families of the unburnt forest were much less abundant (Fig. 3.1). Species of *Macaranga* that were especially abundant in the burnt forests were *M. bancana*, *M. conifera*, *M. gigantea*, *M. hypoleuca* and *M. trichocarpa* (Appendix 1). Other species being abundant in both burnt forests were *Vernonia arborea* (Compositae), *Dillenia borneensis* (Dilleniaceae), *Ficus aurata* (Moraceae) and *Melastoma malabathricum* (Melastomataceae).

Besides species that were abundant in both burnt forests, there were also many species that were only abundant in the twice-burnt forest. Typical examples were *Homalanthus populneus* and *Mallotus paniculatus* (both Euphorbiaceae), *Piper aduncum* (an exotic species of the Piperaceae), *Callicarpa pentandra* (Labiatae), *Ficus obscura* and *F. grossularioides* (Moraceae), *Leea indica* (Vitaceae), *Melicope glabra* (Rutaceae) and *Trema tomentosa* and *T. cannabina* (Ulmaceae s.l.). All these species were absent or rare in the once-burnt forest but among the dominant species in the twice-burnt forest. Apart from *Piper aduncum*, these species were faster-growing than species that were also abundant in the once-burnt forest (Fig. 3.2).

No significant differences between forest types were observed in other types of trees. Palm trees had a very similar abundance in all three forests. Most stems belonged to

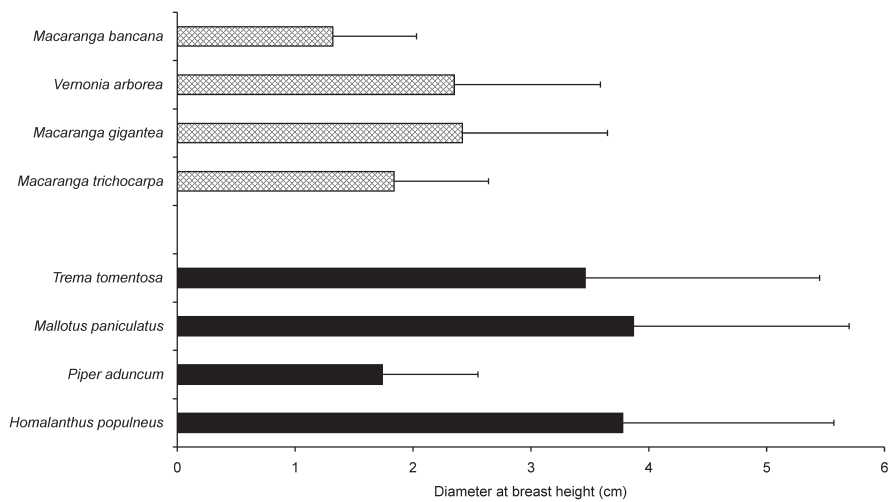


Fig. 3.2. Diameter at breast height (average + standard deviation) of four species abundant in both burnt forests (cross-hatched bars) and of four species abundant only in the twice-burnt forest (solid bars).

Borassodendron borneensis, with *Oncosperma horridum* as the second most abundant species (Appendix 1). Non-climbing bamboos were represented by only one unidentified species of *Gigantochloa*. Stem clusters of this species were present in only one subplot of the unburnt and once-burnt forest, while they were present in three subplots of the twice-burnt forest. Due to its multi-stemmed growth form, total stem densities of this species were nevertheless rather high, particularly in the twice-burnt forest.

Monocot treelets were represented by two species of *Dracaena* (*D. angustifolia* and *D. elliptica*, Dracaenaceae) and an unidentified species of *Pandanus* (Pandanaceae). Gymnosperm trees were represented only by *Nageia wallichii* (Podocarpaceae) and *Gnetum gnemon* (Gnetaceae). All five species occurred in very low densities in the three forest types, although *N. wallichii* was present in six subplots in the unburnt forest. Tree ferns were represented by only one species, *Cyathea reccommata* (Cyatheaceae), that was observed in only one unburnt subplot of the once-burnt forest. Several more individuals were present in the surroundings of this subplot. This area was almost permanently flooded and comprised species characteristic of peat swamp forest, such as the pitcher plant *Nepenthes ampullaria* (Nepenthaceae).

Abundance and composition in different types of lianas

Dicot lianas had a similar abundance in all three forests, with stem densities around 1000 stems ha⁻¹ (Table 3.3). In the unburnt forest, dominant dicot liana families in terms of stem densities were Leguminosae, Annonaceae, Apocynaceae, Celastraceae, Connaraceae and Dilleniaceae (Table 3.6). Species that greatly contributed to the dominance of these families were *Desmos chinensis* and *Cyathostemma excelsum* (Annonaceae),

Parameria laevigata (Apocynaceae), and several species of *Spatholobus* (Leguminosae), *Salacia* (Celastraceae), *Agelaea* (Connaraceae) and *Tetracera* (Dilleniaceae).

Generally, the dominant dicot liana families of the unburnt forest had a lower abundance in the burnt forests (Table 3.6), but the differences between forest types were much less pronounced than in the dominant dicot tree families (Table 3.5). In the burnt forests, and particularly in the once-burnt forest, species of *Uncaria* (Rubiaceae), *Embelia* and *Maesa* (both Myrsinaceae) were strikingly more abundant than in the unburnt forest. Unlike several dicot trees, few dicot lianas were clearly more abundant in the twice-burnt forest when compared to the once-burnt forest. Apparently only *Cayratia japonica* (Vitaceae) had ecological characteristics similar to species such as *Homalanthus populneus* and *Piper aduncum*, as it was fast-growing and particularly abundant in the twice-burnt forest, while being almost absent in the unburnt forest (including canopy gaps, Chapter 2).

Rattans, climbing palms, were the only large plant type being significantly less abundant in the burnt forests (Table 3.3). In the unburnt forest, rattans were almost as abundant as the largest plant family in dicot lianas (Leguminosae), while they had much lower densities in the once- and twice-burnt forest. Typically, the dominant species were different in all three forests (Table 3.6). In the unburnt forest, *Korthalsia ferox*, *Calamus flabellatus* and *Ceratolobus subangulus* were among the dominant species. In the once-burnt forest, *Plectocomiopsis geminiflora* and *Korthalsia echinometra* were most abundant, and in the twice-burnt forest *Ceratolobus concolor*.

Climbing bamboos comprised solely the species *Dinochloa scandens*. This species was never observed in the unburnt forest and was only present outside the subplots in the once-burnt forest. In strong contrast to this, it was present in 47 out of 80 subplots in the twice-burnt forest with up to 520 stems per subplot, making it the dominant liana species of this forest type (Table 3.6).

Monocot lianas had a similar abundance in the unburnt and twice-burnt forest, but were significantly less abundant in the once-burnt forest (Table 3.3). Two unidentified species of *Pothos* (Araceae) and *Freycinetia* (Pandanaeae) were rather abundant in the unburnt forest, while three other species were so in the twice-burnt forest: *Smilax odorata*, *S. barbata* (Smilacaceae) and *Flagellaria indica* (Flagellariaceae). All five species were rare in the once-burnt forest, while other recorded species, including several Araceae, were rare in all three forests.

Gymnosperm lianas comprised six unidentified species of the genus *Gnetum* (Gnetaceae). All six species were rare in the two burnt forests where they were restricted to unburnt forest remnants in floodplains, while no species was observed in the unburnt forest.

Fern lianas comprised mainly stems of *Stenochlaena palustris* (Blechnaceae, Table 3.6), a species that was present in most subplots of the burnt forests and in two subplots in canopy gaps in the unburnt forest. *Stenochlaena palustris* is a stem climber and was therefore never as dominant as other climbers typical of the burnt forests like *Dinochloa scandens* and species of *Lygodium* (Schizaeaceae). Rare fern liana species comprised an unidentified species of *Gleichenia* (Gleicheniaceae) in the once-burnt forest and two species of *Teratophyllum* (*T. ludens* and *T. clemensiae*, Lomariopsidaceae) in the twice-burnt forest. Within these forests, all three species were restricted to unburnt forest remnants in floodplains.

Table 3.7. The ten most abundant families, genera and species of small plants in the unburnt, once-burnt and twice-burnt forest. In columns after each taxon the corresponding abundance (Abun), expressed as the percentage ground cover, and the percentage of the cover of all small plants together (%). Between parentheses behind families the numbers of observed genera and species and behind genera the family it belongs to and the numbers of observed species.

Small plants — Unburnt			Once-burnt			Twice-burnt		
Families	Abun	%	Abun	%	Abun	%	Abun	%
1. Marantaceae (1, 3)	12.8	47.2	1. Nephrolepidaceae (1, 1)	33.2	50.2	1. Zingiberaceae s.l. (1, 29)	15.7	29.3
2. Palmae (2, 2)	6.0	22.1	2. Dennstaedtiaceae (3, 3)	19.4	18.2	2. Marantaceae (1, 3)	8.6	16.0
3. Cyperaceae (3, 7)	5.1	18.8	3. Marantaceae (1, 2)	11.3	17.1	3. Nephrolepidaceae (1, 1)	8.4	15.7
4. Rubiaceae (4, 8)	1.9	7.0	4. Zingiberaceae s.l. (0, 17)	7.7	11.6	4. Compositae (2, 2)	7.0	13.1
5. Zingiberaceae s.l. (0, 11)	1.5	5.5	5. Cyperaceae (3, 9)	7.0	10.6	5. Cyperaceae (3, 8)	6.1	11.4
6. Dryopteridaceae (2, 7)	0.6	2.4	6. Compositae (1, 1)	5.1	7.7	6. Dennstaedtiaceae (2, 2)	5.6	10.5
7. Hypoxidaceae (1, 1)	0.3	1.1	7. Gramineae (2, 2)	4.7	7.1	7. Schizaceae (1, 3)	4.1	7.6
8. Aristolochiaceae (1, 1)	0.3	1.1	8. Schizaceae (1, 2)	3.4	5.1	8. Solanaceae (1, 1)	3.7	6.9
9. Hymenophyllaceae (1, 1)	0.3	1.1	9. Rubiaceae (2, 5)	1.8	2.7	9. Melastomataceae (1, 1)	3.6	6.7
10. Pandanaceae (1, 1)	0.3	1.1	10. Blechnaceae (1, 1)	0.4	0.6	10. Rubiaceae (4, 4)	2.0	3.7
Genera								
1. <i>Phrynium</i> (Mara, 2)	12.7	46.9	1. <i>Nephrolepis</i> (Neph, 1)	33.2	50.2	1. <i>Phrynium</i> (Mara, 2)	8.4	15.7
2. <i>Licuala</i> (Palm, 2)	5.7	21.0	2. <i>Microlepia</i> (Denn, 1)	11.9	18.0	2. <i>Nephrolepis</i> (Neph, 1)	8.4	15.7
3. <i>Mapania</i> (Cype, 5)	4.1	15.1	3. <i>Phrynium</i> (Mara, 2)	11.3	17.1	3. <i>Mikania</i> (Comp, 1)	6.9	12.9
4. <i>Hedyotis</i> (Rubi, 1)	1.2	4.4	4. <i>Pteridium</i> (Denn, 1)	7.3	11.0	4. <i>Microlepia</i> (Denn, 1)	4.4	8.2
5. <i>Scleria</i> (Cype, 1)	0.9	3.3	5. <i>Mikania</i> (Comp, 1)	5.1	7.7	5. <i>Lygodium</i> (Schi, 3)	4.1	7.6
6. <i>Diplazium</i> (Dryo, 4)	0.4	1.5	6. <i>Imperata</i> (Gram, 1)	4.6	7.0	6. <i>Mapania</i> (Cype, 5)	3.8	7.1
7. <i>Lastianthus</i> (Rubi, 3)	0.4	1.5	7. <i>Mapania</i> (Cype, 7)	4.0	6.1	7. <i>Solanum</i> (Sola, 1)	3.7	6.9
8. <i>Pinanga</i> (Palm, 1)	0.3	1.1	8. <i>Lygodium</i> (Schi, 2)	3.4	5.1	8. <i>Clidemia</i> (Mela, 1)	3.6	6.7
9. <i>Curculigo</i> (Hypo, 1)	0.3	1.1	9. <i>Scleria</i> (Cype, 1)	3.0	4.5	9. <i>Costus</i> (Zing, 2)	2.8	5.2
10. <i>Thottea</i> (Aris, 1)	0.3	1.1	10. <i>Hedyotis</i> (Rubi, 1)	1.3	2.0	10. <i>Scleria</i> (Cype, 2)	2.1	3.9
Species								
1. <i>Phrynium jagoriaceum</i>	12.7	46.9	1. <i>Nephrolepis biserrata</i>	33.2	50.2	1. <i>Nephrolepis biserrata</i>	8.4	15.7
2. <i>Licuala sp. 1</i>	5.7	21.0	2. <i>Microlepia spelunceae</i>	11.9	18.0	2. <i>Phrynium jagoriaceum</i>	7.9	14.7
3. <i>Mapania sp. 1</i>	2.4	8.9	3. <i>Phrynium jagoriaceum</i>	9.8	14.8	3. <i>Mikania scandens</i>	6.9	12.9
4. <i>Hedyotis congesta</i>	1.2	4.4	4. <i>Pteridium aquilinum</i>	7.3	11.0	4. <i>Zingiberaceae sp. 2</i>	4.4	8.2
5. <i>Scleria terrestris</i>	0.9	3.3	5. <i>Mikania scandens</i>	5.1	7.7	5. <i>Microlepia spelunceae</i>	4.4	8.2
6. <i>Mapania sp. 2</i>	0.8	3.0	6. <i>Imperata cylindrica</i>	4.6	7.0	6. <i>Solanum jamaicense</i>	3.7	6.9
7. <i>Mapania sp. 4</i>	0.8	3.0	7. <i>Zingiberaceae sp. 1</i>	4.4	6.7	7. <i>Clidemia hirta</i>	3.6	6.7
8. <i>Zingiberaceae sp. 1</i>	0.4	1.5	8. <i>Lygodium microphyllum</i>	3.1	4.7	8. <i>Lygodium microphyllum</i>	3.3	6.2
9. <i>Pinanga sp. 1</i>	0.3	1.1	9. <i>Scleria terrestris</i>	3.0	4.5	9. <i>Costus speciosus</i>	2.7	5.0
10. <i>Curculigo sp. 1</i>	0.3	1.1	10. <i>Phrynium sp. 2</i>	1.8	2.7	10. <i>Zingiberaceae sp. 1</i>	2.4	4.5

Abundance and composition in different small plant types

When compared to the unburnt forest, most small plant types covered significantly more ground surface in either one or both of the burnt forests (Table 3.4). Dicot small climbers comprised solely the species *Mikania scandens* (Compositae, Table 3.7) in the 2 × 4 m subplots. This species was very abundant in both burnt forests and often dominated the vegetation where tree regeneration was absent. Of the same plant type, species of the genera *Tournefortia* (Boraginaceae), *Piper* (Piperaceae), *Cynanchum* and *Dischidia* (Asclepiadaceae) were present in the 10 × 20 m subplots, but were not observed in the 2 × 4 m subplots.

Both dicot shrubs and herbs were significantly more abundant in the twice-burnt forest but not in the once-burnt forest (Table 3.4). This was mainly due to the abundant regeneration of invasive species such as *Chromolaena odorata* (syn. *Eupatorium odoratum*, Compositae), *Clidemia hirta* (Melastomataceae) and *Solanum jamaicense* (Solanaceae) (Table 3.7). All three mentioned species are exotics and have a growth form almost intermediate between herbs and shrubs. Dicot species that were more typically shrubs mainly belonged to genera of the Rubiaceae: *Ixora*, *Lasianthus* and *Psychotria*. The first two genera consisted of species that were mainly restricted to unburnt forest, while *Psychotria viridiflora* was most abundant in the burnt forests.

Of the truly herbaceous dicots, *Hedyotis congesta* (Rubiaceae) was rather common in all three forest types, while other species were always rare. *Thottea grandiflora* (Aristolochiaceae) and *Labisia pumila* (Myrsinaceae) were mainly present in the understorey of the forest, while other rare herbaceous species were restricted to floodplains, both in the unburnt forest and in the unburnt patches of the burnt forests. Examples include unidentified species of *Cyrtandra* (Gesneriaceae), Acanthaceae and Rubiaceae.

Grass-like monocots were most abundant in the once-burnt forest (Table 3.4), mainly due to a high ground cover of *Scleria terrestris* (Cyperaceae) and *Imperata cylindrica* (Gramineae) (Table 3.7). Both species were less abundant in the twice-burnt forest, apparently as a result of shading by the dense overstorey of pioneer trees. In contrast to these species, three unidentified species of *Mapania* (Cyperaceae) were present in all three forest types though clearly most abundant in the unburnt forest (Table 3.7). Other species were rare in all three forests.

Palmlets only included unidentified species of the genera *Licuala* and *Pinanga*. Like climbing palms (rattans) among the large plants, palmlets were the only plant type among the small plants being significantly less abundant in both burnt forests (Table 3.4).

Monocot herbs were only significantly more abundant in the twice-burnt forest (Table 3.4) and this was mainly due to a high ground cover of Zingiberaceae s.l. (Table 3.7). In total, 43 species of Zingiberaceae s.l. were distinguished in the three forests together. *Costus speciosus* was very abundant in the twice-burnt forest (Table 3.7) though absent in the other two forests. A second observed species of this genus was *C. glabra* that was restricted to unburnt subplots in the floodplains of this forest. Of the other genera, *Etlingera* and *Hornstedtia* were particularly abundant in the two burnt forests, while species of *Elettaria* and *Plagiostachys* were more common in the unburnt forest.

The monocot herb *Phrynium jagoriaceum* (Marantaceae) was the most abundant small species of the unburnt forest, while still being almost equally abundant in the two

burnt forests (Table 3.7). This species was especially abundant in temporarily flooded areas where it often formed a continuous field layer. It was much less abundant in areas that were never waterlogged or that were permanently flooded. In the burnt forest, it apparently recovered from the fires by resprouting from rhizomes that survived in the ground. Other species of Marantaceae were much less abundant in all three forests and were mainly restricted to floodplains.

Other monocot herbs included *Mapania cuspidata* (Cyperaceae) and *Leptaspis urceolata* (Gramineae), two broad-leaved species of families that usually have a grass-like habit. These species were rather common in the unburnt forest and in the unburnt floodplains of the burnt forests. Unidentified species that were also rather common at these places were of the genera *Curculigo* (Hypoxidaceae), *Alocasia* (Araceae) and an acaulescent *Pandanus* (Pandanaceae). In addition, several young plants of a species of the Orchidaceae were observed in the burnt parts of the Sungai Wain forest.

Small climbing ferns were limited to four species of the genus *Lygodium* (Schizaeaceae). Similar to the dicot small climber *Mikania scandens*, these species were rare in the unburnt forest, but very abundant in the burnt forests (Table 3.4) and often forming dense tangles at places where pioneer trees were absent.

Fern treelets comprised solely *Cyathea moluccana* (Cyatheaceae), a species that was only observed in one subplot of the twice-burnt forest. Fern treelets were the only small plant type that did not show a significant difference in abundance between forest types (Table 3.4), but this is explained by the fact that this plant type was too rare in the forest to detect any difference.

Herbaceous ferns were clearly most abundant in the once-burnt forest (Table 3.4), where they dominated the vegetation with an average cover of more than 50% in the entirely burnt subplots. This was mainly due to three species: *Pteridium aquilinum* subsp. *caudatum* and *Microlepia speluncae* (Dennstaedtiaceae) and *Nephrolepis biserata* (Nephrolepidaceae) (Table 3.7). Below the dense bushes formed by *Macaranga trichocarpa* (Euphorbiaceae) and in the twice-burnt forest, they apparently suffered from shading as most ferns were almost dying off at these places. Two other herbaceous ferns were also often present in the burnt subplots but were never dominant: *Pteris tripartita* (Pteridaceae) and *Blechnum orientale* (Blechnaceae).

Other herbaceous ferns were rare or absent in all three forest types and only five of them could be reliably identified to the species level: *Trichomanes javanica* (Hymenophyllaceae), *Taenitis blechnoides* (Pteridaceae), *Pleocnemia irregularis* (Dryopteridaceae), *Lycopodium cernuum* (Lycopodiaceae) and *Pityrogramma calomelanus* (Pteridaceae). The latter two species were very abundant along roadsides in the Wanariset area (K.A.O. Eichhorn, pers. obs.), but were rare in the forest itself. Among the most species-rich genera were *Selaginella* (4 species, Selaginellaceae), *Diplazium* (6 species, Dryopteridaceae) and *Tectaria* (4 species, Dryopteridaceae).

Abundance and composition of seeds in the topsoil

In total, 3056 germinated seeds were recorded during the soil seed bank experiment. 51 seedlings, belonging to 6 species, were excluded from the analysis because they probably originated from weeds that were abundant in the nursery and absent in the three forests. Because only 11 germinating seedlings were observed in the control trays,

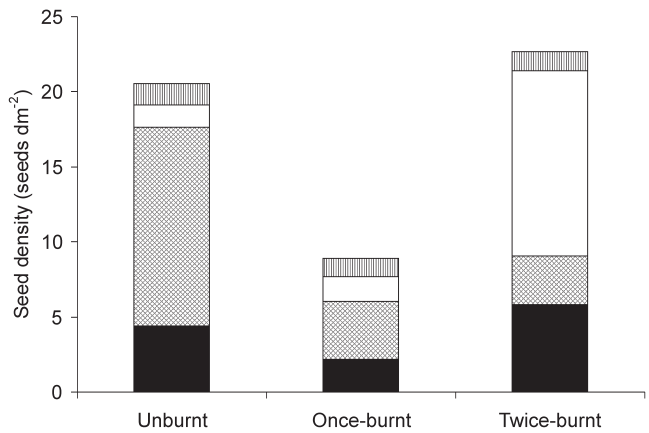


Fig. 3.3. Density of germinated seeds of trees (solid), lianas (cross-hatched), small plants (open) and plants of unknown growth form (hatched) in the topsoil (0–3 cm) of the unburnt, once-burnt and twice-burnt forest.

it was considered likely that few additional seedlings were coming from sources other than the soil samples themselves. Based on morphological similarity 2775 (92.3%) of the remaining 3005 seedlings could be assigned to species that were observed in the standing vegetation of the three forests. The other seedlings could not be assigned to species known from the field because they were either too small or they were apparently species absent in the standing vegetation. Finally, 2548 (84.8%) seedlings belonged to species that could be identified. Percentages of seedlings that could be identified to the species level were high because the great majority of the seedlings belonged to species that were very abundant in the standing vegetation of the burnt forests and easy to recognize.

Trees, lianas and small plants all contributed importantly to overall seed densities in the topsoil, but there were pronounced differences between these growth forms with respect to the forest type that they were most abundant in (Fig. 3.3, Table 3.8). Densities of tree seeds were highest in the twice-burnt forest and lowest in the once-burnt forest with the unburnt forest more or less intermediate. When compared to the standing vegetation (Table 3.3), the two burnt forests had similar ratios between stems and seeds, even though the twice-burnt forest had almost three times higher absolute values. In contrast to this, stem densities in the unburnt and twice-burnt forest were very similar in the standing vegetation, while the twice-burnt forest had clearly more seeds in the topsoil. Species often found in the seed bank of all three forests were *Pternandra coerulescens* and *Melastoma malabathricum* (Melastomataceae), *Pertusadina eurhyncha* and *Urophyllum arborescens* (Rubiaceae) and *Vernonia arborea* (Compositae), while seeds of *Trema tomentosa* (Ulmaceae s.l.) and *Callicarpa pentandra* (Labiatae) were only abundant in the topsoil of the twice-burnt forest (Table 3.8).

In lianas, seed densities were much higher in the unburnt forest than in the burnt forests (Fig. 3.3). Seed densities did not reflect stem densities in the standing vegetation,

Table 3.8. The ten most abundant species in the soil seed bank of the unburnt, once-burnt and twice-burnt forest. In columns after each species the corresponding abundance (Abun), expressed as the number of germinated seeds per dm², and the relative abundance (%), expressed as the percentage of all germinated seeds.

Soil seed bank									
Unburnt	Abun	%	Once-burnt	Abun	%	Twice-burnt	Abun	%	
1. <i>Uncaria cordata</i> (L, Rubi)	43.2	21.0	1. <i>Uncaria barbata</i> (L, Rubi)	16.3	18.3	1. <i>Mikania scandens</i> (S, Comp)	43.8	19.3	
2. <i>Dissochaeta gracilis</i> (L, Mela)	30.0	14.6	2. <i>Pternandra coerulescens</i> (T, Mela)	13.5	15.1	2. <i>Solanum jamaicense</i> (S, Sola)	38.9	17.2	
3. <i>Pternandra coerulescens</i> (T, Mela)	24.1	11.7	3. <i>Uncaria cordata</i> (L, Rubi)	11.8	13.2	3. <i>Chromolaena odorata</i> (S, Comp)	14.1	6.2	
4. <i>Uncaria barbata</i> (L, Rubi)	22.9	11.1	4. <i>Mikania scandens</i> (S, Comp)	11.5	12.9	4. <i>Clidemia hirta</i> (S, Mela)	13.9	6.1	
5. <i>Uncaria borneensis</i> (L, Rubi)	18.9	9.2	5. <i>Dissochaeta gracilis</i> (L, Mela)	4.9	5.5	5. <i>Callicarpa pentandra</i> (T, Labi)	10.8	4.8	
6. <i>Uncaria kunstleri</i> (L, Rubi)	8.2	4.0	6. <i>Uncaria kunstleri</i> (L, Rubi)	2.8	3.1	6. <i>Uncaria canescens</i> (L, Rubi)	10.2	4.5	
7. <i>Hedyotis congesta</i> (S, Rubi)	8.2	4.0	7. <i>Melastoma malabathricum</i> (T, Mela)	2.4	2.7	7. <i>Trema tomentosa</i> (T, Ulma)	10.2	4.5	
8. <i>Pertusadina eurhyncha</i> (T, Rubi)	3.8	1.8	8. <i>Solanum jamaicense</i> (S, Sola)	2.1	2.4	8. <i>Melastoma malabathricum</i> (T, Mela)	9.5	4.2	
9. <i>Urophylllum arborens</i> (T, Rubi)	3.5	1.7	9. <i>Vernonia arborea</i> (T, Comp)	1.6	1.8	9. <i>Gramineae</i> sp. 1 (S, Gram)	8.5	3.7	
10. <i>Curculigo</i> sp. 1 (S, Hypo)	3.3	1.6	10. <i>Uncaria canescens</i> (L, Rubi)	1.0	1.1	10. <i>Uncaria cordata</i> (L, Rubi)	5.6	2.5	
Trees	44.1	21.4	Trees	21.9	24.5	Trees	58.5	25.8	
Lianas	132.5	64.4	Lianas	38.4	43.0	Lianas	31.9	14.1	
Small plants	14.4	7.0	Small plants	16.5	18.5	Small plants	123.6	54.5	
Unknown	14.6	7.1	Unknown	12.5	14.0	Unknown	12.8	5.6	

as stem densities did not differ significantly between any of the three forest types (Table 3.3). The same two families as in trees comprised the most abundant species among lianas (Table 3.8): The Rubiaceae were represented by several abundant *Uncaria* species (*U. barbata*, *U. borneensis*, *U. canescens*, *U. cordata* and *U. kunstleri*) while the Melastomataceae were mainly represented by *Dissochaeta gracilis*.

Seed densities of small plants were by far the highest in the twice-burnt forest, while relatively few seeds were found in the unburnt and once-burnt forest (Fig. 3.3). In the standing vegetation, these differences between forest types mostly reflected the ground cover by small dicots (Table 3.4) that were also the major component of the seed bank of small plants. Small monocot species were generally rare in the seed bank. Species

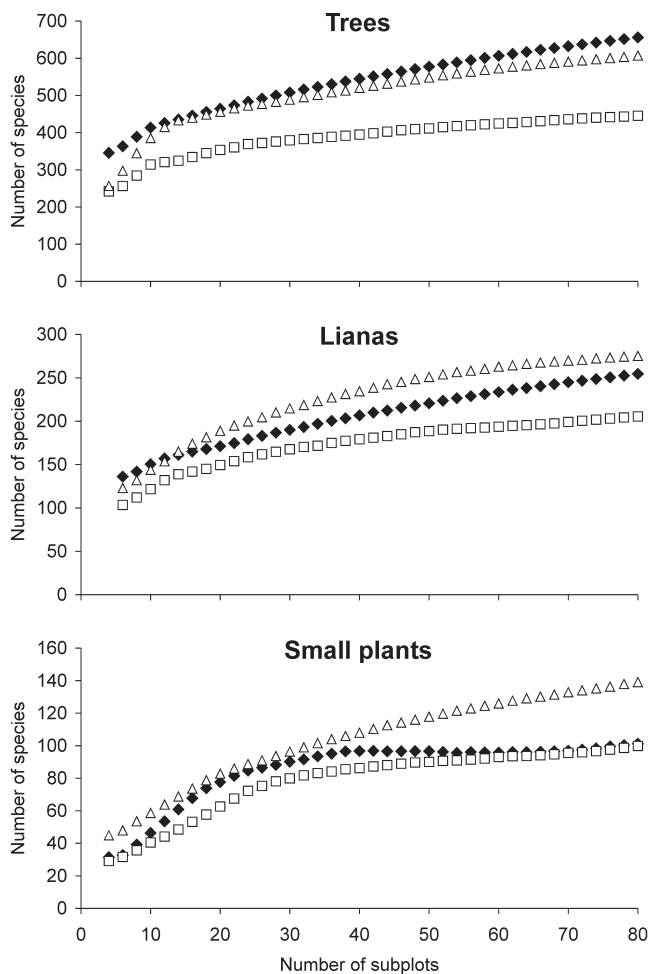


Fig. 3.4. Total species richness in trees, lianas and small plants as a function of the number of subplots used to estimate it with the Incidence-based Coverage Estimator (ICE). Results show the average of 500 random subplot samples of the unburnt (◆), once-burnt (□) and twice-burnt forest (△).

with high seed densities in the twice-burnt forest were *Chromolaena odorata* and *Mikania scandens* (Compositae), *Clidemia hirta* (Melastomataceae), *Solanum jamai-cense* (Solanaceae) and an unidentified species of Gramineae (Table 3.8). In addition, *M. scandens* was also abundant in the topsoil of the once-burnt forest, while *Hedyotis congesta* (Rubiaceae) and an unidentified species of *Curculigo* (Hypoxidaceae) were abundant in the unburnt forest.

Estimating total species richness

It is particularly relevant for species conservation to know whether the two burnt forests still had a high plant diversity when compared to the unburnt forest. Since only 1.6 ha out of 450 ha was sampled (0.35% of the total area) in each forest type, the observed species numbers are likely to be much lower than the total numbers of species that occur in the three forest plots. Two rather different methods were therefore used to extrapolate observed species richness to total species richness at the landscape scale.

The non-parametric ICE-index was used to estimate total species richness from species that were rare in the forest. ICE-estimations of total species richness were still strongly increasing with the numbers of subplots that were used to estimate it (Fig. 3.4). When all 80 subplots were included, total species richness was estimated to be much higher than when fewer subplots were used. This suggests that the ICE-index strongly

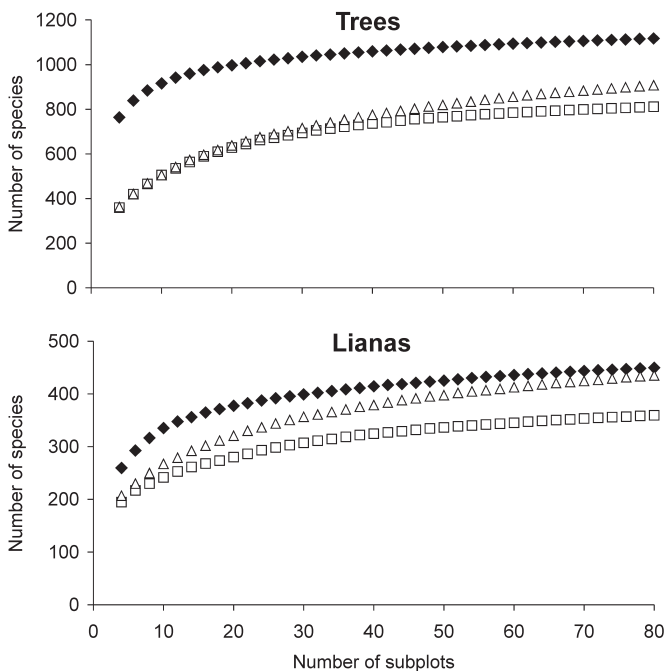


Fig. 3.5. Total species richness in trees and lianas as a function of the number of subplots used to estimate it with Fisher's alpha. Results show the average of 500 random subplot samples of the unburnt (◆), once-burnt (□) and twice-burnt forest (△).

underestimated true species richness due to undersampling. Estimations would thus have been higher when more subplots had been sampled and become reliable when ICE-curves reach the asymptote that corresponds to true species richness in the entire 450 ha plot.

Fisher's alpha was used to estimate total species richness based on the assumption that the relative abundance of species is described by a log-normal distribution. Estimations of total species richness using Fisher's alpha were much higher than when using the ICE-index (Fig. 3.5), but, similar to the ICE-index, species richness was still increasing with the number of subplots used to calculate it until all 80 subplots were included. In addition, Fisher's alpha itself still increased with sample size until all 80 subplots were included. Thus, although estimations of total species richness were much higher than when using the ICE-index, estimations based on Fisher's alpha were still likely to underestimate true species richness, and particularly so in the two burnt forests.

Since Fisher's alpha provided higher estimations than the ICE-index, but still seemed to underestimate true species richness, it was considered likely that alpha was closest to true species richness. Estimations based on Fischer's alpha were therefore used to discuss differences in estimated total species richness in trees and lianas. As Fisher's alpha is calculated from numbers of individuals, it could not be applied to small plants. Total species richness in this group was therefore discussed from estimations by the ICE-index.

Species richness at two spatial scales

Species richness per forest type was assessed at two spatial scales. At the subplot scale, it was calculated by taking the average and standard deviation of the number of species per subplot. At the landscape scale, observed species richness was calculated by taking the total number of species observed in all subplots together. In addition, the total number of species per forest type was estimated by means of the ICE-index in species of small plants and by means of Fisher's alpha in trees and lianas.

At the subplot scale, species richness and abundance differed (significantly) in the same direction between forest types in nearly all comparisons (Table 3.3, 3.4). An exception occurred in dicot trees, where species richness was significantly lower in the twice-burnt forest when compared to the unburnt forest, while there was no difference in abundance. As trees are by far the most numerous in terms of species and individuals, species richness was consequently also lower in all trees, all dicots, and all large species together. A second exception occurred in small monocots, where species richness was significantly higher in the twice-burnt forest without a significant difference in abundance.

At the landscape scale, tree species richness was also highest in the unburnt forest, where 510 species were observed in all subplots together and 1118 were estimated to be present in the entire area (Table 3.3). It was lowest in the once-burnt forest, where 328 species were observed and 812 estimated to be present, and more or less intermediate in the twice-burnt forest, where 423 species were observed and 908 estimated to be present. Families that greatly contributed to the observed differences in species richness were Anacardiaceae, Annonaceae, Dipterocarpaceae, Lauraceae, Meliaceae and Myristicaceae (Table 3.5, Fig. 3.1). In the once-burnt forest, these families had at

least 10 species fewer and were also much less abundant when compared to the unburnt forest. Generally, these families had an equally low abundance though higher species numbers in the twice-burnt forest.

Lianas had much fewer species than trees in all three forests (Table 3.3). Unlike trees, observed species numbers were highest in the twice-burnt forest, where 190 species were observed and 435 estimated to be present. Slightly fewer species (182) were observed in the unburnt forest, but more species (450) were estimated to be present. The lowest species richness was again in the once-burnt forest, where 148 species were observed and 360 estimated to be present. Differences between forest types were mainly a result of rattans and dicot lianas. Rattans had 31 species in the unburnt forest, while they had only 8 and 13 species in the once- and twice-burnt forest, respectively. In dicot lianas, Annonaceae were also most species rich in the unburnt forest, but other large families were so in the twice-burnt forest (Apocynaceae, Celastraceae, Gnetaceae, Rubiaceae and Vitaceae). Nearly all major families had the lowest species numbers in the once-burnt forest.

In small plants, observed species numbers were lower than in trees and lianas (Table 3.4), but it should be noted that these plants were recorded in much smaller subplots and that the total recorded area was only 4% of that for large growth forms. Furthermore, estimations of total species numbers were likely to be more conservative than for large plants, because they were based on the ICE-index that underestimated true species richness more than Fischer's alpha (see above). Species richness was highest in the twice-burnt forest, where 87 species were observed in the subplots and 139 species were estimated to be present in the entire forest. Species numbers in the two other forest types were considerably lower, as 59 species were observed and 101 estimated to be present in the unburnt forest, and 61 observed and 100 estimated to be present in the once-burnt forest. The relatively high species richness in the twice-burnt forest mainly resulted from high species numbers in monocot herbs, especially Zingiberaceae s.l. Also grass-like monocots had most species in the twice-burnt forest, despite the fact that they were more abundant in the once-burnt forest. This was mainly the result of a difference in Gramineae, as Cyperaceae had similar species numbers in all three forest types.

Relative differences in species richness between the three forests were often very different at the two spatial scales. Tree species richness in the once- and twice-burnt forest was respectively 33% (21.0/63.1) and 50% (31.8/63.1) of the unburnt forest at the subplot scale, but respectively 64% (328/510) and 83% (423/510) at the landscape scale. In small plants, it was respectively a factor 2.07 (6.94/3.35) and 3.17 (10.63/3.35) higher in the burnt forests at the subplot scale, but only a factor 1.03 (61/59) and 1.47 (87/59) at the landscape scale. Due to the fires, species richness was apparently decreased in trees and increased in small plants, but this effect was much more pronounced at the subplot scale in both cases. In lianas, differences between the unburnt and twice-burnt forest were even reversed at the different spatial scales, as observed species richness was higher in the unburnt forest at the subplot scale, while it was higher in the twice-burnt forest at the landscape scale (Table 3.3). Differences between forest types were most scale-dependent in herbaceous ferns, where at the subplot scale species richness was 6.0–6.4 times higher in the burnt forests, while the

unburnt forest had the highest species richness at the landscape scale (Table 3.4). All four examples show, to a differing degree, that assessing the impact of fires on species diversity at a small scale provides very different results from those at a large scale.

DISCUSSION

Differences between the three forests due to factors other than fire

The present comparison of the three forest types provides important information on the status of the lowland rain forests after initial and repeated fires in East Kalimantan. But as in most previous studies, reported effects of forest disturbance were deduced from a comparison of forests with a different disturbance history and not from real time series at these sites. Consequently, site-specific characteristics other than fire disturbance history may also contribute to observed differences between the three forest types. We therefore first briefly discuss other site-specific characteristics that may have determined the present status of these forests.

The Sungai Wain and Wanariset forests were probably floristically very similar before the fires, as inventories of unburnt areas within both forests had almost the highest similarity in tree composition among 18 rain-forest inventories in East Kalimantan (Chapter 2; Slik et al., 2003). The number of tall trees (dbh > 10 cm) is very similar for the unburnt forests of Sungai Wain (470–486 stems ha⁻¹) and Wanariset (463–518), suggesting that the impact of (illegal) logging was similar for both forests (Chapter 2). Moreover, both forests were also thought to be very similar with respect to soil type, topography and rainfall (Van Nieuwstadt, 2002). Nevertheless, we found small though significant differences in both elevation and inclination (Table 3.2). As the average elevation of subplots differed no more than about 20 m between sites, we consider this to have no influence on the plant community. Inclination, however, also differed, as slopes were significantly steeper in the twice-burnt Wanariset forest than in the two forests of Sungai Wain. This may have caused more variation in microhabitats resulting in higher species richness in the Wanariset forest (Clark et al., 1999; Svenning, 1999; Webb & Peart, 2000).

Tree diversity was indeed very high in the Wanariset forest before the initial fires in 1982–1983 (Kartawinata et al., 1981; Van Valkenburg, 1997). Unfortunately, no comparable record of the Sungai Wain forest exists and comparison with the present data is of limited value due to a different sampling design. Our own data showed that several plant families typical of undisturbed forest had similar stem densities in the once- and twice-burnt forest though more species in the latter (Fig. 3.1). Assuming that the fires were not highly selective against the dominant species (Cochrane & Schultze, 1999), it would seem reasonable to assume that species richness was somewhat higher in the Wanariset forest before the initial fires of 1982–1983.

Disturbance of the surrounding area may have affected the plant community of the three forests in a different way. The twice-burnt Wanariset forest was mainly surrounded by cultivated land that was often deliberately burnt during recent decades, while the study sites in Sungai Wain were mainly surrounded by forest that remained unburnt until 1998. In the Wanariset forest, seed import may have more strongly affected the soil seed bank and forest composition in favour of species characteristic of

the severely disturbed areas surrounding it. This was also observed in other tropical forests (Saulei & Swaine, 1988; Guariguata & Ostertag, 2001). Examples of species that certainly invaded the twice-burnt forest were exotics such as *Piper aduncum* (Piperaceae), *Solanum jamaicense* (Solanaceae), *Chromolaena odorata* (Compositae) and *Clidemia hirta* (Melastomataceae). It is, however, likely that also species native to Borneo have invaded the forest of Wanariset. Similar to these exotics, species such as *Homalanthus populneus* and *Mallotus paniculatus* (Euphorbiaceae), *Trema tomentosa* (Ulmaceae s.l.) and *Callicarpa pentandra* (Labiatae), are also nearly or completely absent in the unburnt and once-burnt forest of Sungai Wain while they are very abundant in the Wanariset forest (Table 3.7, Appendix 1) and surroundings (K.A.O. Eichhorn, pers. obs.). Therefore, it is very likely that the import of seeds into the Wanariset forest increased species richness and biased species composition towards more severely disturbed areas.

In conclusion, the high similarity with respect to altitude, soil type, rainfall and original tree composition shows that the forests of Sungai Wain and Wanariset are suitable for comparative studies. Since the ENSO fires severely affected the forest structure (Van Nieuwstadt et al., 2001; Cleary, 2002), it is likely that major differences between the plant communities of both forests result from fire disturbance history. It should, however, be realised that factors other than fire did and still do cause minor differences between the three forest disturbance types. The Wanariset forest originally may have had a somewhat higher species diversity that was probably due to a higher variation in inclination. Species richness in the Wanariset forest is further enhanced by seed import that was apparently lower in the Sungai Wain forest. Seed import may also have caused a species composition in the Wanariset forest that was biased towards that of disturbed areas.

Soil seed bank

Van Nieuwstadt (2002) estimated that in the top 4.5 cm of the soil in the Sungai Wain forest in October 1998, 39.7 (95% confidence limits 19.1–82.4) seeds dm^{-2} were present in the unburnt forest, and 20.8 (95% confidence limits 12.0–36.1) in the once-burnt forest. In our samples of April 2000, we found densities of 20.6 and 8.9 seeds dm^{-2} , respectively, in the top 3 cm of the soil. Our lower seed densities are of course partly explained by the fact that less soil per dm^2 was sampled in our experiment, but other factors may also explain part of the different results. The conditions in the nursery were very similar to those of Van Nieuwstadt (2002), making it unlikely that these accounted for them. However, small-scale variation in seed densities may have accounted for differences. The confidence limits of Van Nieuwstadt (2002) show that the variation among his soil samples was high and the same holds for our experiment, where densities were 4.9–87.5 seeds dm^{-2} for subplots in the unburnt forest, and 0.7–35.4 seeds dm^{-2} for subplots in the once-burnt forest. Moreover, it is possible that processes related to post-fire succession partly explain the lower seed densities in our analysis. Our samples were collected about one and a half year later than those of Van Nieuwstadt (2002). It is very likely that some of the seeds in the topsoil germinated or died in the meantime, while seed production in the once-burnt forest was still nearly zero at the end of 1999 (K.A.O. Eichhorn, pers. obs.). This could also explain lower

densities in the unburnt forest, as seeds of species present in the soil seed bank are often well dispersed (e.g. Saulei & Swaine, 1988). Most seeds produced in the unburnt forest may have been transported to the burnt surroundings, while this was not compensated for by any import of seeds.

Interestingly, we found hardly any seedlings of the genus *Macaranga* (Euphorbiaceae) during the soil seed bank analysis. Many species of this genus are often regarded as pioneer species (Chapter 4) and pioneer species are usually the main component of soil seed banks in tropical rain forests (e.g. Whitmore, 1984; Garwood, 1989; Maberley, 1992). Van Nieuwstadt (2002) also found very few seedlings of *Macaranga* during his analysis of the soil seed bank. By collecting an additional sample underneath a mature tree of *Macaranga gigantea*, he ensured that a high density of seeds of this species were present in this sample. He found that most of these seeds appeared to be unviable. However, it remains difficult to know why so many trees of *Macaranga* and *Mallotus* were present in the standing vegetation while so few seedlings were observed during both analyses. A first hypothesis would be that viable seeds of this genus were present in the soil samples while only few of them germinated, because conditions in the nursery were somehow unfavourable for them while they were favourable for other pioneers. Unfortunately, we did not have the opportunity to check for ungerminated seeds of *Macaranga* or other species at the end of our work. Another hypothesis would be that the number of viable seeds of *Macaranga* species strongly decreased in the soil during the two years between the fire and soil sampling since most of them germinated or died while new seeds were hardly produced. This hypothesis is supported by the observation that very few reproductive individuals of species in this genus were observed in the burnt area, but this was also true for many species that were abundant in the soil seed bank and data are lacking on extinction and germination rates of the seeds. A third hypothesis would be that the soil seed bank contains few seeds of *Macaranga* species, but that seedling establishment was very successful after the 1998 fires, while it was much less successful for other pioneers. *Macaranga gigantea*, for example, was among the dominant pioneer trees in the once-burnt forest, but had a stem density of 262 stems ha⁻¹ at this site, corresponding to a minimum seed density of only 0.26 10⁻³ seeds dm⁻². Since only 57.6 dm² of soil was sampled for the seed bank analysis, it is quite possible that by chance no viable seeds of this species were collected in the soil samples, while seed densities in the field were still sufficiently high to account for the observed sapling densities. The third hypothesis is also supported by the fact that seeds of *Macaranga* species are much larger than those of many other pioneers (e.g. species of Rubiaceae and Melastomataceae), while the survival of seedlings is generally positively related to seed size (Garwood, 1989). Thus a small number of large *Macaranga* seeds may well produce more saplings than a large number of small seeds of a species suffering high mortality rates during the seedling stage.

Changes in forest structure and composition after initial and recurrent fires

Tree densities were much lower in the once-burnt forest than in the unburnt forest, but were approximately the same in the twice-burnt forest (Table 3.3). In addition, typical weedy small plant types like grasses (i.e. *Imperata cylindrica*), dicot and fern climbers and herbaceous ferns were very abundant in the once-burnt forest, while they

were much less abundant in the unburnt and twice-burnt forest (Table 3.4). Without information on species composition and diversity, a comparison of the vegetation structure in the three forest types therefore suggested that a second fire largely compensated the strong negative impact of an initial fire. However, we found that only a small number of pioneer trees accounted for the high tree densities in the twice-burnt forest (Table 3.3). The great majority of tree species of the unburnt forest not only occurred at much lower densities in the once-burnt forest, but also in the twice-burnt forest (Appendix 1). Our results therefore show that abundant post-fire regeneration of trees, as was observed at several sites in East Kalimantan (e.g. Siegert et al., 2001), does not, in itself, ensure recovery of the forest's original biodiversity. Information on species composition is needed to know how many species of trees and other plants are able to recover.

Dynamics in the soil seed bank of pioneer trees seem to explain the apparently different effects of an initial and a subsequent fire. Pioneer trees are the main component of the soil tree seed bank, but are relatively scarce in pristine forests when compared to disturbed forests (e.g. Garwood, 1989; Gariguata & Ostertag, 2001). Consequently, few seeds are available in the topsoil for tree establishment after an initial fire in the forest. During our field study (two years after the ENSO fires) pioneer trees were therefore only present as scattered bushes in the once-burnt forest, apparently at places where parent trees were reproductive before the fires. In addition, dense vegetation dominated by herbaceous ferns and dicot lianas surrounded these bushes and prevented further colonisation of pioneer trees by shading, since the germination of pioneer seeds is inhibited by low light intensities (Bazzaz & Pickett, 1980; Vasquez-Yanes & Smith, 1982; Uhl & Clark, 1983; Vasquez-Yanes & Orozco-Segovia, 1993). During post-fire succession, the (already) established pioneer trees become reproductive and seeds will start to accumulate in the topsoil at a much higher rate than they did before the fire. After the second fire in the Wanariset forest, many pioneer tree seeds were therefore likely to be available for tree establishment and this would explain why a dense secondary forest developed before fern-liana tangles could become dominant. This explanation implies that a third fire will also not result in permanent deforestation at Wanariset, since tree seeds in the topsoil were most abundant in this twice-burnt forest (Fig. 3.3).

Apart from a remarkable difference in pioneer tree densities, there is also a remarkable difference in pioneer species composition between the once- and twice-burnt forest. The most abundant pioneer tree species of the once-burnt forest were *Macaranga trichocarpa* and *M. gigantea* (Euphorbiaceae), *Vernonia arborea* (Compositae) and *Dillenia borneensis* (Dilleniaceae) (Table 3.5). Three of these species were also among the ten most abundant species in the twice-burnt forest (Table 3.5), but also other pioneer species, such as *Piper aduncum* (Piperaceae), *Homolanthus populneus* and *Mallotus paniculatus* (Euphorbiaceae), were very abundant in this forest. Generally, species that were only abundant in the twice-burnt forest were faster growing than species that were also abundant in the once-burnt forest (Fig. 3.2), and were far more reproductive at the time of the field study (K.A.O. Eichhorn, pers. obs.). In New Guinea, *Piper aduncum* was shown to be an invasive species that is growing faster than local pioneer species, and to be a threat to the indigenous flora (Rogers & Hartemink, 2000). Their (near) absence in the unburnt and the once-burnt forest, indicates that seeds of these fast growing pioneers invade forests after an initial fire but remain dormant until conditions for

germination become favourable again after the next fire. In the twice-burnt forest of Wanariset, such invasive pioneers thus seem to have become abundant after the second fire. Here, they only co-dominated with the local pioneers, but they seem to have the potential to replace them if fires continue to occur in the forest, which indicates that not only non-pioneer species, but finally also local pioneer species will suffer from recurrent large-scale fires. This process of replacement of the local pioneers by invasive pioneers seems to have been nearly completed along frequently burnt roadsides, where the above-mentioned local pioneers are almost absent while the invasive pioneers usually dominate the vegetation (K.A.O. Eichhorn, pers. obs.).

The impact of fires on plant diversity in relation to spatial scale

Our comparison of two spatial scales strongly suggests that the impact of the ENSO fires on species richness is highly dependent on the scale of assessment (Table 3.3, 3.4, Fig. 3.4, 3.5). Similar scale-dependent effects of disturbance on species diversity have also been reported by other studies that assessed it at different spatial scales, as for example, fish removal in temperate reefs of New Zealand (Syms & Jones, 1999) and bark beetles and logging in pine forests of Finland (Peltonen et al., 1998). In tropical rain forest, the impact of logging on species richness and evenness in butterflies has been shown to be highly scale-dependent too (Hamer & Hill, 2000). Hamer & Hill (2000) also reviewed previous assessments of species richness in tropical Lepidoptera and showed that small- and large-scale studies usually reported opposing effects of disturbance. Interestingly, the authors suggested that scale-dependence is likely to be particularly strong in well-dispersed taxa, though they did not provide an explanatory mechanism. This hypothesis is strongly supported by our results, as herbaceous ferns are among the best dispersing of all plant taxa and show by far the strongest scale-dependent effects of all plant types in this study (Table 3.4).

Scale-dependency strongly limits the interpretation of the results of biodiversity studies on the impact of large-scale disturbance events like the 1997–1998 fires in East Kalimantan. On the one hand, small-scale studies seem to reflect changes in abundance rather than true changes in species richness. On the other hand, large-scale biodiversity studies may reflect true changes in species richness but lack the replication showing that results are generally valid. However, even without replication, our results do show that plant diversity can still be remarkably high in severely burnt forests. In the burnt forests, tree species richness was lower than in the unburnt forest, but the landscape-scale assessments indicated that most tree species were still present (although in much lower densities). Species richness in lianas was not clearly lower at any spatial scale, while species richness in small plants was even higher in the burnt forests, although it did not compensate for the lower diversity in tree species.

Burnt tropical rain forests: plant diversity and its conservation

Despite being severely damaged by the ENSO fires, both burnt rain forests of our study still showed a high regenerative power:

- 1) Fires have not resulted in permanent deforestation of the study sites. Trees were still abundantly regenerating and many tree seeds were found in the topsoil.

- 2) Species composition was clearly affected, but most species of the unburnt forest were still present in the burnt forests.
- 3) The landscape-scale assessments showed that both burnt forests were still floristically very diverse and indicated that the ENSO fires affected the abundance of species rather than species richness itself.

These observations suggest that tropical rain forests to some extent conserve their high biodiversity during periods of recurrent fires. It is, however, questionable how many species may become extinct during the coming years, as a result of reduced reproduction and growth, increased predation, decreased pollination, edge-effects etc. (Curran et al., 1999; Laurance et al., 2000; Bruna et al., 2002; Bruna, 2003; Ashworth et al., 2004). Long-term monitoring is necessary to prove that recently burnt rain forests are able to maintain their high biodiversity. Moreover, most burnt rain forests soon become burnt again, as today tropical wildfires occur at exceptional high frequencies due to interaction with destructive human activities and positive feedbacks (Cochrane & Schultze, 1998; Cochrane et al., 1999; Goldammer, 1999; Nepstad et al., 1999, 2001; Cochrane, 2001; Laurance & Williamson, 2001). At these frequencies, newly established pioneer trees are often burnt before reproduction and subsequent post-fire stands have a more open structure. Consequently, subsequent fires have a much higher intensity and destroy unburnt forest remnants and tall trees that survived the initial fires (Cochrane & Schultze, 1998; Goldammer, 1999). Resprouting is also lost as a mechanism to conserve plant diversity as it is very sensitive to repeated disturbance at high frequencies (Van Nieuwstadt et al., 2001). Rather than ENSO fires themselves, supplemental high-frequency wildfires therefore have the potential to cause permanent deforestation and loss of plant diversity.

**THE PLANT COMMUNITIES OF
BURNT RAIN FOREST IN RELATION TO
TOPOGRAPHY AND FOREST REMNANTS**

SUMMARY

Patterns in the species richness and composition of tree and liana communities were studied in two rain forests that had been burnt during the 1997–1998 El-Niño fires in East Kalimantan, Indonesia. In both burnt forests, two sets of 40 randomly located subplots within areas of 18 ha and 450 ha were examined for woody plants, topographic variation, and the cover by unburnt remnant forest.

Diversity and composition of tree and lianas were both related to topographic variation, as species numbers and scores on the first axis of a Detrended Correspondence Analysis (DCA) were related to both elevation and inclination. The observed relations between plant community characteristics and topographic variation resulted from strongly contrasting distribution patterns between abundant pioneer species and infrequent non-pioneer species. As a result of increased numbers of infrequent species, species richness increased and species composition changed at lower elevations and in flatter areas.

Within both burnt forest reserves, a network of unburnt remnant forest was present in the floodplains of larger streams. The topographic position and plant composition of the network in combination were the prime explanation for the observed relations between the plant community characteristics and topography. The network contained high densities of infrequent species and had a much higher species richness than the surrounding burnt matrix.

Outside the unburnt forest network in the burnt matrix, post-fire regeneration of infrequent species was more abundant at lower elevations and below tall trees. Abundant pioneer species apparently did not affect the regeneration of infrequent non-pioneer species.

INTRODUCTION

The recovery of burnt tropical rain forests can take place by means of remnant populations, resprouting individuals, establishment from the soil seed bank, and seed dispersal (Uhl et al., 1981; Stocker, 1981; Uhl & Jordan, 1984; Saulei & Swaine, 1988; Riswan & Kartawinata, 1991; Van Nieuwstadt et al., 2001). Species can recolonise burnt areas from outside, but if the burnt area is very large, recovery from surviving plants and seeds in the area itself is likely to be more important. Pioneer species are able to colonise severely disturbed areas from the soil seed bank (Chapter 3; Uhl et al., 1981; Gariguata & Ostertag, 2001). Due to a fast growth rate, photosynthetic characteristics, growth form, early reproduction and other adaptations (Bazzaz & Pickett, 1980; Whitmore, 1984; Mabberley, 1992; Davies, 1998), these species increase strongly in abundance after fire (Uhl et al., 1981; Goldammer et al., 1996).

The great majority of plants, however, comprises non-pioneer species. These species do not have a soil seed bank (Swaine & Whitmore, 1988; Garwood, 1989) and seed import from surrounding unburnt areas is likely to be low since huge areas were destroyed by the fires. Remnant populations and resprouting individuals will then be the major source for recovery after large-scale disturbance by fires. Non-pioneer species

that mainly occur in floodplains will survive the fires in remnant forest (Chapter 3) and those capable of abundant resprouting are able to recover their original densities (Van Nieuwstadt et al., 2001). However, most species mainly occur outside floodplains and are not capable of resprouting, and are therefore strongly reduced in abundance by fire (Chapter 3; Goldammer et al., 1996).

The probability that a large area of burnt tropical rain forest is able to recover its original plant biodiversity mainly depends on the densities and distribution patterns of this majority of reduced species. The question arises as to whether these infrequent species are randomly distributed within burnt forest areas or mainly restricted to certain patches, and if so, if these patches can be characterised in terms of vegetation structure (e.g. forest remnants) and environmental factors (e.g. topography). From a conservation point of view, it is essential to know which patches still contain high concentrations of infrequent species, as these patches can serve as the main sources for recovery of the original biodiversity in the future.

Many studies have included an analysis of the impact of fire on plant diversity in tropical rain forest, either by comparing the status of a forest before and after fire (e.g. Uhl et al., 1981; Peres, 1999), or by comparing burnt and unburnt forests (e.g. Cochrane & Schultze, 1998; Van Nieuwstadt, 2002; Slik et al., 2002). Chapter 3 of this thesis describes another study on the impact of fire on plant diversity using the latter approach. None of these studies, however, focused on patterns of plant diversity within burnt rain forest areas. Here I present a detailed analysis of the landscape-scale patterns in tree and liana communities of two rain forests that were severely burnt by the ENSO fires of 1998 in East Kalimantan, Indonesia. Patterns in species diversity and composition are related to topography and forest remnants, as well as to the successional status of individual species. Three questions are addressed:

- 1) Which spatial patterns are present in the species diversity and composition of the tree and liana communities within these two forests?
- 2) Are these patterns related to topography and forest remnants?
- 3) Are these patterns different for abundant (often called pioneer) species and infrequent (often called non-pioneer) species?

METHODS

Within both burnt forests, data on plants (trees and lianas), topographic variables (elevation and inclination), and the cover of unburnt remnant forest, were systematically recorded in two sets of 40 subplots (10 × 20 m) that were randomly located in plots of 18 ha and 450 ha (see Chapter 1 for details). Patterns in species composition were studied by means of Detrended Correspondence Analysis (DCA), an indirect gradient analysis technique that detects gradients from species abundance data (Hill & Gauch, 1980; Jongman et al., 1995). DCA was performed using CANOCO software for Windows, version 4.02 (Ter Braak, 1988; Ter Braak & Smilauer, 1998). All species with five or more stems in the dataset (corresponding to a stem density of 3.1 stems ha⁻¹ or higher) were included in the analysis. Data were used untransformed and detrending was carried out by segments. Other statistical analyses were based on all recorded species and were performed using SPSS 10.0 software for Windows.

RESULTS

Species composition and richness

Patterns in the species composition were analysed for trees and lianas separately and for both forests separately. Subplot scores on the first and second DCA-axis showed that unburnt remnant forest had a species composition different from the burnt matrix, while partially burnt subplots tended to have intermediate scores (Fig. 4.1). In all four cases, the first DCA-axis explained much more variation in species composition than did the next three axes (Table 4.1). The percentage of variance explained by the first axes varied from 11.3% to 15.9%, while the next axes never explained more than 7.4%. This showed that there was always one major gradient present in the species composition, while additional gradients were much less pronounced.

Furthermore, DCA subplot scores on the first axis were in all four cases significantly related to the number of species in these subplots. The first DCA-axes thus not only reflected a strong gradient in species composition, but a gradient in species richness as well. Other DCA-axes were rarely significantly related to species richness.

Relations with topographic variation

Both species richness and composition were then related to two topographic variables: elevation and inclination (Table 4.2). Similar relations were again found for both trees and lianas and for both forest reserves. Species diversity, expressed as the number of species per subplot, showed a significant negative relation to both elevation and inclination. Thus, species richness was increasing at lower elevations and in flatter areas. The explained amount of variation in species richness ranged between 7% and 30%.

Species composition, expressed as the subplot scores on the first DCA-axis, also showed highly significant negative relations with elevation and inclination (Table 4.2). Thus, species composition was changing at lower elevations and in flatter areas. The explained amount of variation ranged between 7% and 19%.

Table 4.1. Explained variation and correlation with species richness of the first four axes of a Detrended Correspondence Analysis (DCA). Results shown for trees and lianas and for both forest reserves separately.

Significance levels: *) $p < 0.05$, **) $p < 0.01$, ***) $p < 0.005$, NS not significant (n = 80).

		Sungai Wain Trees	Sungai Wain Lianas	Wanariset Trees	Wanariset Lianas
Explained variation (%)	DCA 1	12.1	13.3	15.9	11.3
	DCA 2	4.3	7.0	7.4	5.6
	DCA 3	3.2	5.0	4.4	4.5
	DCA 4	3.0	4.0	3.3	3.3
Correlation with species richness	DCA 1	$r = +0.57^{***}$	$r = +0.72^{***}$	$r = +0.74^{***}$	$r = +0.49^{***}$
	DCA 2	NS	NS	$r = +0.31^{**}$	NS
	DCA 3	$r = +0.28^*$	NS	$r = +0.46^{***}$	NS
	DCA 4	NS	NS	NS	NS

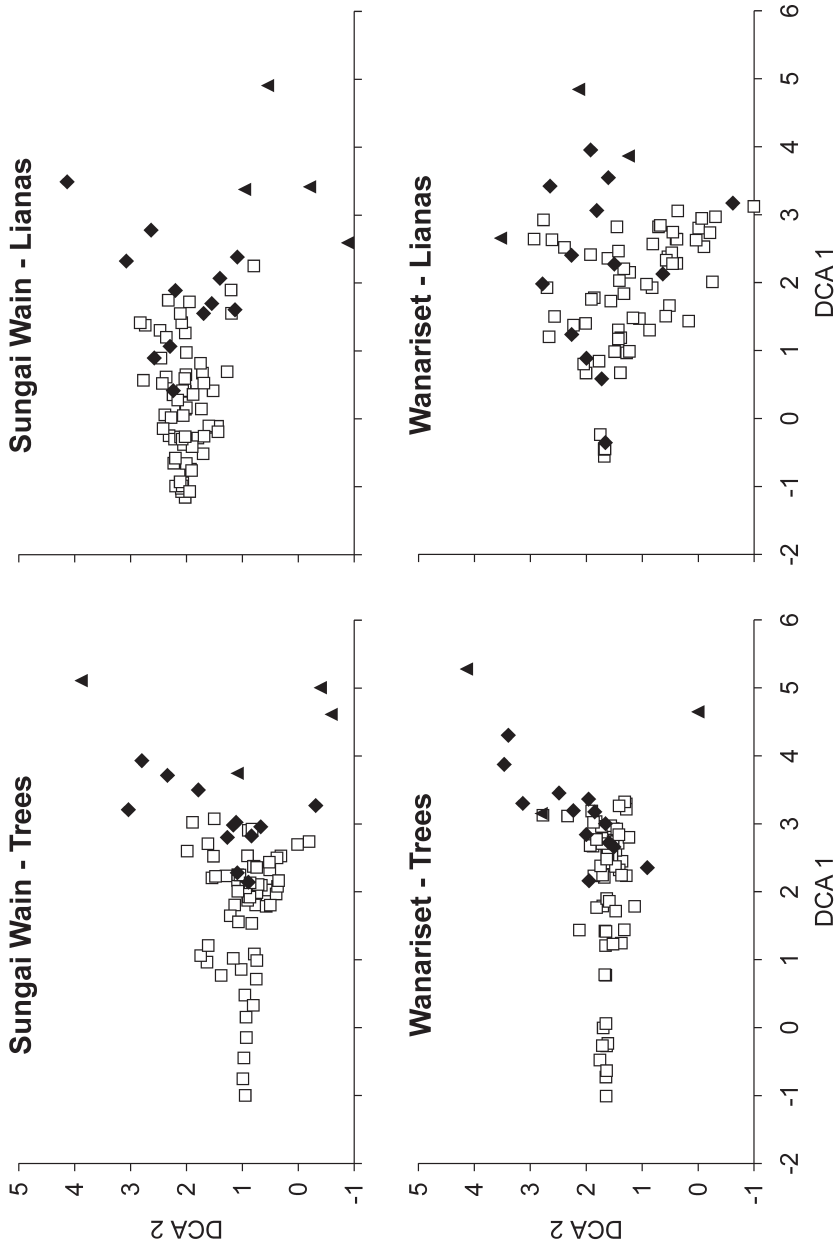


Fig. 4.1. Detrended Correspondence Analyses (DCA) of the species composition. DCA 2 plotted against DCA 1. Results shown for both trees and lianas and for both forest reserves. □: entirely burnt subplots; ◆: partially burnt subplots; ▲: unburnt subplots.

Table 4.2. Regression analysis of the relation between species richness and composition and two topographic variables: elevation and inclination. Species richness expressed as the number of species per subplot, species composition as the subplot scores on the first DCA-axis. Significance levels: *) $p < 0.05$, **) $p < 0.01$, ***) $p < 0.005$ ($n = 80$).

	Sungai Wain Trees	Sungai Wain Lianas	Wanariset Trees	Wanariset Lianas
Elevation				
Species richness	$-0.202x + 37.3$ $r^2 = 0.097^{***}$	$-0.143x + 23.1$ $r^2 = 0.136^{***}$	$-0.526x + 61.6$ $r^2 = 0.303^{***}$	$-0.296x + 29.7$ $r^2 = 0.256^{***}$
DCA 1	$-0.030x + 4.53$ $r^2 = 0.204^{***}$	$-0.030x + 3.01$ $r^2 = 0.162^{***}$	$-0.039x + 4.47$ $r^2 = 0.304^{***}$	$-0.019x + 3.04$ $r^2 = 0.095^{**}$
Inclination				
Species richness	$-0.416x + 25.3$ $r^2 = 0.072^*$	$-0.372x + 15.4$ $r^2 = 0.161^{***}$	$-0.786x + 43.9$ $r^2 = 0.114^{***}$	$-0.622x + 22.6$ $r^2 = 0.192^{***}$
DCA 1	$-0.065x + 2.78$ $r^2 = 0.169^{***}$	$-0.071x + 1.36$ $r^2 = 0.165^{***}$	$-0.047x + 2.99$ $r^2 = 0.076^*$	$-0.041x + 2.58$ $r^2 = 0.073^*$

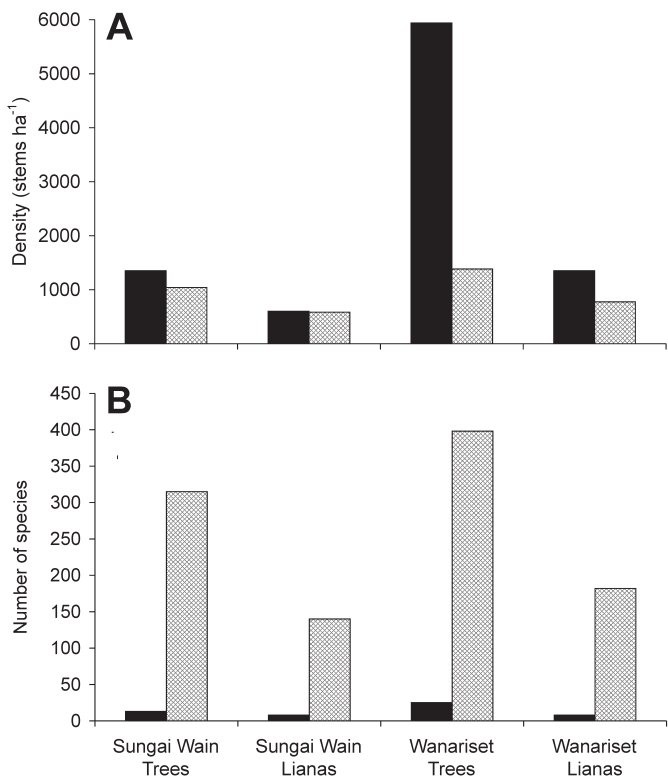


Fig. 4.2. Stem density (A) and total observed species number (B) of abundant (solid bars) and infrequent (cross-hatched bars) species. Results shown for both trees and lianas and for both forest reserves.

Abundant versus infrequent species

Patterns in species richness and composition were further analysed by classifying all observed species as either abundant (densities 30 or more stems ha⁻¹ when calculated as the average of all 80 – burnt and unburnt – subplots in a forest reserve) or infrequent (less than 30 stems ha⁻¹). Several species were classified as abundant species for both forest reserves, but most species were only so in one reserve. A striking number of species in *Macaranga* (trees, Euphorbiaceae) and *Uncaria* (lianas, Rubiaceae) were abundant, either in one or in both forest reserves. Other genera with more than one abundant species were *Ficus* (Moraceae) in trees and *Embelia* (Myrsinaceae) in lianas.

A comparison of abundant and infrequent species showed that abundant species dominated the burnt forests in stem numbers, while the great majority of species was infrequent (Fig. 4.2). This was again observed in both trees and lianas and in both forest reserves. Only 4.0–5.9% of the species were classified as being abundant, but these species accounted for 51–81% of all recorded stems. Dominance by abundant tree and liana species was much stronger in Wanariset than in Sungai Wain, as a result of respectively 2.2 and 4.4 times higher stem densities, while for both trees and lianas stem densities in infrequent species were 1.3 times higher in Wanariset than in Sungai Wain.

Among infrequent species, stem numbers per subplot were related to patterns in overall plant community characteristics (this including both abundant and infrequent species) and to topographic variation (Table 4.3). Results were again similar for both

Table 4.3. Relation of stem numbers in infrequent and abundant species with species richness and composition and with two topographic variables: elevation and inclination. Relations with plant variables were analysed by means of correlation and those with topographic variables by means of regression analysis.

Significance levels: ** p < 0.01, *** p < 0.005, NS not significant (n = 80).

	Sungai Wain Trees	Sungai Wain Lianas	Wanariset Trees	Wanariset Lianas
Infrequent species				
Species richness	r = +0.890***	r = +0.810***	r = +0.898***	r = +0.865***
DCA 1	r = +0.689***	r = +0.779***	r = +0.614***	r = +0.537***
Elevation	-0.417x + 54.5 r ² = 0.142***	-0.325x + 37.9 r ² = 0.131***	-0.807x + 73.3 r ² = 0.214***	-0.595x + 49.2 r ² = 0.210***
Inclination	-1.022x + 31.4 r ² = 0.149***	-0.940x + 21.4 r ² = 0.191***	-0.156x + 51.8 r ² = 0.136***	-1.402x + 37.2 r ² = 0.199***
Abundant species				
Species richness	NS	NS	r = +0.460***	NS
DCA 1	r = -0.559***	r = -0.306**	r = -0.681***	r = -0.416***
Elevation	NS	NS r ² = 0.242***	2.51x - 23.1	NS
Inclination	NS	NS	NS	NS

trees and lianas and for both forest reserves. Highly significant positive relations were observed with species numbers per subplot and with subplot scores on the first DCA-axis. Thus, species richness increased and composition changed with increased stem numbers of infrequent species. Not surprisingly, stem numbers in infrequent species were related to topographic variation in a similar way as overall species richness and composition were: they were higher at lower elevations and in flatter areas. The observed relations were all highly significant and explained 13–21% of the variation.

In contrast, stem numbers of abundant species were usually only related to species composition and not at all related to topography and species richness (Table 4.3). Significant negative relations with subplot scores on the first DCA-axis were observed in both trees and lianas and in both forest reserves. For trees in the Wanariset forest, however, stem numbers of abundant species were also positively related to elevation and negatively related to species richness. When compared to the infrequent species, abundant species were thus inversely related to the plant community characteristics and topographic variation if they were related at all.

Unburnt remnant forest

Unburnt remnant forest was still present throughout the burnt forest reserves and effectively constituted networks along the larger streams (Fig. 4.3). In both burnt forest reserves, 16 subplots were either partially or entirely covered by unburnt remnant forest. On average, 10.6% of the subplots was covered by unburnt forest in the Sungai Wain forest while this was 8.1% in the Wanariset forest.

The position of unburnt remnant forest showed a highly significant negative relation with both elevation (Linear Regression Analysis (LRA), Sungai Wain: $y = -0.420x + 44.5$, $r^2 = 0.066$, $p < 0.05$; Wanariset: $y = -0.467x + 34.5$, $r^2 = 0.124$, $p < 0.005$) and inclination (LRA, Sungai Wain: $y = -1.629x + 27.4$, $r^2 = 0.175$, $p < 0.005$; Wanariset: $y = -1.402x + 29.8$, $r^2 = 0.189$, $p < 0.005$). There were differences between entirely burnt subplots, subplots being partially covered by unburnt remnant forest, and subplots being entirely covered (Fig. 4.4). Entirely burnt subplots were present at all levels of elevation and inclination, but were apparently more common on steeper slopes and higher elevations. Subplots being partially covered by unburnt remnant forest were found at all levels of inclination, but only at the lower elevations of the landscape. Finally, subplots being entirely covered by unburnt remnant forest were restricted to almost flat areas at low elevations.

Composition expressed as abundant and infrequent species differed strongly between the unburnt forest network and the surrounding burnt matrix (Fig. 4.5). Unburnt patches were dominated by stems of infrequent species, while burnt patches were dominated by abundant species. Results were very similar for trees and lianas, but the burnt patches in Sungai Wain were less strongly dominated by abundant species than in Wanariset. This was a result of much higher stem densities in abundant species at the latter site (Fig. 4.2). In unburnt patches, however, the ratio between abundant and infrequent species was very similar for both forest reserves.

The topographic position of unburnt remnant forest in combination with its plant composition was the major underlying factor causing the observed relations between the plant community characteristics and topographic variation (Table 4.4). Species numbers

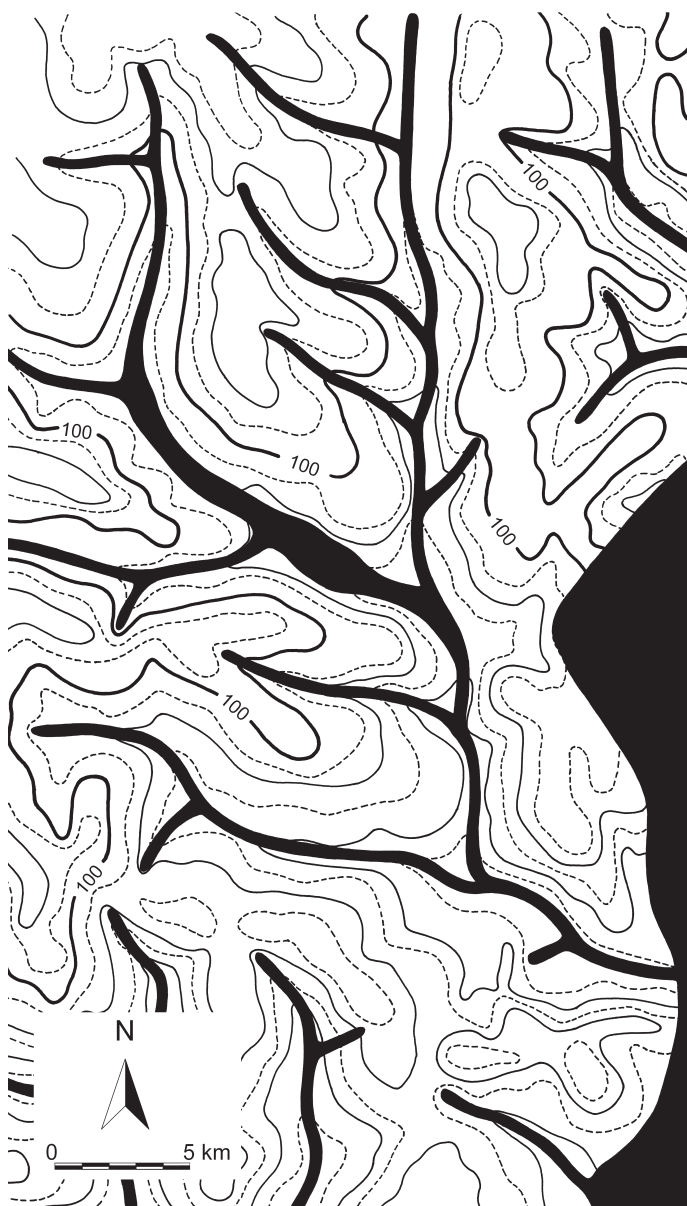


Fig. 4.3. Position of unburnt remnant forest (black) in the once-burnt 450 ha plot of Sungai Wain.

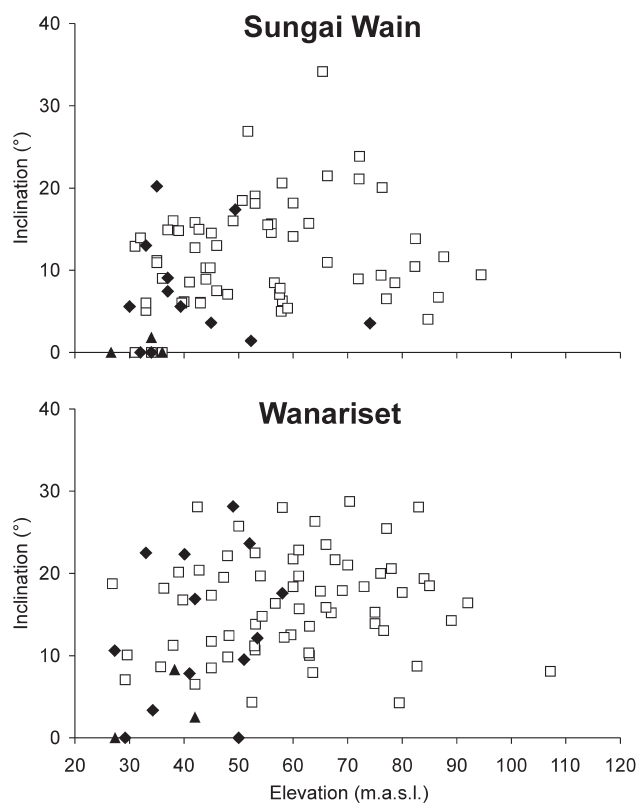


Fig. 4.4. Position of unburnt remnant forest in relation to variation in two topographic variables: elevation and inclination. Results shown for both forest reserves. □: entirely burnt subplots; ◆: partially burnt subplots; ▲: unburnt subplots.

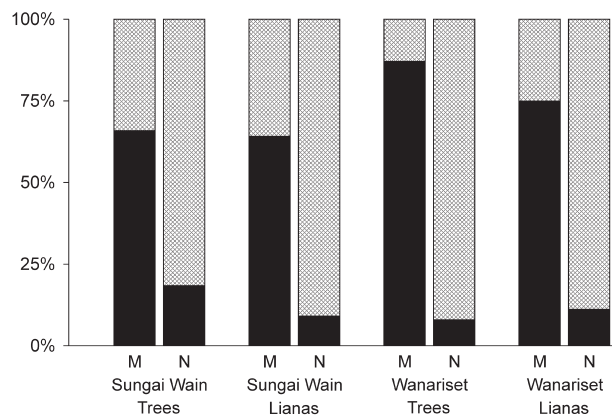


Fig. 4.5. Composition of the burnt matrix (M) and the network of unburnt remnant forest (N) expressed as the stem percentages of abundant (solid) and infrequent (cross-hatched) species. Results shown for trees and lianas and for both forest reserves.

Table 4.4. Regression analysis of the relations between species richness, species composition, stem numbers of infrequent species and unburnt remnant forest.

Significance levels: ***) $p < 0.005$ ($n = 80$).

	Sungai Wain Trees	Sungai Wain Lianas	Wanariset Trees	Wanariset Lianas
Species richness	$0.258x + 18.3$ $r^2 = 0.423^{***}$	$0.157x + 9.89$ $r^2 = 0.439^{***}$	$0.453x + 28.1$ $r^2 = 0.394^{***}$	$0.298x + 10.7$ $r^2 = 0.466^{***}$
DCA 1	$0.026x + 1.84$ $r^2 = 0.397^{***}$	$0.029x + 0.32$ $r^2 = 0.428^{***}$	$0.026x + 2.05$ $r^2 = 0.231^{***}$	$0.020x + 1.78$ $r^2 = 0.189^{***}$
Infrequent species	$0.551x + 15.0$ $r^2 = 0.656^{***}$	$0.426x + 7.17$ $r^2 = 0.593^{***}$	$1.049x + 19.2$ $r^2 = 0.637^{***}$	$0.786x + 9.27$ $r^2 = 0.648^{***}$

per subplot, subplot scores on the first DCA-axis, and stem numbers in infrequent species were in all cases closely related to the cover by unburnt remnant forest. Results were again very similar for trees and lianas and for both forest reserves. Relations were always highly significant and explained 39–47% of the variation in species richness, 19–43% of the variation in the first DCA-axis, and even 59–66% of the variation in the densities of infrequent species.

However, unburnt remnant forest was not the only factor explaining the observed relations between the plant community characteristics and topographic variation. After exclusion of all subplots that were partially or entirely covered by unburnt forest, species richness and composition and stem numbers of infrequent species were still related to topographic variation in the burnt matrix (Table 4.5). Species numbers per

Table 4.5. Regression analysis of the relations of species richness, species composition, and stem numbers in infrequent species with two topographic variables (elevation and inclination), when only the entirely burnt subplots were included.

Significance levels: *) $p < 0.05$, **) $p < 0.01$, ***) $p < 0.005$, NS not significant ($n = 64$).

	Sungai Wain Trees	Sungai Wain Lianas	Wanariset Trees	Wanariset Lianas
Elevation				
Species richness	$-0.130x + 28.7$ $r^2 = 0.068^*$	$-0.070x + 15.2$ $r^2 = 0.083^*$	$-0.376x + 50.3$ $r^2 = 0.263^{***}$	$-0.200x + 22.5$ $r^2 = 0.256^{***}$
DCA 1	$-0.018x + 3.25$ $r^2 = 0.109^{**}$	NS	$-0.031x + 3.87$ $r^2 = 0.204^{***}$	NS
Infrequent species	$-0.200x + 31.5$ $r^2 = 0.103^{**}$	$-0.091x + 14.3$ $r^2 = 0.087^*$	$-0.376x + 41.9$ $r^2 = 0.190^{***}$	$-0.275x + 26.3$ $r^2 = 0.277^{***}$
Inclination				
Species richness	NS	NS	NS	$-0.332x + 15.9$ $r^2 = 0.096^*$
DCA 1	NS	NS	NS	NS
Infrequent species	NS	$-0.195x + 8.97$ $r^2 = 0.063^*$	NS	NS

subplot, subplot scores on the first DCA-axis, and stem numbers of infrequent species were still showing a negative relation with both elevation and inclination in all cases. Relations were, however, much weaker than when all subplots were included. Elevation usually accounted for a significant amount of explained variation in the plant variables, but much less when compared to the analyses including all 80 subplots (Table 4.2, 4.3). Inclination was apparently only a minor factor influencing the plant community characteristics in the burnt matrix, as only two out of twelve relations (these being all negative) were significant at the 0.05 level.

Post-fire regeneration within the burnt matrix

The regeneration of infrequent species in the burnt matrix will mainly determine the prospects for recovery of the original plant diversity. For both infrequent trees and lianas and in both forest reserves, diameter classes up to 2 cm at breast height had many more stems than other classes (Fig. 4.6). In lianas, the 0–1 cm diameter class was again much larger than the 1–2 cm class. This indicates that many newly established stems of infrequent tree species had already passed the 1 cm class two years after the fires, but not yet the 2 cm class, while most stems of liana species were still smaller than 1 cm dbh.

When only entirely burnt subplots were included in the analysis, stem densities in small diameter classes (dbh = 0–2 cm) of infrequent species were negatively related to both elevation and inclination (Table 4.6). Post-fire regeneration of infrequent species was thus more abundant at lower elevations and in flatter areas. But little variation in the plant community characteristics was usually explained by these topographic variables and relations were not always significant. In general, small diameter classes were related in a very similar way to topographic variation within the burnt matrix as were all diameter classes together (Table 4.5).

Finally, I studied the relationship between the regeneration of infrequent species and three main components of the vegetation structure, tall trees (all species, dbh > 10

Table 4.6. Relations of small stem numbers (dbh < 2 cm) of infrequent species in the burnt matrix with two topographic variables and three characteristics of the vegetation structure. Relations with topographic variables were analysed by means of regression analysis, those with the vegetation structure by means of correlation using both elevation and inclination as covariables. Significance levels: *) p < 0.05, ***) p < 0.005, NS not significant (n = 64).

	Sungai Wain Trees	Sungai Wain Lianas	Wanariset Trees	Wanariset Lianas
Elevation	$-0.104x + 16.1$ $r^2 = 0.093^*$	$-0.092x + 14.2$ $r^2 = 0.101^*$	$-0.246x + 28.4$ $r^2 = 0.148^{***}$	$-0.287x + 26.7$ $r^2 = 0.312^{***}$
Inclination	NS	$-0.184x + 8.63$ $r^2 = 0.064^*$	NS	$-0.363x + 15.3$ $r^2 = 0.067^*$
Large trees	$r = +0.329^{***}$	$r = +0.255^*$	$r = +0.451^{***}$	$r = +0.358^{***}$
Abundant trees	NS	NS	NS	NS
Abundant lianas	NS	NS	NS	NS

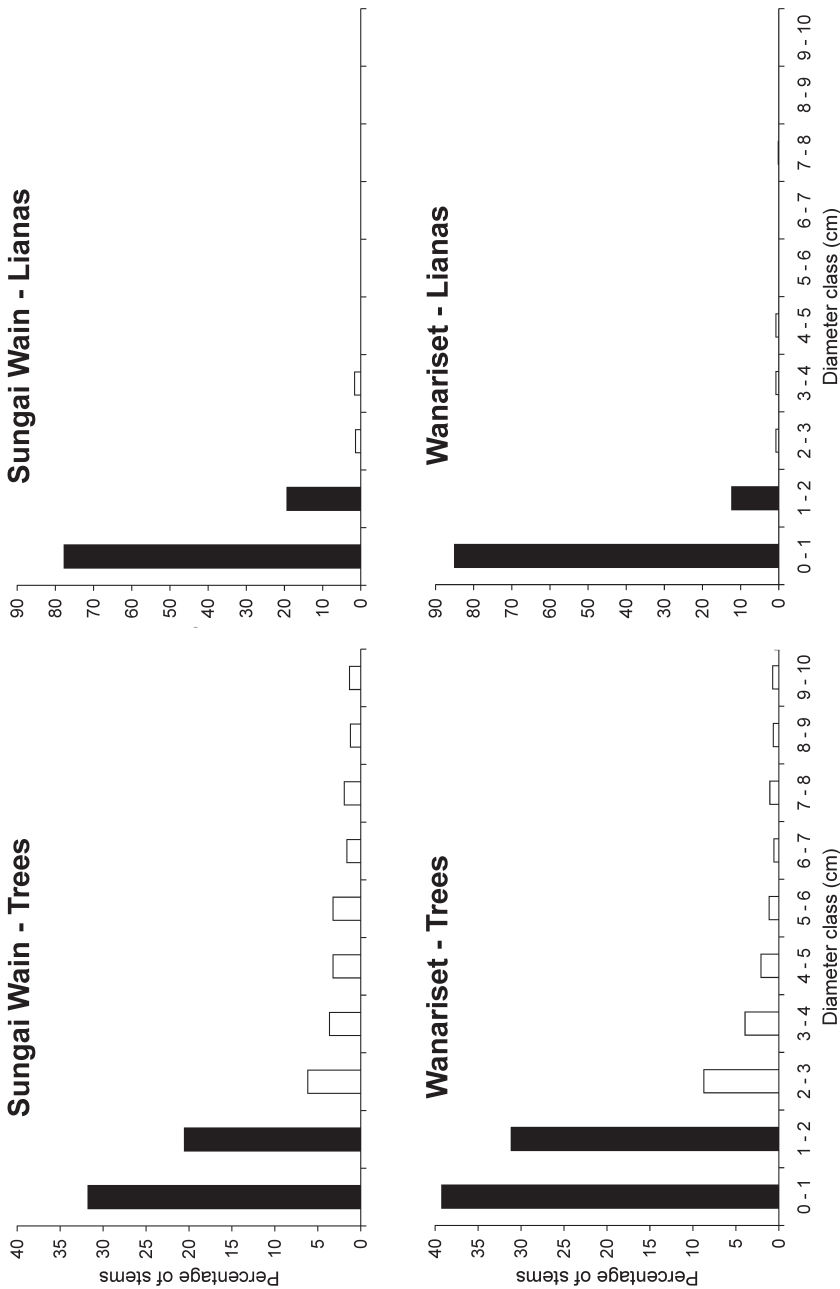


Fig. 4.6. Distribution of stems of infrequent species over dbh classes up to 10 cm. Results shown for trees and lianas and for both forest reserves. Stem numbers expressed as the percentages of all stems in entirely burnt subplots (n = 64). Solid bars indicate classes included in the analyses of post-fire regeneration.

cm), stems of abundant tree species (dbh < 10 cm) and stems of abundant liana species (Table 4.6). In order to exclude indirect relations with topographic variation, partial correlations were performed using both elevation and inclination as covariables. Stem numbers in infrequent species showed a significant positive relation to the number of tall trees. Relations were highly significant, except for lianas in the Sungai Wain forest. In contrast, no significant relations were found with stem numbers in abundant tree and liana species. Thus, post-fire regeneration of infrequent species within the burnt matrix was clearly more abundant below tall trees but was not at all related to variation in the density of abundant species.

DISCUSSION

Abundant versus infrequent species

A few abundant plant species dominated the burnt matrix of the forest, while the great majority of the species was infrequent and mainly restricted to the unburnt forest network. It is a generally observed phenomenon that early successional stages are dominated by a rather limited set of pioneer species (e.g. Uhl, 1987; Brown & Lugo, 1990; Guariguata & Ostertag, 2001). Most abundant tree species in the burnt forests were indeed referred to as pioneer species (Table 4.7). In contrast to this, few infrequent species were classified as pioneer species. More evidence for the pioneer status of most abundant species and the non-pioneer status of most infrequent species was provided by the soil seed bank analyses and preferences of the species for canopy gaps. Pioneer species typically have a soil seed bank and establish exclusively in canopy gaps in forests, in contrast to non-pioneer species (Swaine & Whitmore, 1988). In the burnt forests of my study, most abundant species were indeed observed in the soil seed bank ($23/42 = 55\%$), while only a small fraction of the non-pioneer species were so ($20/732 = 3\%$) (Chapter 3). In addition, of the 17 species that were shown to be associated with canopy gaps (Chapter 2), 13 were among the abundant species while only four species were not.

However, not all abundant species seemed to be typical pioneer species. *Fordia splendidissima* (Leguminosae), *Gironniera nervosa* (Ulmaceae s.l.) and *Macaranga lowii* (Euphorbiaceae) also had high stem densities in unburnt forest (Chapter 3). These abundant species were able to recover from fire by resprouting of their burnt stems (Van Nieuwstadt et al., 2001). *Syzygium nigricans* (Myrtaceae) was almost restricted to wet areas in nearby unburnt forests and thus apparently little affected by the fires. *Pternandra coeruleascens* (Melastomataceae) also had high concentrations of individuals in the floodplains of unburnt forests, was capable of recovering from fire by resprouting and was frequently observed in the soil seed bank (Chapter 3).

Plant diversity and topographic variation

For both trees and lianas in both burnt forests, species richness increased and composition changed at lower elevations and in flatter areas. These patterns are, however, not restricted to burnt forests, as there is much evidence that topography can be a factor determining species richness and composition in unburnt forests too, by being related

Table 4.7. List of tree species that are abundant in at least one of the forest reserves. Abundant was defined as having at least 30 stems per hectare on average in the subplots. After each species name if it was abundant in Sungai Wain (SW) and Wanariset (Wan), observed in the soil seed bank (SSB), associated with canopy gaps in the unburnt forest of Sungai Wain (Gap), and references to publications where the species was explicitly classified as a pioneer.

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Species name	SW	Wan	SSB	Gap	Pioneer
<i>Blumea balsamifera</i> (Compositae)	+	–	–	–	1
<i>Cratoxylum formosum</i> (Hypericaceae)	–	+	+	–	2
<i>Dillenia borneensis</i> (Dilleniaceae)	+	–	–	+	3, 41
<i>Ficus aurata</i> (Moraceae)	+	+	+	–	
<i>Ficus grossularioides</i> (Moraceae)	–	+	+	–	4, 5
<i>Ficus obscura</i> (Moraceae)	–	+	–	–	
<i>Ficus</i> sp. 3 (Moraceae)	–	+	+	–	
<i>Fordia splendidissima</i> (Leguminosae)	+	+	–	–	
<i>Callicarpa pentandra</i> (Labiatae)	–	+	+	–	6
<i>Gigantochloa</i> sp. 1 (Gramineae)	–	+	–	–	
<i>Gironiera nervosa</i> (Ulmaceae s.l.)	+	+	–	–	
<i>Homalanthus populneus</i> (Euphorbiaceae)	–	+	+	–	7–10
<i>Leea indica</i> (Vitaceae)	–	+	–	–	4, 7, 11
<i>Macaranga bancana</i> (Euphorbiaceae)	+	+	–	+	2, 5, 7, 9, 12–25, 41
<i>Macaranga conifera</i> (Euphorbiaceae)	–	+	–	+	9, 15, 24–29, 41
<i>Macaranga gigantea</i> (Euphorbiaceae)	+	+	–	+	1, 3, 5, 7, 12–17, 19–28, 30–33, 41
<i>Macaranga hypoleuca</i> (Euphorbiaceae)	–	+	+	+	5, 13, 16, 19–22, 24, 25–28, 30–36, 41
<i>Macaranga lowii</i> (Euphorbiaceae)	+	+	+	–	
<i>Macaranga pearsonii</i> (Euphorbiaceae)	–	+	–	–	24–25
<i>Macaranga trichocarpa</i> (Euphorbiaceae)	+	+	+	+	3, 5, 7, 8, 14, 24–25, 41
<i>Mallotus paniculatus</i> (Euphorbiaceae)	–	+	–	–	5, 7–9, 24, 33
<i>Melastoma malabathricum</i> (Melastomataceae)	+	+	+	–	2, 9, 14, 16, 33, 37, 38
<i>Melicope glabra</i> (Rutaceae)	–	+	–	–	
<i>Pertusadina eurhyncha</i> (Rubiaceae)	–	+	+	–	39
<i>Piper aduncum</i> (Piperaceae)	–	+	+	–	9, 40
<i>Pternandra coerulescens</i> (Melastomataceae)	+	+	+	–	
<i>Syzygium nigricans</i> (Myrtaceae)	+	–	–	–	
<i>Trema tomentosa</i> (Ulmaceae s.l.)	–	+	+	–	16
<i>Vernonia arborea</i> (Compositae)	+	+	+	+	41

to gradients in, for example, soil type and hydrology (Ashton, 1976; Clark et al., 1999; Svenning, 1999; Webb & Peart, 2000). In the unburnt forest of Sungai Wain, both species richness and composition were related to topography too (Chapter 2), but much less variation in these plant community parameters was explained by topography than in the burnt forests of both Sungai Wain and Wanariset (Table 4.2). Thus, topography seems to determine the patterns in species richness and composition of burnt forests much more than of unburnt forests.

The observed relations between plant community characteristics and topography resulted from an increased stem density of infrequent species at lower elevations and in flatter areas. In contrast, abundant species were only weakly or not at all related to topography. Stem densities in infrequent species were also much more closely related to species richness and composition than were stem densities in abundant species, showing that the infrequent species particularly determined the patterns in the overall plant community characteristics. This can be explained by two factors:

- 1) the great majority of species was infrequent (Fig. 4.2); and
- 2) particularly the distribution of infrequent species was related to topography (Table 4.3).

Unburnt remnant forest

In Sungai Wain, 10.6% of the recorded surface (1.6 ha) was covered by unburnt remnant forest and in Wanariset 8.1%. These estimates included only the interconnected patches that together constituted the network. Since patches of unburnt remnant forest outside the network were scarce and usually not larger than 1–5 m² (K.A.O. Eichhorn, pers. obs.), the real cover of unburnt forest in the subplots was assumed to be only slightly higher than recorded. However, it remains questionable to what extent my subplots were representative of the whole study area, as the variation in cover was high. Based on additional field studies in East Kalimantan it was estimated that the cover of unburnt remnant forest after the 1998 fires varied roughly between 5% and 30% (K.A.O. Eichhorn, D.F.R. Cleary, J.W.F. Slik, unpublished data).

The cover of unburnt remnant forest showed a negative relation to both elevation and inclination. These negative relations could be explained by the fact that the unburnt forest network was mainly restricted to floodplains: flat areas in the valleys of streams. The underlying factor explaining the position of remnant forest is likely to be the relatively high water content of floodplain soils. Interestingly, floodplains of streams less than 0.5 m wide were usually entirely burnt during the fires (K.A.O. Eichhorn, pers. obs.). Along smaller streams, the soils were apparently completely dry after six months of drought during the ENSO event of 1998, while floodplains of larger streams were still sufficiently wet to prevent fires. Thus floodplains of large streams seem to be much less vulnerable to fire than those of small streams.

The combination of the topographic position and plant composition of the network was the main explanation for the observed relations between the plant community characteristics and topography. The unburnt forest network was dominated by stems of infrequent species, while the surrounding burnt matrix was dominated by abundant species. As the network was mainly restricted to flat areas at lower elevations, species

composition shifted from abundant to infrequent species and species richness increased at lower elevations and in flatter areas. Besides the unburnt forest network, variation within the burnt matrix itself was a second factor explaining the observed relations. When only the entirely burnt subplots were included in the analyses, species richness and stem densities in infrequent species were still increasing and species composition was still changing at lower elevations. Field observations indicated that, within the burnt matrix, fire damage was generally less severe in the valleys (K.A.O. Eichhorn, pers. obs.). Tree mortality has been shown to be positively related to fire intensity (Cochrane & Schultze, 1999) and more stems may have survived in the lower parts of the burnt landscape.

Post-fire regeneration in the burnt matrix

Within the burnt matrix surrounding the unburnt forest network, post-fire regeneration was dominated by a few abundant pioneer species, but significant numbers of infrequent non-pioneer species were present as well. Assessment of post-fire regeneration was complicated in this study by the fact that small stems of infrequent species in the burnt matrix not only comprised saplings and resprouting individuals that established after the fires, but also slow-growing individuals that survived the fires. It is nevertheless very likely that for infrequent species, stems up to 2 cm dbh almost entirely comprised post-fire regeneration. Since mortality due to fire strongly increases with decreasing diameter class, small diameter classes have hardly any individuals directly after fire (Uhl & Kauffman, 1990; Peres, 1999; Van Nieuwstadt et al., 2001; Cleary, 2002). In the burnt matrix of my study sites, dbh classes above 2 cm contained much fewer stems in the burnt matrix than those below this level, indicating that only a few trees that established after the fires exceeded 2 cm dbh. Uhl (1987) recorded an average increase in diameter of trees after fire of about 0.7 cm year^{-1} . Considering the fact that I studied the burnt forest about two years after the fires, this growth rate indeed predicts that most saplings will be in the 1–2 cm classes recorded in this study. In lianas, most stems did not yet exceed 1 cm dbh.

Post-fire regeneration of infrequent species increased at lower elevations and in flatter areas, where fires were apparently less intense due to a relatively high humidity. As the ability to produce new shoots is likely to be dependent on the amount of fire damage to trees and other plants, densities of newly produced shoots may have been higher in the valleys. In addition, more new seedlings may have germinated there, as the soil seed bank is usually less damaged when fire intensity is low (Uhl et al., 1981), although few seeds of the infrequent species were found in the topsoil (Chapter 3).

Post-fire regeneration of infrequent species was positively associated with the stem density of tall trees. This association did not result from indirect relations between the two plant variables and topography, as was shown by the partial correlations using both elevation and inclination as covariables. Guevara et al. (1986, 1992) showed that tall trees can function as regeneration nuclei by attracting birds which import seeds from surrounding areas. This may explain why the regeneration was better developed below tall trees, although other mechanisms could also account for the observed positive association: patches in the burnt matrix which have been subjected to a relatively low fire intensity may contain more tall trees due to higher survival, as tall tree mortality

is higher when fires become more intensive (Cochrane & Schultze, 1998; Goldammer, 1999). But these patches are also likely to contain more post-fire regeneration (see above). As I could not score any parameter that is a more direct measure of fire intensity, I was not able to study associations between post-fire regeneration and tall trees with the exclusion of indirect relationships with fire intensity. However, the fact that stem densities of tall trees and post-fire regeneration of infrequent species were positively associated (Table 4.6) nevertheless shows that tall trees indicate a relatively well-developed post-fire regeneration of infrequent species.

Abundant species had apparently little influence on the post-fire regeneration of infrequent species, as I found no significant relationships between both groups of species. In contrast to my results, most of the abundant species are regarded as pioneer species and these have been shown to shelter the regeneration of non-pioneer species against droughts in *Imperata* grasslands in Kalimantan (Otsamo et al., 1996; Tolkamp & Aldrianto, 1997). Because of this sheltering effect, pioneer species are widely applied in reforestation projects to enhance the survival and growth of non-pioneer species such as Dipterocarps. However, the burnt matrix of my study sites was probably not dry enough to cause a high mortality among the infrequent non-pioneer species and a sheltering effect of abundant pioneer species.

SUMMARY, CONCLUSIONS AND OUTLOOK FOR FUTURE RESEARCH

INTRODUCTION

The combination of human activity and fire has resulted in a dramatic increase of forest destruction in tropical regions. During El-Niño Southern Oscillation (ENSO) events, especially large areas have been destroyed by fire. It has been demonstrated that the most extensive fires have occurred in the Indonesian province of East Kalimantan (Siegert et al., 2001), where 3.5 million ha of vegetation were destroyed in 1982–1983 (Goldammer et al., 1996) and 5.2 million ha in 1998, this including 2.6 million ha of forest (Hoffmann et al., 1999). Contemporary large-scale ENSO fires have also been recorded elsewhere in Indonesia (Legg & Laumonier, 1999) as well as in the Amazon region (Cochrane & Schultze, 1998; Hammond & Ter Steege, 1998; Laurance, 1998; Cochrane, 2003). As with forest concessions and plantations, national parks and many other forest reserves were also largely or entirely destroyed in East Kalimantan (Goldammer et al., 1996; Hoffmann et al., 1999; Siegert et al., 2001). The question now arises as to whether areas with burnt forest still harbour enough biodiversity to justify maintaining their conservation status, or whether all efforts should be focused on the protection of so-called ‘pristine’ forests so as to reduce the risk of those being destroyed by future fires. So far, data on the impact of the fires on species diversity have been scarce (Chapter 1). I have studied two burnt forests in detail and compared them with one of the few unburnt lowland rain forests left in East Kalimantan. Particular emphasis was placed on plant diversity and forest structure at the landscape scale. In order to extrapolate the results of this study to other burnt forests in East Kalimantan, I compared several forests using high-resolution Synthetic Aperture Radar (SAR-) images and additional field studies.

FIELD STUDY

The field study was executed in two forest reserves north of the city of Balikpapan (see Chapter 1 for more details). Plant diversity was studied in unburnt and once-burnt forest of the Sungai Wain reserve, and in twice-burnt forest of the Wanariset reserve. In 1998 both forests were heavily damaged by fires over most of their area as stems of small diameter classes were almost entirely absent after the fires (Van Nieuwstadt et al., 2001). From January to May 2000, these three forests were recorded using the same method: all terrestrial plants were sampled and identified in two sets of 40 subplots (10 × 20 m) randomly located in plots of 18 ha and 450 ha. Apart from the field survey, soil samples of all subplots in the three 450 ha plots were analysed as to their content of germinating seeds in the nursery (see Chapter 3 for details).

UNBURNT REMNANT FOREST

Remnants of unburnt forest are often observed in burnt forest areas (Goldammer et al., 1996; Cochrane & Schultze, 1998, 1999). Until now it is unknown how it is structured in the burnt landscape and it has been questioned to what degree its biotic integrity is maintained during post-fire succession (Cochrane & Schultze, 1999). From the strong contrast in the vegetation structure and the absence of burnt wood fragments, unburnt forest patches were still easily recognizable in my study sites and their limits could usually be mapped in the subplots to 1 m accuracy. In the burnt forests of Sungai Wain and Wanariset, I found that unburnt forest patches covered respectively 10.6% and 8.1% of the studied area (Chapter 4). Nearly all unburnt forest was found to be in the floodplains of small rivers and streams. As streams form an integrated network in the burnt landscape, unburnt remnant forest did not comprise isolated fragments but effectively constituted networks of interconnected patches (Chapter 4: Fig. 4.3).

The species composition of the unburnt forest network was studied by assigning them to two abundance classes defined by arbitrary limits: abundant species (densities 30 or more stems ha^{-1} when calculated as the average of all 80 – burnt and unburnt – subplots in a forest reserve) and infrequent species (less than 30 stems ha^{-1}) (see Chapter 4 for further details). These two classes seemed to reflect to a high degree two contrasting ecological plant types, as most abundant species were often referred to as pioneer species, while few infrequent species were so (Chapter 4: Table 4.7). A comparison of the unburnt network with the burnt matrix showed that the network contained high concentrations of infrequent species, while the matrix was dominated by abundant species (Chapter 4: Fig. 4.5). Stem densities in infrequent species therefore showed highly significant positive correlations with the cover of unburnt remnant forest, while abundant species were negatively or not correlated with its cover (Chapter 4: Table 4.3). While the unburnt network covered only c. 10% of the area, the majority of all species was present and many infrequent species were even restricted to it. It thereby made an important contribution to overall plant diversity in the burnt forests. Other elements that contribute importantly to the recovery of plant diversity are both tall trees, that survived the fires and droughts (Chapter 3), and resprouting primary forest species (Van Nieuwstadt et al., 2001; Guariguata & Ostertag, 2001).

In the twice-burnt Wanariset forest, the network was still present 18 years after the initial fires in 1982–1983 and mainly comprised infrequent non-pioneer species (Chapter 4: Fig. 4.5). This shows that it has been able to survive recurrent fires and that its composition has been very persistent during post-fire succession. Since many species being critically reduced by the fires maintain high stem concentrations in this network, it may well facilitate their future recovery in the burnt matrix. There is an interesting historical analogue here, in that tropical riparian forests are thought to have functioned as persistent forest refuges during Pleistocene dry periods, and subsequently to have enabled the conversion of surrounding savannah into forest (Meave et al., 1991).

PLANT REGENERATION AND DIVERSITY

Two years after the fires, succession was developed far enough to permit study of the initial forest recovery. Forest regeneration was better developed in the twice-burnt matrix of the Wanariset forest than it was in the once-burnt matrix of the Sungai Wain forest (Fig. 5.1). The density of young trees was more than three times higher and even exceeded tree density in the unburnt forest (Chapter 3: Table 3.3). In addition, typically weedy growth forms like ferns, vines and grasses were less abundant in the matrix of the twice-burnt forest (Chapter 3: Table 3.4), even though they were common in the surrounding cultivated land. This striking difference between the two burnt sites would appear to reflect the densities of tree seeds in the soil seed bank before the 1998 fires. The Wanariset forest was then dominated by pioneer trees as a result of the initial fires in 1982–1983, while such trees were relatively scarce in the unburnt Sungai Wain forest. As pioneer species typically have a well-developed soil seed bank (Swaine & Whitmore, 1988; Garwood, 1989), many more tree seeds may have been present in the topsoil of the Wanariset forest. Similarly, post-clearing regeneration is generally better developed when a site has previously been occupied by successional vegetation rather than old-growth forest (Guariguata & Ostertag, 2001). This explanation implies that even a third fire will not lead to permanent deforestation, since tree seeds in the topsoil were most abundant at this site (Chapter 3: Table 3.8). Thus far, recurrent fires have not led to permanent deforestation and it seems unlikely that subsequent fires will change this very soon.

In order to study whether changes in the forest structure were accompanied by changes in plant diversity, species richness was assessed both at the subplot scale (0.02 ha) – by taking the average number of species per subplot, and at the landscape scale (450 ha) – by taking the total number of observed species in each of the three forests (see Chapter 3 for further details). In addition, the total number of species per forest type was estimated by means of the ICE-index (Lee & Chao, 1994) and Fisher's alpha (Fisher et al., 1943). At the subplot scale, observed species richness was considerably lower in the two burnt forests, while at the landscape scale, differences between sites were much smaller (Chapter 3: Table 3.3, 3.4). Differences between forest types were also much smaller when the total number of species was estimated with the above-mentioned indices. Only trees accounted for a higher overall plant diversity in the unburnt forest, while the number of species in lianas and herbaceous plants was often higher in the burnt forests.

These results show that the scale of assessment strongly determines the relative differences in species richness between the three forests. Although the forest structure was severely affected in the burnt forests, species numbers were not much lower than in the unburnt forest. The main difference was that the majority of the species occurred at lower densities. Studies below the landscape scale are therefore expected to reveal much higher extinction rates than the actual values will be. Efforts to provide further evidence about the impact of large-scale disturbance events like the 1997–1998 fires should therefore focus on additional large-scale biodiversity assessments rather than on highly replicated small-scale studies, as only large-scale studies can paint the full picture.



Fig. 5.1. The structure of two burnt forests in East Kalimantan two years after the 1998 fires. — A. The once-burnt forest of Sungai Wain: Scattered bushes of young pioneer trees and (mostly dead) tall trees in a dense vegetation of herbaceous ferns and climbers. — B. The twice-burnt forest of Wanariset: A dense young forest consisting of pioneer trees up to six metres high, with few herbaceous plants in the understorey and scattered (mostly dead) tall trees in between.



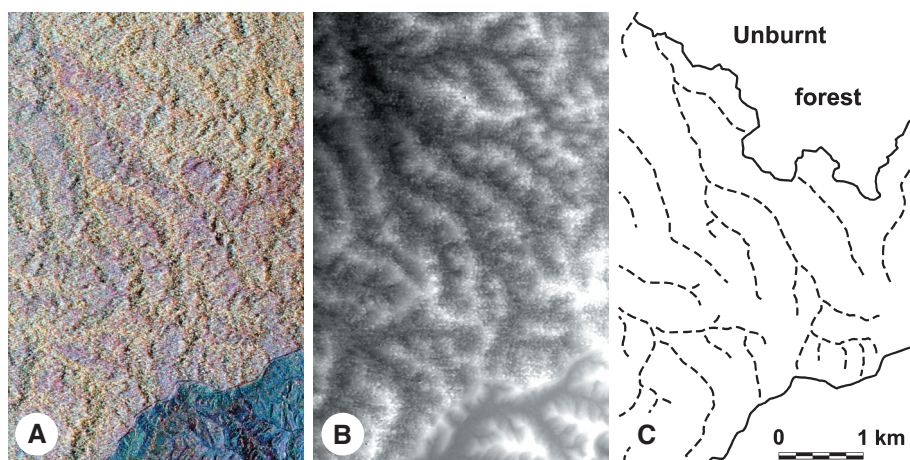


Fig. 5.2. Detail of the unburnt forest network in Sungai Wain and its relation to topography. — A. Polarimetric radar image in orthographic projection with intensity corrections for slope effects: red P-band, green L-band, blue C-band. Vegetations types: yellow unburnt forest, pink burnt forest, blue severely burnt rubber plantation. Note that large trees are distinguishable in both forest types. — B. High-resolution Digital Elevation Model (DEM) of the same area: grey-scale from low (black) to high (white) altitude of terrain plus vegetation. — C. Map of the same area based on visual interpretation of the SAR-image and on information from the field.

FIRE FREQUENCY AND DEFORESTATION

The observed high regenerative power of the burnt forests is in accordance with Neotropical forest succession (Guariguata & Ostertag, 2001), but superficially seems to conflict with the findings in papers describing recurrent fires that become increasingly destructive and finally result in permanent deforestation (Goldammer, 1999; Cochrane et al., 1999). The key factor explaining these divergent findings has been suggested to be fire frequency (Cochrane, 2003). If fires occur at high frequency, new pioneer trees will be eliminated before reproduction (Cochrane & Schultze, 1998, 1999). Their soil seed bank declines with each new fire and subsequent post-fire stands will have a more open structure. During dry periods, more open stands are more vulnerable to later fires. These fires are also more intense and can destroy even tall trees (Goldammer, 1999) and unburnt forest remnants (Cochrane & Schultze, 1998). This positive feedback in the fire dynamics will finally lead to permanent deforestation (Goldammer, 1999; Cochrane et al., 1999; Nepstad et al., 2001). However, if fires occur at lower frequencies, pioneer trees become reproductive and can replenish the seed bank before the next fire. Subsequent pioneer stands will not have a more open structure and deforestation will not occur. It would appear that post-fire stands will then remain humid enough during dry periods to prevent high-intensity fires that destroy tall trees and unburnt remnant forest. Plant diversity is then further conserved by the resprouting of primary forest trees, which has also been shown to be especially sensitive to repeated disturbance at high frequencies (Van Nieuwstadt et al., 2001).

SYNTHETIC APERTURE RADAR (SAR-)IMAGES AND ADDITIONAL FIELD STUDIES

Remote sensing images and additional field studies provide evidence that the observed high diversity of the once- and twice-burnt forest is also present in many other burnt forests of East Kalimantan. On 16 September 2000, two representative areas (each 1,200 km² in size) in the burnt region of East Kalimantan were observed using the airborne NASA/JPL AirSAR imaging radar centred at Meratus and Sungai Wain. Compared with other existing images these SAR-images have a very rich information content and enable the recognition of remnant forest and individual tall trees (Hoekman & Quiñones, 1999; Hoekman, 2001). Tall remnant trees and unburnt remnant forest networks were visible in all burnt forests that were studied: Sungai Wain (Fig. 5.2), Wanariset, Bukit Bankirai, and PT.ITCI concession (Meratus).

In November and December 1999, I visited burnt lowland rain forests throughout the burnt region in East Kalimantan. Elements that were shown to be major contributors to plant diversity in burnt forests were still present at all sites, usually to the same levels as in the burnt forests of Sungai Wain and Wanariset. Unburnt remnant forest, tall remnant trees and resprouting individuals of typical primary forest species were seen to be common in burnt forests around the bay of Balikpapan, in the PT.ITCI concession, Bukit Bankirai, Bukit Soeharto, Kutai National Park and to the very north of the burnt region near Sangkulirang. Similar observations were also made by other researchers at several sites in the burnt region (J.W.F. Slik and D.F.R. Cleary, pers. comm.).

Both the remote sensing images and the additional field studies showed that remnant forest networks, tall trees and resprouting stems were present at all sites studied in the burnt region. This is a strong indication that most of the plant diversity was also conserved there and probably at many other burnt sites in East Kalimantan.

BURNT FORESTS AND BIODIVERSITY CONSERVATION

In the absence of further disturbance the burnt tropical rain forests in East Kalimantan seem to be able to conserve most of their high plant species richness. Species richness is still high in the two burnt forests studied in detail and elements that contribute importantly to plant diversity are present in various other burnt forests. Logged rain forest in Borneo is also shown to be richer in tree species than has been assumed before (Cannon et al., 1998) and this has motivated Chazdon to stress the importance of disturbed and fragmented tropical rain forests for the conservation of biodiversity (Chazdon, 1998). With the expectation that hardly any unburnt lowland forest (logged or not) will be left in Kalimantan in the near future (Siegert et al., 2001; Jepson et al., 2001), I predict that burnt forests will soon be deemed conservationally important ecosystems too. In my opinion, this strongly advocates their protection from further destructive human activities.

Such activities seem to have greatly increased since the 1997–1998 fires in East Kalimantan. Salvage felling, the harvesting of dead timber, is stimulated by government regulations and has now become a threat to regenerating burnt forests as a result of the heavy machinery used and the illegal harvesting of living trees (Hoffmann et

al., 1999; Van Nieuwstadt et al., 2001; Curran et al., 2004). High-frequency wildfires associated with land reclamation has also increased and these have the potential to cause permanent deforestation. Earlier reports from the Amazon region and East Kalimantan have described the processes leading to permanent deforestation (Goldammer, 1999; Cochrane et al., 1999; Nepstad et al., 2001) and to the alarming consequences for those regions (Jepson et al., 2001; Laurance et al., 2001; Carvalho et al., 2001). On the one hand I consider these publications invaluable for drawing attention to the severe impact of wildfires on tropical rain forests. But, I would like to stress that too pessimistic a view will only stimulate further destructive human activities as they will reinforce the opinion that disturbed forests are not worth considering for biodiversity conservation. The results of this study show that even after severe damage by ENSO fires, burnt tropical rain forests can still harbour high plant diversity, but that it must be realized that the major threats to that diversity will come from subsequent destructive human activities.

FUTURE RESEARCH

Although integration of my field study with remote sensing studies was not an objective at the moment that my field study started, this integration proved to be able to generate important additional information on the status of the burnt rain forests in East Kalimantan. The fact that my study of plant diversity was executed at scales up to 450 ha, a much larger scale than was usual at that time, made it possible to show that within two burnt forest reserves most of the original species richness was conserved in unburnt remnant forest networks and tall remnant trees that survived the fires. The added value of remote sensing studies is that they enable diversity assessments at even larger spatial scales. Since unburnt forest networks and tall remnant trees were visible at all sites studied within the burnt area that was surveyed by remote sensing, it is very likely that plant diversity was also largely conserved there. However, in order to obtain stronger evidence that most of the rain-forest biodiversity is conserved in forest remnants throughout the burnt region, studies of SAR-images should be integrated with biodiversity field studies using small subplots that are scattered throughout the remotely sensed area. Especially in such very large-scale field studies statistical dependence between ecological and spatial variables should be avoided (see Chapter 1 for a discussion of this problem). Perhaps such studies will not only show that my results are of general value, but also detect new biodiversity patterns at even larger spatial scales. The results of such large-scale studies will help us to better predict which areas should be prioritised for biodiversity conservation.

Other studies could provide important additional information on questions concerning the plant diversity of burnt rain forests in Borneo. My study did not include mosses and vascular epiphytes, for example. Both plant types can be important components of overall plant diversity (e.g. Richards, 1996) and may well show diversity patterns different from plant types included in my study. Furthermore, ecological studies that focus on the underlying processes explaining the plant diversity patterns observed in my study can help us to better understand how such patterns arise. An interesting example of such a study will be one on the spatial relationships between hydrology,

topography, and the impact of fires on plant diversity. My study detected relationships between topography, forest remnants and plant diversity, but many of the observed relationships between plant diversity and topography apparently reflected relationships with hydrology.

Another important question is how plant diversity develops during post-fire succession. My field study was restricted to only a single record of the subplots, about two years after the ENSO fires of 1998. At that time, plant diversity was still high in the burnt forests. However, an unknown proportion of the species may become extinct during the coming years, as a result of reduced reproduction and growth, increased predation, edge-effects etc. (see Chapter 1). On the other hand, new (invasive) species and (temporally) extinct species can (re-)colonise the burnt areas from the surrounding areas. A series of records during a time span of at least some decades may reveal to what extent such processes lead to post-fire extinction and (re-)colonisation. Such a study will be especially informative if executed in the same plots, but this requires continuity in the field project for a long period of time. If such a time series of records is executed in small permanent sample plots that are widely scattered throughout the burnt area, changes of plant diversity in time can be related to changes in the whole region as detected by remote sensing. Finally, all future research should aim at greater integration of studies of biodiversity, ecological relationships and remote sensing.

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Appendix 1

List of all species recorded in the 10 × 20 m subplots. After each family, genus and species name respectively plant type, observed number of stems (N) and number of subplots having at least one stem exceeding 1.3 m in height of this species (S) per forest disturbance type (0 = unburnt, 1 = once-burnt, 2 = twice-burnt) (n = 80). Notes: ¹⁾ incl. *Gomphia*, ²⁾ syn. *Anthocephalus chinensis*, ³⁾ subsp. *caudatum*.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Actinidiaceae	<i>Saurauia</i>	<i>glabra</i>	dicot tree	0	0	5	0	0	5
Alangiaceae	<i>Alangium</i>	<i>ridleyi</i>	dicot tree	23	0	29	11	0	10
Anacardiaceae	<i>Bouea</i>	<i>oppositifolia</i>	dicot tree	12	4	2	11	4	2
Anacardiaceae	<i>Buchanania</i>	<i>sessifolia</i>	dicot tree	1	0	3	1	0	2
Anacardiaceae	<i>Camposperma</i>	<i>auriculatum</i>	dicot tree	1	0	0	1	0	0
Anacardiaceae	<i>Dracontomelon</i>	<i>dao</i>	dicot tree	0	0	3	0	0	3
Anacardiaceae	<i>Drimycarpus</i>	<i>luridus</i>	dicot tree	27	1	1	18	1	1
Anacardiaceae	<i>Gluta</i>	<i>macrocarpa</i>	dicot tree	46	4	2	31	4	2
Anacardiaceae	<i>Gluta</i>	<i>renghas</i>	dicot tree	1	0	0	1	0	0
Anacardiaceae	<i>Gluta</i>	<i>wallichii</i>	dicot tree	42	3	0	16	3	0
Anacardiaceae	<i>Mangifera</i>	<i>foetida</i>	dicot tree	3	0	0	3	0	0
Anacardiaceae	<i>Melanochyla</i>	<i>fulvinervis</i>	dicot tree	91	10	6	36	8	4
Anacardiaceae	<i>Parishia</i>	<i>insignis</i>	dicot tree	3	0	0	3	0	0
Anacardiaceae	<i>Pentaspadon</i>	<i>motleyi</i>	dicot tree	1	0	0	1	0	0
Anacardiaceae	<i>Swintonia</i>	<i>acuta</i>	dicot tree	1	0	0	1	0	0
Anacardiaceae	<i>Indet</i>	<i>sp. 7</i>	dicot tree	1	0	0	1	0	0
Anacardiaceae	<i>Indet</i>	<i>sp. 8</i>	dicot tree	0	0	1	0	0	1
Anacardiaceae	<i>Indet</i>	<i>sp. 9</i>	dicot tree	0	0	1	0	0	1
Anacardiaceae	<i>Indet</i>	<i>sp. 10</i>	dicot tree	0	0	1	0	0	1
Anacardiaceae	<i>Indet</i>	<i>sp. 16</i>	dicot tree	0	0	5	0	0	5
Ancistrocladaceae	<i>Ancistrocladus</i>	<i>tectorius</i>	dicot liana	24	42	17	11	22	9
Annonaceae	<i>Artabotrys</i>	<i>macranthus</i>	dicot liana	14	1	1	9	1	1
Annonaceae	<i>Artabotrys</i>	<i>suaveolens</i>	dicot liana	10	35	39	9	29	21
Annonaceae	<i>Cananga</i>	<i>odorata</i>	dicot tree	0	0	10	0	0	9
Annonaceae	<i>Cyathocalyx</i>	<i>carinatus</i>	dicot tree	0	0	4	0	0	2
Annonaceae	<i>Cyathocalyx</i>	<i>sumatrana</i>	dicot tree	2	0	0	2	0	0
Annonaceae	<i>Cyathocalyx</i>	<i>sp. 8</i>	dicot tree	0	0	5	0	0	4
Annonaceae	<i>Cyathocalyx</i>	<i>sp. 10</i>	dicot tree	0	0	1	0	0	1
Annonaceae	<i>Cyathostemma</i>	<i>excelsum</i>	dicot liana	55	8	16	30	8	9
Annonaceae	<i>Desmos</i>	<i>chinensis</i>	dicot liana	57	3	8	37	3	7
Annonaceae	<i>Desmos</i>	<i>cochinensis</i>	dicot liana	22	8	11	15	5	5
Annonaceae	<i>Enicosanthum</i>	<i>paradoxum</i>	dicot tree	48	2	4	25	2	3
Annonaceae	<i>Enicosanthum</i>	<i>sp. 6</i>	dicot tree	3	0	4	1	0	1
Annonaceae	<i>Enicosanthum</i>	<i>sp. 7</i>	dicot tree	0	0	4	0	0	3
Annonaceae	<i>Fissistigma</i>	<i>manubriatum</i>	dicot liana	23	0	5	19	0	4
Annonaceae	<i>Fissistigma</i>	<i>sp. 1</i>	dicot liana	4	6	0	4	5	0
Annonaceae	<i>Fissistigma</i>	<i>sp. 2</i>	dicot liana	4	0	0	4	0	0
Annonaceae	<i>Fissistigma</i>	<i>sp. 3</i>	dicot liana	0	1	0	0	1	0
Annonaceae	<i>Fissistigma</i>	<i>sp. 6</i>	dicot liana	0	0	1	0	0	1
Annonaceae	<i>Fissistigma</i>	<i>sp. 7</i>	dicot liana	0	1	0	0	1	0
Annonaceae	<i>Friesodielsia</i>	<i>glabra</i>	dicot liana	2	8	2	2	5	1
Annonaceae	<i>Goniothalamus</i>	<i>macrophyllus</i>	dicot tree	4	0	0	4	0	0
Annonaceae	<i>Goniothalamus</i>	<i>sp. 1</i>	dicot tree	11	2	1	7	2	1
Annonaceae	<i>Mezzettia</i>	<i>parvifolia</i>	dicot tree	3	0	0	3	0	0
Annonaceae	<i>Mitrella</i>	<i>kentii</i>	dicot liana	1	4	246	1	3	35
Annonaceae	<i>Monocarpia</i>	<i>euneura</i>	dicot tree	6	2	1	4	1	1
Annonaceae	<i>Neouvaria</i>	<i>acuminatissima</i>	dicot tree	15	0	2	10	0	2

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Annonaceae	<i>Phaeanthus</i>	<i>splendens</i>	dicot tree	1	3	3	1	3	3
Annonaceae	<i>Polyalthia</i>	<i>cauliflora</i>	dicot tree	10	0	0	7	0	0
Annonaceae	<i>Polyalthia</i>	<i>lateriflora</i>	dicot tree	45	6	4	28	5	3
Annonaceae	<i>Polyalthia</i>	<i>microtus</i>	dicot tree	1	0	0	1	0	0
Annonaceae	<i>Polyalthia</i>	<i>rumphii</i>	dicot tree	44	2	8	27	2	4
Annonaceae	<i>Polyalthia</i>	<i>sumatrana</i>	dicot tree	71	3	0	39	3	0
Annonaceae	<i>Popowia</i>	<i>hirta</i>	dicot tree	8	0	2	8	0	2
Annonaceae	<i>Popowia</i>	<i>pisocarpa</i>	dicot tree	11	0	8	7	0	6
Annonaceae	<i>Pyramidanthe</i>	<i>prismatica</i>	dicot liana	1	11	5	1	6	4
Annonaceae	<i>Uvaria</i>	<i>sp. 5</i>	dicot liana	3	0	0	3	0	0
Annonaceae	<i>Uvaria</i>	<i>sp. 7</i>	dicot liana	2	0	0	2	0	0
Annonaceae	<i>Uvaria</i>	<i>sp. 9</i>	dicot liana	5	4	2	4	3	2
Annonaceae	<i>Uvaria</i>	<i>sp. 11</i>	dicot liana	0	0	1	0	0	1
Annonaceae	<i>Uvaria</i>	<i>sp. 12</i>	dicot liana	3	0	0	3	0	0
Annonaceae	<i>Uvaria</i>	<i>sp. 13</i>	dicot liana	4	0	0	3	0	0
Annonaceae	<i>Uvaria</i>	<i>sp. 14</i>	dicot liana	1	0	3	1	0	3
Annonaceae	<i>Xylopia</i>	<i>elliptica</i>	dicot tree	22	5	2	21	5	2
Annonaceae	<i>Xylopia</i>	<i>ferruginea</i>	dicot tree	23	2	3	17	2	3
Annonaceae	<i>Xylopia</i>	<i>malayana</i>	dicot tree	29	3	6	21	3	4
Apocynaceae	<i>Alstonia</i>	<i>iwahigensis</i>	dicot tree	8	5	4	7	4	4
Apocynaceae	<i>Alstonia</i>	<i>pneumatophora</i>	dicot tree	2	0	0	2	0	0
Apocynaceae	<i>Dyera</i>	<i>costulata</i>	dicot tree	1	0	0	1	0	0
Apocynaceae	<i>Kibatalia</i>	<i>villosa</i>	dicot tree	0	1	0	0	1	0
Apocynaceae	<i>Parameria</i>	<i>laevigata</i>	dicot liana	98	14	2	30	7	2
Apocynaceae	<i>Tabernaemontana</i>	<i>macrocarpa</i>	dicot tree	7	0	1	5	0	1
Apocynaceae	<i>Willughbeia</i>	<i>angustifolia</i>	dicot liana	21	1	1	15	1	1
Apocynaceae	<i>Willughbeia</i>	<i>sp. 1</i>	dicot liana	16	1	9	9	1	4
Apocynaceae	<i>Willughbeia</i>	<i>sp. 2</i>	dicot liana	3	0	8	3	0	3
Apocynaceae	<i>Willughbeia</i>	<i>sp. 3</i>	dicot liana	2	0	0	2	0	0
Apocynaceae	<i>Willughbeia</i>	<i>sp. 5</i>	dicot liana	1	0	0	1	0	0
Apocynaceae	<i>cf. Alyxia</i>	<i>sp. 1</i>	dicot liana	1	0	0	1	0	0
Apocynaceae	<i>cf. Alyxia</i>	<i>sp. 2</i>	dicot liana	0	1	0	0	1	0
Apocynaceae	<i>cf. Parameria</i>	<i>sp. 5</i>	dicot liana	9	0	2	8	0	2
Apocynaceae	<i>cf. Parameria</i>	<i>sp. 6</i>	dicot liana	0	0	2	0	0	2
Apocynaceae	<i>cf. Parameria</i>	<i>sp. 7</i>	dicot liana	2	0	4	2	0	2
Apocynaceae	<i>Indet</i>	<i>sp. 4</i>	dicot tree	0	0	1	0	0	1
Apocynaceae	<i>Indet</i>	<i>sp. 7</i>	dicot liana	0	0	1	0	0	1
Apocynaceae	<i>Indet</i>	<i>sp. 8</i>	dicot liana	0	1	0	0	1	0
Apocynaceae	<i>Indet</i>	<i>sp. 9</i>	dicot liana	0	1	0	0	1	0
Apocynaceae	<i>Indet</i>	<i>sp. 11</i>	dicot liana	0	0	1	0	0	1
Aquifoliaceae	<i>Ilex</i>	<i>cymosa</i>	dicot tree	18	13	7	11	12	6
Araceae	<i>Pothos</i>	<i>sp. 1</i>	monocot liana	23	2	3	18	2	2
Araceae	<i>cf. Amydrium</i>	<i>sp. 1</i>	monocot liana	1	0	0	1	0	0
Araceae	<i>cf. Pothos</i>	<i>sp. 2</i>	monocot liana	0	3	0	0	3	0
Araceae	<i>cf. Pothos</i>	<i>sp. 3</i>	monocot liana	0	0	2	0	0	2
Araceae	<i>Indet</i>	<i>sp. 2</i>	monocot liana	0	1	1	0	1	1
Araceae	<i>Indet</i>	<i>sp. 3</i>	monocot liana	2	3	1	2	3	1
Araceae	<i>Indet</i>	<i>sp. 4</i>	monocot liana	4	1	6	4	1	2
Araceae	<i>Indet</i>	<i>sp. 5</i>	monocot liana	1	0	0	1	0	0
Araceae	<i>Indet</i>	<i>sp. 7</i>	monocot liana	0	2	0	0	2	0
Araceae	<i>Indet</i>	<i>sp. 8</i>	monocot liana	0	1	1	0	1	1
Araceae	<i>Indet</i>	<i>sp. 9</i>	monocot liana	0	0	1	0	0	1
Araceae	<i>Indet</i>	<i>sp. 10</i>	monocot liana	3	0	0	1	0	0
Araceae	<i>Indet</i>	<i>sp. 11</i>	monocot liana	0	1	0	0	1	0
Araliaceae	<i>Schefflera</i>	<i>sp. 1</i>	dicot liana	0	2	0	0	2	0
Asclepiadaceae	<i>Cynanchum</i>	<i>cf. ovalifolium</i>	dicot vine	0	1	0	0	1	0

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Asclepiadaceae	<i>Cynanchum</i>	<i>sp. 1</i>	dicot vine	1	0	0	1	0	0
Asclepiadaceae	<i>Cynanchum</i>	<i>sp. 2</i>	dicot vine	0	1	1	0	1	1
Asclepiadaceae	<i>Dischidia</i>	<i>indica</i>	dicot vine	1	0	0	1	0	0
Asclepiadaceae	<i>Dischidia</i>	<i>latifolia</i>	dicot vine	1	0	0	1	0	0
Asclepiadaceae	<i>Dischidia</i>	<i>sp. 1</i>	dicot vine	0	3	0	0	2	0
Asclepiadaceae	<i>Hoya</i>	<i>sp. 1</i>	dicot liana	0	0	1	0	0	1
Blechnaceae	<i>Stenochlaena</i>	<i>palustris</i>	fern liana	2	156	164	2	54	44
Bombacaceae	<i>Durio</i>	<i>acutifolius</i>	dicot tree	183	36	7	55	31	6
Bombacaceae	<i>Durio</i>	<i>dulcis</i>	dicot tree	12	2	3	10	2	3
Bombacaceae	<i>Durio</i>	<i>graveolens</i>	dicot tree	2	1	1	2	1	1
Bombacaceae	<i>Durio</i>	<i>griffithii</i>	dicot tree	1	1	0	1	1	0
Bombacaceae	<i>Durio</i>	<i>kutejensis</i>	dicot tree	2	0	1	2	0	1
Bombacaceae	<i>Durio</i>	<i>lanceolatus</i>	dicot tree	14	1	0	10	1	0
Bombacaceae	<i>Durio</i>	<i>oxleyanus</i>	dicot tree	31	5	0	11	5	0
Bombacaceae	<i>Durio</i>	<i>sp. 1</i>	dicot tree	3	2	4	2	2	3
Bombacaceae	<i>Durio</i>	<i>sp. 3</i>	dicot tree	0	1	1	0	1	1
Bombacaceae	<i>Neesia</i>	<i>synandra</i>	dicot tree	0	0	1	0	0	1
Boraginaceae	<i>Tournefortia</i>	<i>sp. 1</i>	dicot vine	0	1	32	0	1	17
Burseraceae	<i>Canarium</i>	<i>denticulatum</i>	dicot tree	40	3	0	28	3	0
Burseraceae	<i>Canarium</i>	<i>littorale</i>	dicot tree	4	0	3	3	0	3
Burseraceae	<i>Canarium</i>	<i>megalanthum</i>	dicot tree	1	0	0	1	0	0
Burseraceae	<i>Canarium</i>	<i>odonthophyllum</i>	dicot tree	5	1	2	4	1	2
Burseraceae	<i>Canarium</i>	<i>pilosum</i>	dicot tree	18	0	1	15	0	1
Burseraceae	<i>Dacryodes</i>	<i>costata</i>	dicot tree	74	4	0	38	4	0
Burseraceae	<i>Dacryodes</i>	<i>expansa</i>	dicot tree	3	0	0	3	0	0
Burseraceae	<i>Dacryodes</i>	<i>incurvata</i>	dicot tree	1	0	0	1	0	0
Burseraceae	<i>Dacryodes</i>	<i>rostrata</i>	dicot tree	304	21	30	69	14	18
Burseraceae	<i>Dacryodes</i>	<i>rubiginosa</i>	dicot tree	18	3	0	14	3	0
Burseraceae	<i>Dacryodes</i>	<i>rugosa</i>	dicot tree	0	0	6	0	0	5
Burseraceae	<i>Dacryodes</i>	<i>sp. 8</i>	dicot tree	0	0	1	0	0	1
Burseraceae	<i>Dacryodes</i>	<i>sp. 9</i>	dicot tree	2	1	0	1	1	0
Burseraceae	<i>Santiria</i>	<i>griffithii</i>	dicot tree	18	3	4	15	3	3
Burseraceae	<i>Santiria</i>	<i>megaphylla</i>	dicot tree	2	0	0	2	0	0
Burseraceae	<i>Santiria</i>	<i>oblongifolia</i>	dicot tree	11	1	0	7	1	0
Burseraceae	<i>Santiria</i>	<i>tomentosa</i>	dicot tree	3	2	2	3	2	1
Burseraceae	<i>Santiria</i>	<i>sp. 1</i>	dicot tree	1	0	0	1	0	0
Burseraceae	<i>Triomma</i>	<i>malaccensis</i>	dicot tree	2	0	2	2	0	2
Capparidaceae	<i>Capparis</i>	<i>sp. 1</i>	dicot liana	1	0	0	1	0	0
Caprifoliaceae	<i>Viburnum</i>	<i>sp. 1</i>	dicot tree	1	1	0	1	1	0
Caprifoliaceae	<i>Viburnum</i>	<i>sp. 2</i>	dicot tree	1	0	0	1	0	0
Caprifoliaceae	<i>Viburnum</i>	<i>sp. 3</i>	dicot tree	8	1	0	5	1	0
Caprifoliaceae	<i>Viburnum</i>	<i>sp. 4</i>	dicot tree	0	0	1	0	0	1
Cecropiaceae	<i>Poikilospermum</i>	<i>sp. 1</i>	dicot liana	2	1	3	2	1	2
Celastraceae	<i>Bhesa</i>	<i>paniculata</i>	dicot tree	13	5	1	11	4	1
Celastraceae	<i>Bhesa</i>	<i>robusta</i>	dicot tree	0	0	2	0	0	2
Celastraceae	<i>Euonymus</i>	<i>castaneifolius</i>	dicot tree	16	2	0	15	2	0
Celastraceae	<i>Kokoona</i>	<i>ochracea</i>	dicot tree	7	0	0	7	0	0
Celastraceae	<i>Kokoona</i>	<i>reflexa</i>	dicot tree	1	0	1	1	0	1
Celastraceae	<i>Lophopetalum</i>	<i>beccarianum</i>	dicot tree	9	0	0	5	0	0
Celastraceae	<i>Lophopetalum</i>	<i>javanicum</i>	dicot tree	5	1	0	5	1	0
Celastraceae	<i>Lophopixis</i>	<i>maingayi</i>	dicot liana	7	0	0	6	0	0
Celastraceae	<i>Salacia</i>	<i>chinensis</i>	dicot liana	8	0	0	7	0	0
Celastraceae	<i>Salacia</i>	<i>korthalsiana</i>	dicot liana	4	0	0	2	0	0
Celastraceae	<i>Salacia</i>	<i>macrophylla</i>	dicot liana	1	0	0	1	0	0
Celastraceae	<i>Salacia</i>	<i>sp. 1</i>	dicot liana	118	16	1	49	7	1
Celastraceae	<i>Salacia</i>	<i>sp. 2</i>	dicot liana	1	0	2	1	0	2

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Celastraceae	<i>Salacia</i>	<i>sp. 3</i>	dicot liana	16	2	1	10	2	1
Celastraceae	<i>Salacia</i>	<i>sp. 5</i>	dicot liana	2	0	0	1	0	0
Celastraceae	<i>Salacia</i>	<i>sp. 7</i>	dicot liana	1	0	0	1	0	0
Celastraceae	<i>Salacia</i>	<i>sp. 10</i>	dicot liana	0	0	8	0	0	7
Celastraceae	<i>Salacia</i>	<i>sp. 11</i>	dicot liana	0	0	1	0	0	1
Celastraceae	<i>Salacia</i>	<i>sp. 12</i>	dicot liana	0	1	0	0	1	0
Celastraceae	<i>Salacia</i>	<i>sp. 13</i>	dicot liana	0	0	2	0	0	2
Celastraceae	<i>Salacia</i>	<i>sp. 14</i>	dicot liana	0	0	3	0	0	2
Celastraceae	<i>Salacia</i>	<i>sp. 15</i>	dicot liana	0	0	1	0	0	1
Celastraceae	<i>Salacia</i>	<i>sp. 16</i>	dicot liana	0	1	0	0	1	0
Chrysobalanaceae	<i>Atuna</i>	<i>racemosa</i>	dicot tree	12	1	2	11	1	1
Chrysobalanaceae	<i>Atuna</i>	<i>sp. 1</i>	dicot tree	1	0	0	1	0	0
Chrysobalanaceae	<i>Licania</i>	<i>splendens</i>	dicot tree	6	2	4	6	2	4
Chrysobalanaceae	<i>Licania</i>	<i>sp. 1</i>	dicot tree	1	0	0	1	0	0
Chrysobalanaceae	<i>Maranthus</i>	<i>corymbosa</i>	dicot tree	0	0	1	0	0	1
Chrysobalanaceae	<i>Parinari</i>	<i>oblongifolia</i>	dicot tree	2	1	0	2	1	0
Chrysobalanaceae	<i>Parinari</i>	<i>sp. 1</i>	dicot tree	1	0	0	1	0	0
Chrysobalanaceae	<i>Indet</i>	<i>sp. 1</i>	dicot tree	0	0	1	0	0	1
Combretaceae	<i>Combretum</i>	<i>nigricans</i>	dicot liana	20	2	54	7	2	23
Combretaceae	<i>Combretum</i>	<i>sp. 5</i>	dicot liana	0	1	2	0	1	2
Combretaceae	<i>Combretum</i>	<i>sp. 6</i>	dicot liana	4	0	0	3	0	0
Combretaceae	<i>Combretum</i>	<i>sp. 7</i>	dicot liana	4	1	12	1	1	3
Combretaceae	<i>Combretum</i>	<i>sp. 8</i>	dicot liana	3	0	0	1	0	0
Combretaceae	<i>Terminalia</i>	<i>sp. 1</i>	dicot tree	0	0	1	0	0	1
Commelinaceae	<i>Amischotolype</i>	<i>mollissima</i>	monocot liana	0	0	3	0	0	2
Compositae	<i>Blumea</i>	<i>balsamifera</i>	dicot tree	0	49	10	0	18	10
Compositae	<i>Chromolaena</i>	<i>odorata</i>	dicot shrub	0	21	101	0	14	26
Compositae	<i>Mikania</i>	<i>scandens</i>	dicot vine	0	332	1018	0	52	64
Compositae	<i>Vernonia</i>	<i>arborea</i>	dicot tree	7	278	371	2	65	68
Compositae	<i>cf. Gynura</i>	<i>sp. 1</i>	dicot liana	0	1	2	0	1	2
Connaraceae	<i>Agelaea</i>	<i>borneensis</i>	dicot liana	39	5	12	21	5	4
Connaraceae	<i>Agelaea</i>	<i>trinervis</i>	dicot liana	31	4	31	20	4	8
Connaraceae	<i>Agelaea</i>	<i>sp. 1</i>	dicot liana	1	3	3	1	3	3
Connaraceae	<i>Cnestis</i>	<i>sp. 1</i>	dicot liana	11	15	18	8	15	15
Connaraceae	<i>Connarus</i>	<i>sucus</i>	dicot liana	2	1	3	1	1	3
Connaraceae	<i>Ellipanthus</i>	<i>beccarii</i> var. <i>peltatus</i>	dicot tree	43	5	2	26	4	2
Connaraceae	<i>Rourea</i>	<i>acupetala</i>	dicot liana	27	9	20	16	8	17
Connaraceae	<i>Rourea</i>	<i>sp. 1</i>	dicot liana	1	5	0	1	5	0
Connaraceae	<i>Rourea</i>	<i>sp. 3</i>	dicot liana	1	1	4	1	1	2
Connaraceae	<i>Rourea</i>	<i>sp. 4</i>	dicot liana	0	0	1	0	0	1
Connaraceae	<i>Rourea</i>	<i>sp. 5</i>	dicot liana	0	0	3	0	0	3
Connaraceae	<i>Rourea</i>	<i>sp. 11</i>	dicot liana	9	2	0	5	2	0
Connaraceae	<i>Rourea</i>	<i>sp. 12</i>	dicot liana	5	0	0	1	0	0
Connaraceae	<i>cf. Cnestis</i>	<i>sp. 2</i>	dicot liana	1	0	0	1	0	0
Connaraceae	<i>Indet</i>	<i>sp. 2</i>	dicot liana	0	0	1	0	0	1
Convolvulaceae	<i>Erycibe</i>	<i>borneensis</i>	dicot tree	3	0	0	3	0	0
Convolvulaceae	<i>Erycibe</i>	<i>grandiflora</i>	dicot liana	1	0	2	1	0	2
Convolvulaceae	<i>Erycibe</i>	<i>sp. 1</i>	dicot liana	25	4	1	18	4	1
Convolvulaceae	<i>Erycibe</i>	<i>sp. 2</i>	dicot liana	9	0	0	9	0	0
Convolvulaceae	<i>Erycibe</i>	<i>sp. 3</i>	dicot tree	4	0	0	3	0	0
Convolvulaceae	<i>Erycibe</i>	<i>sp. 4</i>	dicot tree	3	0	2	3	0	2
Convolvulaceae	<i>Erycibe</i>	<i>sp. 6</i>	dicot tree	1	5	9	1	4	7
Convolvulaceae	<i>Erycibe</i>	<i>sp. 10</i>	dicot liana	0	0	1	0	0	1
Convolvulaceae	<i>Erycibe</i>	<i>sp. 13</i>	dicot liana	18	0	3	8	0	1
Convolvulaceae	<i>cf. Erycibe</i>	<i>sp. 11</i>	dicot liana	0	1	0	0	1	0

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Convolvulaceae	<i>cf. Erycibe</i>	<i>sp. 12</i>	dicot liana	2	2	1	1	1	1
Cornaceae	<i>Mastixia</i>	<i>rostrata</i>	dicot tree	0	0	1	0	0	1
Crypteroniaceae	<i>Crypteronia</i>	<i>borneensis</i>	dicot tree	14	3	0	13	3	0
Crypteroniaceae	<i>Crypteronia</i>	<i>griffithii</i>	dicot tree	0	0	1	0	0	1
Crypteroniaceae	<i>Crypteronia</i>	<i>macrophylla</i>	dicot tree	13	0	1	8	0	1
Crypteroniaceae	<i>Dactylocladus</i>	<i>stenostachys</i>	dicot tree	1	0	0	1	0	0
Cucurbitaceae	<i>Trichosanthes</i>	<i>borneensis</i>	dicot liana	0	3	11	0	3	10
Cyatheaceae	<i>Cyathea</i>	<i>recommunata</i>	fern tree	0	1	0	0	1	0
Cyperaceae	<i>Scleria</i>	<i>terrestris</i>	monocot grass	305	334	659	3	6	31
Cyperaceae	<i>Scleria</i>	<i>sp. 1</i>	monocot grass	0	0	842	0	0	36
Datisaceae	<i>Otomeles</i>	<i>sumatrana</i>	dicot tree	0	0	1	0	0	1
Dichapetalaceae	<i>Dichapetalum</i>	<i>timoriense</i>	dicot tree	1	0	5	1	0	3
Dilleniaceae	<i>Dillenia</i>	<i>borneensis</i>	dicot tree	8	168	14	6	54	8
Dilleniaceae	<i>Dillenia</i>	<i>excelsa</i>	dicot tree	22	0	21	14	0	14
Dilleniaceae	<i>Dillenia</i>	<i>reticulata</i>	dicot tree	2	0	0	1	0	0
Dilleniaceae	<i>Tetracera</i>	<i>scandens</i>	dicot liana	23	5	7	14	5	7
Dilleniaceae	<i>Tetracera</i>	<i>sp. 10</i>	dicot liana	20	20	30	13	18	21
Dilleniaceae	<i>Tetracera</i>	<i>sp. 11</i>	dicot liana	30	14	23	17	8	14
Dilleniaceae	<i>Tetracera</i>	<i>sp. 12</i>	dicot liana	41	5	6	24	4	5
Dipterocarpaceae	<i>Shorea</i>	<i>seminis</i>	dicot tree	0	0	3	0	0	3
Dipterocarpaceae	<i>Anisoptera</i>	<i>marginata</i>	dicot tree	1	0	1	1	0	1
Dipterocarpaceae	<i>Anisoptera</i>	<i>sp. 1</i>	dicot tree	0	0	1	0	0	1
Dipterocarpaceae	<i>Cotylelobium</i>	<i>melanoxylum</i>	dicot tree	79	19	6	25	10	6
Dipterocarpaceae	<i>Dipterocarpus</i>	<i>confertus</i>	dicot tree	347	27	30	70	23	22
Dipterocarpaceae	<i>Dipterocarpus</i>	<i>cornutus</i>	dicot tree	19	0	17	10	0	14
Dipterocarpaceae	<i>Dipterocarpus</i>	<i>gracilis</i>	dicot tree	1	0	0	1	0	0
Dipterocarpaceae	<i>Dipterocarpus</i>	<i>tempehes</i>	dicot tree	0	0	15	0	0	3
Dipterocarpaceae	<i>Dipterocarpus</i>	<i>cf. humeratus</i>	dicot tree	0	0	2	0	0	2
Dipterocarpaceae	<i>Hopea</i>	<i>dryobalanoides</i>	dicot tree	3	0	0	1	0	0
Dipterocarpaceae	<i>Hopea</i>	<i>mengerawan</i>	dicot tree	34	0	0	13	0	0
Dipterocarpaceae	<i>Hopea</i>	<i>rudiformis</i>	dicot tree	11	0	4	1	0	1
Dipterocarpaceae	<i>Shorea</i>	<i>gibbosa</i>	dicot tree	0	0	1	0	0	1
Dipterocarpaceae	<i>Shorea</i>	<i>johorensis</i>	dicot tree	5	1	4	3	1	4
Dipterocarpaceae	<i>Shorea</i>	<i>laevis</i>	dicot tree	429	17	13	63	15	11
Dipterocarpaceae	<i>Shorea</i>	<i>lamellata</i>	dicot tree	15	2	0	9	2	0
Dipterocarpaceae	<i>Shorea</i>	<i>leprosula</i>	dicot tree	4	1	0	3	1	0
Dipterocarpaceae	<i>Shorea</i>	<i>ovalis</i>	dicot tree	121	7	13	39	5	8
Dipterocarpaceae	<i>Shorea</i>	<i>parvifolia</i>	dicot tree	51	5	4	20	4	3
Dipterocarpaceae	<i>Shorea</i>	<i>parvistipulata</i>	dicot tree	70	2	0	29	1	0
Dipterocarpaceae	<i>Shorea</i>	<i>pauciflora</i>	dicot tree	5	0	0	4	0	0
Dipterocarpaceae	<i>Shorea</i>	<i>smithiana</i>	dicot tree	119	6	10	40	6	5
Dipterocarpaceae	<i>Shorea</i>	<i>sp. 5</i>	dicot tree	0	0	1	0	0	1
Dipterocarpaceae	<i>Shorea</i>	<i>sp. 6</i>	dicot tree	0	0	1	0	0	1
Dipterocarpaceae	<i>Shorea</i>	<i>sp. 8</i>	dicot tree	2	0	0	2	0	0
Dipterocarpaceae	<i>Vatica</i>	<i>javanica</i>	dicot tree	2	0	0	2	0	0
Dipterocarpaceae	<i>Vatica</i>	<i>odorata</i> ssp.							
		<i>odorata</i>	dicot tree	18	0	19	8	0	5
Dipterocarpaceae	<i>Vatica</i>	<i>rassak</i>	dicot tree	5	0	2	3	0	2
Dipterocarpaceae	<i>Vatica</i>	<i>umbonata</i>	dicot tree	213	17	12	58	14	10
Dracaenaceae	<i>Dracaena</i>	<i>angustifolia</i>	monocot tree	3	0	1	3	0	1
Dracaenaceae	<i>Dracaena</i>	<i>sp. 3</i>	monocot tree	0	1	0	0	1	0
Ebenaceae	<i>Diospyros</i>	<i>borneensis</i>	dicot tree	31	7	14	18	6	8
Ebenaceae	<i>Diospyros</i>	<i>buxifolia</i>	dicot tree	35	3	0	23	3	0
Ebenaceae	<i>Diospyros</i>	<i>elliptifolia</i>	dicot tree	1	2	20	1	2	8
Ebenaceae	<i>Diospyros</i>	<i>macrophylla</i>	dicot tree	6	2	0	5	2	0
Ebenaceae	<i>Diospyros</i>	<i>oblonga</i>	dicot tree	1	0	0	1	0	0

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Ebenaceae	<i>Diospyros</i>	<i>pilosanthera</i>	dicot tree	4	2	0	3	2	0
Ebenaceae	<i>Diospyros</i>	<i>sumatrana</i>	dicot tree	59	2	9	34	2	4
Ebenaceae	<i>Diospyros</i>	<i>wallichii</i>	dicot tree	1	0	0	1	0	0
Ebenaceae	<i>Diospyros</i>	<i>sp. 3</i>	dicot tree	1	0	0	1	0	0
Ebenaceae	<i>Diospyros</i>	<i>sp. 10</i>	dicot tree	1	2	2	1	2	2
Ebenaceae	<i>Diospyros</i>	<i>sp. 11</i>	dicot tree	1	0	0	1	0	0
Ebenaceae	<i>Diospyros</i>	<i>sp. 12</i>	dicot tree	0	0	6	0	0	3
Ebenaceae	<i>Diospyros</i>	<i>sp. 21</i>	dicot tree	0	0	3	0	0	1
Ebenaceae	<i>Diospyros</i>	<i>sp. 23</i>	dicot tree	0	1	0	0	1	0
Ebenaceae	<i>cf. Diospyros</i>	<i>sp. 22</i>	dicot tree	0	0	1	0	0	1
Elaeocarpaceae	<i>Elaeocarpus</i>	<i>clementis</i>	dicot tree	1	0	0	1	0	0
Elaeocarpaceae	<i>Elaeocarpus</i>	<i>cupreus</i>	dicot tree	3	0	4	3	0	4
Elaeocarpaceae	<i>Elaeocarpus</i>	<i>macrocerus</i>	dicot tree	2	0	1	1	0	1
Elaeocarpaceae	<i>Elaeocarpus</i>	<i>stipularis</i>	dicot tree	6	2	2	4	2	2
Elaeocarpaceae	<i>Elaeocarpus</i>	<i>valetonii</i>	dicot tree	1	3	0	1	2	0
Elaeocarpaceae	<i>Sloanea</i>	<i>javanica</i>	dicot tree	0	0	1	0	0	1
Euphorbiaceae	<i>Antidesma</i>	<i>neurocarpum</i>	dicot tree	32	1	6	20	1	5
Euphorbiaceae	<i>Antidesma</i>	<i>sp. 5</i>	dicot tree	0	0	1	0	0	1
Euphorbiaceae	<i>Aporosa</i>	<i>frutescens</i>	dicot tree	38	4	12	29	3	10
Euphorbiaceae	<i>Aporosa</i>	<i>grandistipulata</i>	dicot tree	36	5	8	23	5	4
Euphorbiaceae	<i>Aporosa</i>	<i>lunata</i>	dicot tree	90	4	3	38	4	2
Euphorbiaceae	<i>Aporosa</i>	<i>nitida</i>	dicot tree	107	28	17	48	24	12
Euphorbiaceae	<i>Aporosa</i>	<i>octandra</i>	dicot tree	48	1	0	22	1	0
Euphorbiaceae	<i>Aporosa</i>	<i>subcaudata</i>	dicot tree	156	10	22	53	8	13
Euphorbiaceae	<i>Aporosa</i>	<i>sp. 5</i>	dicot tree	0	0	1	0	0	1
Euphorbiaceae	<i>Aporosa</i>	<i>sp. 15</i>	dicot tree	0	0	1	0	0	1
Euphorbiaceae	<i>Baccaurea</i>	<i>bracteata</i>	dicot tree	6	0	0	5	0	0
Euphorbiaceae	<i>Baccaurea</i>	<i>macrocarpa</i>	dicot tree	11	7	1	10	3	1
Euphorbiaceae	<i>Baccaurea</i>	<i>minor</i>	dicot tree	18	2	2	8	2	2
Euphorbiaceae	<i>Baccaurea</i>	<i>odorata</i>	dicot tree	25	0	0	11	0	0
Euphorbiaceae	<i>Baccaurea</i>	<i>pubera</i>	dicot tree	0	0	1	0	0	1
Euphorbiaceae	<i>Baccaurea</i>	<i>pyriformis</i>	dicot tree	5	1	0	4	1	0
Euphorbiaceae	<i>Baccaurea</i>	<i>cf. dulcis</i>	dicot tree	1	0	0	1	0	0
Euphorbiaceae	<i>Baccaurea</i>	<i>cf. javanica</i>	dicot tree	6	0	0	4	0	0
Euphorbiaceae	<i>Baccaurea</i>	<i>cf. parviflora</i>	dicot tree	0	0	1	0	0	1
Euphorbiaceae	<i>Baccaurea</i>	<i>cf. sarawakensis</i>	dicot tree	23	10	10	15	8	4
Euphorbiaceae	<i>Baccaurea</i>	<i>cf. tetrandra</i>	dicot tree	150	7	2	52	7	2
Euphorbiaceae	<i>Baccaurea</i>	<i>sp. 4</i>	dicot tree	0	0	1	0	0	1
Euphorbiaceae	<i>Blumeodendron</i>	<i>calophyllum</i>	dicot tree	11	1	0	4	1	0
Euphorbiaceae	<i>Bridelia</i>	<i>glauca</i>	dicot tree	1	0	0	1	0	0
Euphorbiaceae	<i>Chaetocarpus</i>	<i>castanicarpus</i>	dicot tree	41	2	2	22	2	2
Euphorbiaceae	<i>Cleistanthus</i>	<i>erycibifolius</i>	dicot tree	64	11	6	31	8	1
Euphorbiaceae	<i>Cleistanthus</i>	<i>myrianthus</i>	dicot tree	94	10	6	48	8	2
Euphorbiaceae	<i>Cleistanthus</i>	<i>paxii</i>	dicot tree	0	0	15	0	0	8
Euphorbiaceae	<i>Cleistanthus</i>	<i>vestitus</i>	dicot tree	8	0	0	4	0	0
Euphorbiaceae	<i>Cleistanthus</i>	<i>cf. sumatranus</i>	dicot tree	0	2	0	0	2	0
Euphorbiaceae	<i>Croton</i>	<i>griffitii</i>	dicot tree	0	0	8	0	0	2
Euphorbiaceae	<i>Dicoelia</i>	<i>sp. 1</i>	dicot tree	0	1	4	0	1	1
Euphorbiaceae	<i>Dimorphocalyx</i>	<i>muricatus</i>	dicot tree	0	0	30	0	0	10
Euphorbiaceae	<i>Drypetes</i>	<i>crassipes</i>	dicot tree	20	0	1	16	0	1
Euphorbiaceae	<i>Drypetes</i>	<i>kikir</i>	dicot tree	173	26	3	68	18	3
Euphorbiaceae	<i>Drypetes</i>	<i>polyneura</i>	dicot tree	0	0	1	0	0	1
Euphorbiaceae	<i>Elateriospermum</i>	<i>tapos</i>	dicot tree	1	0	0	1	0	0
Euphorbiaceae	<i>Endospermum</i>	<i>diadenum</i>	dicot tree	0	11	16	0	11	9
Euphorbiaceae	<i>Fahrenheitia</i>	<i>pendula</i>	dicot tree	43	0	12	19	0	7
Euphorbiaceae	<i>Glochidion</i>	<i>arborescens</i>	dicot tree	4	8	12	3	8	8

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Euphorbiaceae	<i>Glochidion</i>	<i>sericeum</i>	dicot tree	1	3	19	1	3	12
Euphorbiaceae	<i>Glochidion</i>	<i>cf. glomerulata</i>	dicot tree	0	3	2	0	2	2
Euphorbiaceae	<i>Glochidion</i>	<i>cf. obscurum</i>	dicot tree	0	5	17	0	4	13
Euphorbiaceae	<i>Homalanthus</i>	<i>populneus</i>	dicot tree	1	9	1953	1	8	77
Euphorbiaceae	<i>Macaranga</i>	<i>bancana</i>							
		(syn. <i>triloba</i>)	dicot tree	4	68	104	4	34	39
Euphorbiaceae	<i>Macaranga</i>	<i>conifera</i>	dicot tree	4	10	65	3	7	36
Euphorbiaceae	<i>Macaranga</i>	<i>depressa</i>	dicot tree	0	0	6	0	0	6
Euphorbiaceae	<i>Macaranga</i>	<i>gigantea</i>	dicot tree	2	420	605	2	73	64
Euphorbiaceae	<i>Macaranga</i>	<i>hulletii</i>	dicot tree	0	2	2	0	1	1
Euphorbiaceae	<i>Macaranga</i>	<i>hypoleuca</i>	dicot tree	9	17	229	5	13	61
Euphorbiaceae	<i>Macaranga</i>	<i>lowii</i>	dicot tree	703	61	74	74	29	18
Euphorbiaceae	<i>Macaranga</i>	<i>motleyana</i>	dicot tree	4	8	5	4	4	4
Euphorbiaceae	<i>Macaranga</i>	<i>pearsonii</i>	dicot tree	1	14	76	1	14	36
Euphorbiaceae	<i>Macaranga</i>	<i>pruinosa</i>	dicot tree	0	2	4	0	2	4
Euphorbiaceae	<i>Macaranga</i>	<i>tanarius</i>	dicot tree	0	0	27	0	0	15
Euphorbiaceae	<i>Macaranga</i>	<i>trichocarpa</i>	dicot tree	5	674	3100	3	30	36
Euphorbiaceae	<i>Mallotus</i>	<i>mollisimus</i>	dicot tree	0	0	20	0	0	8
Euphorbiaceae	<i>Mallotus</i>	<i>paniculatus</i>	dicot tree	2	7	408	2	4	39
Euphorbiaceae	<i>Mallotus</i>	<i>penangensis</i>	dicot tree	1	1	10	1	1	4
Euphorbiaceae	<i>Neoscortechinia</i>	<i>kingii</i>	dicot tree	86	12	2	43	9	2
Euphorbiaceae	<i>Omphalea</i>	<i>bracteata</i>	dicot liana	88	11	16	39	8	12
Euphorbiaceae	<i>Pimelodendron</i>	<i>griffithianum</i>	dicot tree	32	2	0	24	2	0
Euphorbiaceae	<i>Ptychopyxis</i>	<i>glochidifolia</i>	dicot tree	1	0	2	1	0	1
Euphorbiaceae	<i>Ptychopyxis</i>	<i>javanica</i>	dicot tree	12	2	0	9	2	0
Euphorbiaceae	<i>Trigonopleura</i>	<i>malayana</i>	dicot tree	4	0	1	3	0	1
Euphorbiaceae	<i>Trigonostemon</i>	<i>laevigatus</i>	dicot tree	2	0	0	2	0	0
Euphorbiaceae	<i>cf. Blumeodendron</i>	<i>sp. 2</i>	dicot tree	1	0	0	1	0	0
Euphorbiaceae	<i>cf. Blumeodendron</i>	<i>sp. 3</i>	dicot tree	0	0	1	0	0	1
Euphorbiaceae	<i>cf. Blumeodendron</i>	<i>sp. 4</i>	dicot tree	0	0	2	0	0	1
Euphorbiaceae	<i>cf. Blumeodendron</i>	<i>sp. 5</i>	dicot tree	22	0	0	14	0	0
Euphorbiaceae	<i>Indet</i>	<i>sp. 12</i>	dicot tree	1	0	0	1	0	0
Euphorbiaceae	<i>Indet</i>	<i>sp. 13</i>	dicot tree	0	1	0	0	1	0
Fagaceae	<i>Castanopsis</i>	<i>fulva</i>	dicot tree	15	5	0	13	5	0
Fagaceae	<i>Castanopsis</i>	<i>oviformis</i>	dicot tree	1	4	0	1	3	0
Fagaceae	<i>Castanopsis</i>	<i>sp. 1</i>	dicot tree	1	0	0	1	0	0
Fagaceae	<i>Castanopsis</i>	<i>sp. 2</i>	dicot tree	7	0	0	6	0	0
Fagaceae	<i>Lithocarpus</i>	<i>conocarpus</i>	dicot tree	3	1	2	2	1	2
Fagaceae	<i>Lithocarpus</i>	<i>coopertus</i>	dicot tree	42	6	7	30	6	5
Fagaceae	<i>Lithocarpus</i>	<i>gracilis</i>	dicot tree	33	0	1	21	0	1
Fagaceae	<i>Lithocarpus</i>	<i>hystrix</i>	dicot tree	19	1	3	14	1	2
Fagaceae	<i>Lithocarpus</i>	<i>leptogyne</i>	dicot tree	12	3	1	10	2	1
Fagaceae	<i>Lithocarpus</i>	<i>nieuwenhuisii</i>	dicot tree	1	3	4	1	3	4
Fagaceae	<i>Quercus</i>	<i>argentata</i>	dicot tree	3	0	0	2	0	0
Fagaceae	<i>Quercus</i>	<i>gaharuensis</i>	dicot tree	2	1	0	2	1	0
Fagaceae	<i>Quercus</i>	<i>sp. 1</i>	dicot tree	1	0	0	1	0	0
Fagaceae	<i>Quercus</i>	<i>sp. 2</i>	dicot tree	1	0	0	1	0	0
Flacourtiaceae	<i>Flacourtia</i>	<i>rukam</i>	dicot tree	5	0	0	5	0	0
Flacourtiaceae	<i>Flacourtia</i>	<i>sp. 1</i>	dicot tree	0	0	1	0	0	1
Flacourtiaceae	<i>Hydnocarpus</i>	<i>polypetala</i>	dicot tree	17	0	5	9	0	4
Flacourtiaceae	<i>Hydnocarpus</i>	<i>sp. 1</i>	dicot tree	1	0	0	1	0	0
Flagellariaceae	<i>Flagellaria</i>	<i>indica</i>	monocot liana	2	8	13	1	7	11
Gentianaceae	<i>Fagraea</i>	<i>racemosa</i>	dicot tree	18	4	4	15	4	3
Gentianaceae	<i>Fagraea</i>	<i>sp. 1</i>	dicot liana	1	0	0	1	0	0
Gleicheniaceae	<i>Gleichenia</i>	<i>sp. 1</i>	fern liana	0	24	0	0	3	0
Gnetaceae	<i>Gnetum</i>	<i>gnemon</i>	gymno tree	1	0	1	1	0	1

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Gnetaceae	<i>Gnetum</i>	<i>sp. 2</i>	gymno liana	0	0	2	0	0	1
Gnetaceae	<i>Gnetum</i>	<i>sp. 3</i>	gymno liana	0	2	2	0	1	2
Gnetaceae	<i>Gnetum</i>	<i>sp. 4</i>	gymno liana	0	0	5	0	0	1
Gnetaceae	<i>Gnetum</i>	<i>sp. 5</i>	gymno liana	0	1	3	0	1	2
Gnetaceae	<i>Gnetum</i>	<i>sp. 6</i>	gymno liana	0	0	1	0	0	1
Gnetaceae	<i>Gnetum</i>	<i>sp. 7</i>	gymno liana	0	0	1	0	0	1
Graminae	<i>Gigantochloa</i>	<i>sp. 1</i>	bambu tree	1	6	65	1	1	3
Gramineae	<i>Dinochloa</i>	<i>scandens</i>	bambu liana	0	0	1408	0	0	47
Gramineae	<i>Saccharum</i>	<i>spontaneum</i>	monocot grass	3	88	81	1	10	9
Guttiferae	<i>Calophyllum</i>	<i>gracilipes</i>	dicot tree	0	1	0	0	1	0
Guttiferae	<i>Calophyllum</i>	<i>nodosum</i>	dicot tree	23	0	0	16	0	0
Guttiferae	<i>Calophyllum</i>	<i>woodii</i>	dicot tree	6	0	0	6	0	0
Guttiferae	<i>Calophyllum</i>	<i>sp. 2</i>	dicot tree	2	0	0	2	0	0
Guttiferae	<i>Cratoxylum</i>	<i>arborescens</i>	dicot tree	0	4	4	0	4	3
Guttiferae	<i>Cratoxylum</i>	<i>formosum</i>	dicot tree	3	12	65	2	11	26
Guttiferae	<i>Cratoxylum</i>	<i>glaucum</i>	dicot tree	1	2	4	1	2	3
Guttiferae	<i>Cratoxylum</i>	<i>sumatranum</i>	dicot tree	5	9	6	4	6	4
Guttiferae	<i>Garcinia</i>	<i>beccarii</i>	dicot tree	2	1	0	2	1	0
Guttiferae	<i>Garcinia</i>	<i>griffithii</i>	dicot tree	2	0	3	1	0	3
Guttiferae	<i>Garcinia</i>	<i>lateriflora</i>	dicot tree	1	0	0	1	0	0
Guttiferae	<i>Garcinia</i>	<i>nigrolineata</i>	dicot tree	18	1	2	12	1	2
Guttiferae	<i>Garcinia</i>	<i>nitida</i>	dicot tree	15	0	2	10	0	2
Guttiferae	<i>Garcinia</i>	<i>parvifolia</i>	dicot tree	14	0	0	12	0	0
Guttiferae	<i>Garcinia</i>	<i>cf. nervosa</i>	dicot tree	3	1	0	3	1	0
Guttiferae	<i>Garcinia</i>	<i>sp. 12</i>	dicot tree	0	0	2	0	0	1
Guttiferae	<i>Garcinia</i>	<i>sp. 15</i>	dicot tree	0	1	0	0	1	0
Guttiferae	<i>Mammea</i>	<i>acuminata</i>	dicot tree	9	2	2	7	2	1
Guttiferae	<i>Mesua</i>	<i>borneensis</i>	dicot tree	0	0	3	0	0	2
Guttiferae	<i>cf. Mesua</i>	<i>sp. 1</i>	dicot tree	1	0	0	1	0	0
Icacinaceae	<i>Gonocaryum</i>	<i>calleryanum</i>	dicot tree	6	0	2	4	0	2
Icacinaceae	<i>Phytocrene</i>	<i>borneensis</i>	dicot liana	5	2	4	5	2	4
Icacinaceae	<i>Phytocrene</i>	<i>sp. 1</i>	dicot liana	39	4	2	21	4	2
Icacinaceae	<i>Platea</i>	<i>excelsa</i>	dicot tree	0	0	2	0	0	2
Icacinaceae	<i>Stemonurus</i>	<i>scorpioides</i>	dicot tree	2	30	0	2	9	0
Illiciaceae	<i>Illicium</i>	<i>sp. 1</i>	dicot liana	0	6	0	0	4	0
Irvingiaceae	<i>Irvingia</i>	<i>malayana</i>	dicot tree	2	1	1	2	1	1
Juglandaceae	<i>Engelhardtia</i>	<i>serrata</i>	dicot tree	1	0	0	1	0	0
Labiatae	<i>Callicarpa</i>	<i>glabrifolia</i>	dicot tree	0	0	8	0	0	7
Labiatae	<i>Callicarpa</i>	<i>cf. pentandra</i>	dicot tree	0	14	161	0	10	49
Labiatae	<i>Callicarpa</i>	<i>sp. 5</i>	dicot tree	0	0	41	0	0	18
Labiatae	<i>Callicarpa</i>	<i>sp. 6</i>	dicot tree	0	0	4	0	0	3
Labiatae	<i>Clerodendrum</i>	<i>disparifolium</i>	dicot tree	2	0	12	2	0	10
Labiatae	<i>Clerodendrum</i>	<i>sp. 1</i>	dicot tree	0	1	2	0	1	2
Labiatae	<i>Teijsmannio-</i> <i>dendron</i>	<i>bogoriense</i>	dicot tree	0	2	0	0	2	0
Labiatae	<i>Teijsmannio-</i> <i>dendron</i>	<i>coriaceum</i>	dicot tree	20	0	0	11	0	0
Labiatae	<i>Vitex</i>	<i>vestita</i>	dicot tree	1	0	0	1	0	0
Labiatae	<i>Indet</i>	<i>sp. 1</i>	dicot liana	1	0	0	1	0	0
Labiatae	<i>Indet</i>	<i>sp. 2</i>	dicot liana	5	1	0	4	1	0
Labiatae	<i>Indet</i>	<i>sp. 3</i>	dicot liana	0	0	5	0	0	3
Lauraceae	<i>Actinodaphne</i>	<i>glabra</i>	dicot tree	0	1	3	0	1	2
Lauraceae	<i>Actinodaphne</i>	<i>cf. procera</i>	dicot tree	2	2	0	2	1	0
Lauraceae	<i>Actinodaphne</i>	<i>sp. 4</i>	dicot tree	3	1	0	3	1	0
Lauraceae	<i>Actinodaphne</i>	<i>sp. 5</i>	dicot tree	2	0	4	2	0	2
Lauraceae	<i>Actinodaphne</i>	<i>sp. 6</i>	dicot tree	1	2	2	1	2	2

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Lauraceae	<i>Alseodaphne</i>	<i>elmeri</i>	dicot tree	21	5	6	15	4	5
Lauraceae	<i>Alseodaphne</i>	<i>peduncularis</i>	dicot tree	29	0	1	22	0	1
Lauraceae	<i>Alseodaphne</i>	<i>sp. 20</i>	dicot tree	3	0	1	3	0	1
Lauraceae	<i>Beilschmiedia</i>	<i>dictyoneura</i>	dicot tree	13	3	0	7	2	0
Lauraceae	<i>Beilschmiedia</i>	<i>glabra</i>	dicot tree	1	1	3	1	1	3
Lauraceae	<i>Beilschmiedia</i>	<i>kunstleri</i>	dicot tree	4	0	3	3	0	2
Lauraceae	<i>Beilschmiedia</i>	<i>sp. 1</i>	dicot tree	12	1	3	11	1	3
Lauraceae	<i>Beilschmiedia</i>	<i>sp. 2</i>	dicot tree	9	3	4	8	3	3
Lauraceae	<i>Beilschmiedia</i>	<i>sp. 10</i>	dicot tree	0	0	4	0	0	4
Lauraceae	<i>Beilschmiedia</i>	<i>sp. 11</i>	dicot tree	4	0	2	2	0	1
Lauraceae	<i>Beilschmiedia</i>	<i>sp. 12</i>	dicot tree	1	0	0	1	0	0
Lauraceae	<i>Cinnamomum</i>	<i>cuspidatum</i>	dicot tree	4	0	1	3	0	1
Lauraceae	<i>Cinnamomum</i>	<i>javanicum</i>	dicot tree	1	0	0	1	0	0
Lauraceae	<i>Cinnamomum</i>	<i>subavenicum</i>	dicot tree	2	0	0	2	0	0
Lauraceae	<i>Cryptocarya</i>	<i>crassinervia</i>	dicot tree	29	4	3	20	4	3
Lauraceae	<i>Cryptocarya</i>	<i>sp. 20</i>	dicot tree	2	1	0	2	1	0
Lauraceae	<i>Dehaasia</i>	<i>caesia</i>	dicot tree	11	0	0	10	0	0
Lauraceae	<i>Dehaasia</i>	<i>peduncularis</i>	dicot tree	10	5	1	8	5	1
Lauraceae	<i>Dehaasia</i>	<i>sp. 2</i>	dicot tree	0	0	3	0	0	3
Lauraceae	<i>Endiandra</i>	<i>kingiana</i>	dicot tree	38	5	2	20	5	2
Lauraceae	<i>Endiandra</i>	<i>rubescens</i>	dicot tree	17	6	0	12	6	0
Lauraceae	<i>Endiandra</i>	<i>sp. 1</i>	dicot tree	1	0	1	1	0	1
Lauraceae	<i>Eusideroxylon</i>	<i>zwageri</i>	dicot tree	39	1	12	17	1	9
Lauraceae	<i>Litsea</i>	<i>caulocarpa</i>	dicot tree	2	0	0	1	0	0
Lauraceae	<i>Litsea</i>	<i>elliptica</i>	dicot tree	1	0	2	1	0	2
Lauraceae	<i>Litsea</i>	<i>ferruginea</i>	dicot tree	3	1	1	3	1	1
Lauraceae	<i>Litsea</i>	<i>firma</i>	dicot tree	14	29	22	12	19	12
Lauraceae	<i>Litsea</i>	<i>grandis</i>	dicot tree	1	3	0	1	2	0
Lauraceae	<i>Litsea</i>	<i>ochrea</i>	dicot tree	2	1	0	2	1	0
Lauraceae	<i>Litsea</i>	<i>resinosa</i>	dicot tree	0	0	4	0	0	4
Lauraceae	<i>Litsea</i>	<i>robusta</i>	dicot tree	21	0	2	14	0	1
Lauraceae	<i>Litsea</i>	<i>sp. 2</i>	dicot tree	4	2	0	3	2	0
Lauraceae	<i>Litsea</i>	<i>sp. 11</i>	dicot tree	9	18	1	7	4	1
Lauraceae	<i>Litsea</i>	<i>sp. 20</i>	dicot tree	3	3	0	2	3	0
Lauraceae	<i>Neolitsea</i>	<i>sp. 1</i>	dicot tree	1	0	0	1	0	0
Lauraceae	<i>Neolitsea</i>	<i>sp. 2</i>	dicot tree	3	0	3	3	0	2
Lauraceae	<i>Neolitsea</i>	<i>sp. 3</i>	dicot tree	6	1	0	4	1	0
Lauraceae	<i>Nothaphoebe</i>	<i>umbelliflora</i>	dicot tree	11	0	5	11	0	5
Lauraceae	<i>Phoebe</i>	<i>apaca</i>	dicot tree	15	12	18	11	11	12
Lauraceae	<i>Indet</i>	<i>sp. 22</i>	dicot tree	1	2	0	1	2	0
Lecythidaceae	<i>Barringtonia</i>	<i>lanceolata</i>	dicot tree	26	2	10	17	2	8
Lecythidaceae	<i>Barringtonia</i>	<i>macrostachya</i>	dicot tree	113	42	17	49	19	11
Lecythidaceae	<i>Barringtonia</i>	<i>pendula</i>	dicot tree	2	0	0	2	0	0
Lecythidaceae	<i>Planchonia</i>	<i>valida</i>	dicot tree	0	2	1	0	2	1
Leguminosae	<i>Acacia</i>	<i>mangium</i>	dicot tree	0	0	6	0	0	2
Leguminosae	<i>Archidendron</i>	<i>clypearia</i>	dicot tree	3	1	2	3	1	1
Leguminosae	<i>Archidendron</i>	<i>ellipticum</i>	dicot tree	0	0	25	0	0	7
Leguminosae	<i>Archidendron</i>	<i>microcarpum</i>	dicot tree	41	6	17	23	6	11
Leguminosae	<i>Archidendron</i>	<i>cf. havilandii</i>	dicot tree	0	1	0	0	1	0
Leguminosae	<i>Archidendron</i>	<i>cf. triplinervium</i>	dicot tree	1	1	0	1	1	0
Leguminosae	<i>Archidendron</i>	<i>sp. 2</i>	dicot tree	1	0	0	1	0	0
Leguminosae	<i>Archidendron</i>	<i>sp. 3</i>	dicot tree	9	0	0	9	0	0
Leguminosae	<i>Bauhinia</i>	<i>sp. 1</i>	dicot liana	10	23	16	8	15	15
Leguminosae	<i>Callerya</i>	<i>sp. 1</i>	dicot liana	0	1	0	0	1	0
Leguminosae	<i>Crudia</i>	<i>reticulata</i>	dicot tree	84	39	45	26	19	19
Leguminosae	<i>Dialium</i>	<i>indum</i>	dicot tree	24	1	2	18	1	2

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Leguminosae	<i>Dialium</i>	<i>kunstleri</i>	dicot tree	15	3	0	15	2	0
Leguminosae	<i>Dialium</i>	<i>platysepalum</i>	dicot tree	0	1	0	0	1	0
Leguminosae	<i>Entada</i>	<i>sp. 1</i>	dicot liana	4	3	6	2	2	1
Leguminosae	<i>Fordia</i>	<i>splendidissima</i>	dicot tree	410	76	245	75	43	61
Leguminosae	<i>Koompassia</i>	<i>malaccensis</i>	dicot tree	52	5	12	33	4	10
Leguminosae	<i>Leucomphalos</i>	<i>callicarpus</i>	dicot liana	3	0	1	2	0	1
Leguminosae	<i>Mucuna</i>	<i>sp. 1</i>	dicot liana	6	12	11	4	7	4
Leguminosae	<i>Parkia</i>	<i>speciosa</i>	dicot tree	1	0	1	1	0	1
Leguminosae	<i>Sindora</i>	<i>leiocarpa</i>	dicot tree	7	0	1	6	0	1
Leguminosae	<i>Sindora</i>	<i>velutina</i>	dicot tree	16	0	0	13	0	0
Leguminosae	<i>Spatholobus</i>	<i>ferrugineus</i>	dicot liana	14	16	17	10	15	13
Leguminosae	<i>Spatholobus</i>	<i>sp. 1</i>	dicot liana	213	18	24	56	15	11
Leguminosae	<i>Spatholobus</i>	<i>sp. 2</i>	dicot liana	16	12	19	12	11	12
Leguminosae	<i>Spatholobus</i>	<i>sp. 3</i>	dicot liana	28	16	7	15	14	3
Leguminosae	<i>Spatholobus</i>	<i>sp. 4</i>	dicot liana	39	25	25	14	16	18
Leguminosae	<i>Spatholobus</i>	<i>sp. 5</i>	dicot liana	13	0	17	7	0	8
Leguminosae	<i>Spatholobus</i>	<i>sp. 10</i>	dicot liana	2	1	1	2	1	1
Leguminosae	<i>Spatholobus</i>	<i>sp. 11</i>	dicot liana	0	0	1	0	0	1
Leguminosae	<i>Indet</i>	<i>sp. 3</i>	dicot liana	2	0	4	1	0	3
Leguminosae	<i>Indet</i>	<i>sp. 5</i>	dicot tree	2	2	0	1	2	0
Leguminosae	<i>Indet</i>	<i>sp. 6</i>	dicot tree	1	0	0	1	0	0
Leguminosae	<i>Indet</i>	<i>sp. 7</i>	dicot tree	0	1	0	0	1	0
Lomariopsidaceae	<i>Teratophyllum</i>	<i>clemensiae</i>	dicot liana	0	0	1	0	0	1
Lomariopsidaceae	<i>Teratophyllum</i>	<i>ludens</i>	fern liana	0	0	3	0	0	2
Magnoliaceae	<i>Magnolia</i>	<i>lasia</i>	dicot tree	6	2	0	6	2	0
Magnoliaceae	<i>Magnolia</i>	<i>liliifera</i>	dicot tree	2	0	0	2	0	0
Magnoliaceae	<i>Magnolia</i>	<i>tsiampacca</i>	dicot tree	0	0	4	0	0	3
Malvaceae	<i>Grewia</i>	<i>fibrocarpa</i>	dicot tree	14	1	2	13	1	2
Malvaceae	<i>Grewia</i>	<i>sp. 1</i>	dicot liana	0	0	1	0	0	1
Malvaceae	<i>Microcos</i>	<i>cinnamomifolia</i>	dicot tree	60	0	2	36	0	2
Malvaceae	<i>Microcos</i>	<i>crassifolia</i>	dicot tree	31	1	0	20	1	0
Malvaceae	<i>Microcos</i>	<i>tomentosa</i>	dicot tree	22	10	5	16	6	5
Malvaceae	<i>Pentace</i>	<i>erectinervia</i>	dicot tree	10	4	1	7	3	1
Malvaceae	<i>Pentace</i>	<i>laxiflora</i>	dicot tree	34	5	42	11	3	20
Melastomataceae	<i>Clidemia</i>	<i>hirta</i>	dicot herb	0	0	162	0	0	36
Melastomataceae	<i>Diplectria</i>	<i>sp. 1</i>	dicot liana	4	0	0	3	0	0
Melastomataceae	<i>Diplectria</i>	<i>sp. 2</i>	dicot liana	1	1	0	1	1	0
Melastomataceae	<i>Diplectria</i>	<i>sp. 3</i>	dicot liana	0	0	1	0	0	1
Melastomataceae	<i>Diplectria</i>	<i>sp. 4</i>	dicot liana	0	3	0	0	3	0
Melastomataceae	<i>Diplectria</i>	<i>sp. 5</i>	dicot liana	0	0	1	0	0	1
Melastomataceae	<i>Dissochaeta</i>	<i>gracilis</i>	dicot liana	1	65	15	1	28	10
Melastomataceae	<i>Macrolenes</i>	<i>sp. 1</i>	dicot liana	0	3	0	0	3	0
Melastomataceae	<i>Macrolenes</i>	<i>sp. 2</i>	dicot liana	0	7	1	0	3	1
Melastomataceae	<i>Maclostoma</i>	<i>malabathricum</i>	dicot tree	0	97	185	0	37	49
Melastomataceae	<i>Memecylon</i>	<i>borneense</i>	dicot tree	5	0	0	3	0	0
Melastomataceae	<i>Memecylon</i>	<i>edule</i>	dicot tree	36	8	0	20	8	0
Melastomataceae	<i>Memecylon</i>	<i>oleifolium</i>	dicot tree	10	1	0	7	1	0
Melastomataceae	<i>Memecylon</i>	<i>paniculatum</i>	dicot tree	1	0	0	1	0	0
Melastomataceae	<i>Memecylon</i>	<i>sp. 1</i>	dicot tree	7	0	0	6	0	0
Melastomataceae	<i>Memecylon</i>	<i>sp. 2</i>	dicot tree	1	0	0	1	0	0
Melastomataceae	<i>Memecylon</i>	<i>sp. 4</i>	dicot tree	4	1	0	4	1	0
Melastomataceae	<i>Memecylon</i>	<i>sp. 5</i>	dicot tree	4	1	0	3	1	0
Melastomataceae	<i>Memecylon</i>	<i>sp. 6</i>	dicot tree	1	0	0	1	0	0
Melastomataceae	<i>Memecylon</i>	<i>sp. 7</i>	dicot tree	0	0	1	0	0	1
Melastomataceae	<i>Memecylon</i>	<i>sp. 8</i>	dicot tree	0	0	1	0	0	1
Melastomataceae	<i>Pternandra</i>	<i>azurea</i>	dicot tree	57	8	29	25	2	1

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Melastomataceae	<i>Pternandra</i>	<i>coerulescens</i>	dicot tree	31	105	69	17	33	29
Melastomataceae	<i>Pternandra</i>	<i>galeata</i>	dicot tree	2	0	0	1	0	0
Melastomataceae	<i>Pternandra</i>	<i>rostrata</i>	dicot tree	63	4	5	27	1	4
Melastomataceae	<i>Indet</i>	<i>sp. 1</i>	dicot shrub	1	0	0	1	0	0
Meliaceae	<i>Aglaia</i>	<i>crassinervia</i>	dicot tree	9	0	6	8	0	3
Meliaceae	<i>Aglaia</i>	<i>forbesii</i>	dicot tree	106	0	3	39	0	3
Meliaceae	<i>Aglaia</i>	<i>odorata</i>	dicot tree	2	0	0	2	0	0
Meliaceae	<i>Aglaia</i>	<i>silvestris</i>	dicot tree	17	0	0	7	0	0
Meliaceae	<i>Aglaia</i>	<i>simplicifolia</i>	dicot tree	79	3	1	36	3	1
Meliaceae	<i>Aglaia</i>	<i>tomentosa</i>	dicot tree	88	5	6	39	3	2
Meliaceae	<i>Aglaia</i>	<i>cf. leucophylla</i>	dicot tree	13	1	1	5	1	1
Meliaceae	<i>Aglaia</i>	<i>sp. 1</i>	dicot tree	8	0	0	6	0	0
Meliaceae	<i>Aglaia</i>	<i>sp. 2</i>	dicot tree	7	0	1	6	0	1
Meliaceae	<i>Aglaia</i>	<i>sp. 12</i>	dicot tree	2	2	0	2	1	0
Meliaceae	<i>Aglaia</i>	<i>sp. 13</i>	dicot tree	5	0	1	5	0	1
Meliaceae	<i>Aglaia</i>	<i>sp. 15</i>	dicot tree	1	0	0	1	0	0
Meliaceae	<i>Aphanamixis</i>	<i>borneensis</i>	dicot tree	0	0	1	0	0	1
Meliaceae	<i>Aphanamixis</i>	<i>polystachya</i>	dicot tree	29	0	0	16	0	0
Meliaceae	<i>Chisocheton</i>	<i>ceramicus</i>	dicot tree	6	1	0	5	1	0
Meliaceae	<i>Chisocheton</i>	<i>lansiiifolius</i>	dicot tree	5	0	11	5	0	9
Meliaceae	<i>Chisocheton</i>	<i>patens</i>	dicot tree	3	1	1	2	1	1
Meliaceae	<i>Chisocheton</i>	<i>sp. 6</i>	dicot tree	3	0	0	2	0	0
Meliaceae	<i>Dysoxylum</i>	<i>alliaceum</i>	dicot tree	24	3	0	15	3	0
Meliaceae	<i>Dysoxylum</i>	<i>brachybotrys</i>	dicot tree	4	0	0	3	0	0
Meliaceae	<i>Dysoxylum</i>	<i>cauliflorum</i>	dicot tree	1	0	0	1	0	0
Meliaceae	<i>Dysoxylum</i>	<i>cyrtobotryum</i>	dicot tree	1	0	0	1	0	0
Meliaceae	<i>Dysoxylum</i>	<i>pachyrhache</i>	dicot tree	3	0	0	2	0	0
Meliaceae	<i>Dysoxylum</i>	<i>rigidum</i>	dicot tree	5	0	0	4	0	0
Meliaceae	<i>Dysoxylum</i>	<i>cf. excelsum</i>	dicot tree	2	8	1	1	2	1
Meliaceae	<i>Lansium</i>	<i>domesticum</i>	dicot tree	1	0	1	1	0	1
Meliaceae	<i>Pseudoclausena</i>	<i>chrysogyne</i>	dicot tree	9	0	7	6	0	5
Meliaceae	<i>Reinwardtia</i>	<i>dendron</i>	dicot tree	8	1	1	4	1	1
Meliaceae	<i>Sandoricum</i>	<i>koetjape</i>	dicot tree	4	4	1	4	4	1
Meliaceae	<i>Walsura</i>	<i>pinnata</i>	dicot tree	0	0	1	0	0	1
Meliaceae	<i>cf. Dysoxylum</i>	<i>sp. 12</i>	dicot tree	3	0	0	2	0	0
Menispermaceae	<i>Albertisia</i>	<i>papuana</i>	dicot liana	1	1	0	1	1	0
Menispermaceae	<i>Fibraurea</i>	<i>tinctoria</i>	dicot liana	0	1	3	0	1	2
Menispermaceae	<i>Stephania</i>	<i>sp. 1</i>	dicot liana	0	0	7	0	0	5
Menispermaceae	<i>Tinomiscium</i>	<i>petiolare</i>	dicot liana	3	1	1	1	1	1
Menispermaceae	<i>Indet</i>	<i>sp. 2</i>	dicot liana	1	7	5	1	4	4
Menispermaceae	<i>Indet</i>	<i>sp. 3</i>	dicot liana	5	0	0	4	0	0
Menispermaceae	<i>Indet</i>	<i>sp. 4</i>	dicot liana	2	5	4	2	5	2
Menispermaceae	<i>Indet</i>	<i>sp. 5</i>	dicot liana	2	0	1	2	0	1
Menispermaceae	<i>Indet</i>	<i>sp. 6</i>	dicot liana	1	1	0	1	1	0
Menispermaceae	<i>Indet</i>	<i>sp. 7</i>	dicot liana	0	0	1	0	0	1
Menispermaceae	<i>Indet</i>	<i>sp. 8</i>	dicot liana	0	0	1	0	0	1
Menispermaceae	<i>Indet</i>	<i>sp. 1</i>	dicot liana	7	5	1	7	5	1
Moraceae	<i>Artocarpus</i>	<i>anisophyllus</i>	dicot tree	107	6	8	51	5	8
Moraceae	<i>Artocarpus</i>	<i>dadah</i>	dicot tree	1	1	1	1	1	1
Moraceae	<i>Artocarpus</i>	<i>elasticus</i>	dicot tree	1	0	10	1	0	2
Moraceae	<i>Artocarpus</i>	<i>integer</i>	dicot tree	20	16	2	13	10	2
Moraceae	<i>Artocarpus</i>	<i>nitidus</i>	dicot tree	6	7	12	6	6	9
Moraceae	<i>Artocarpus</i>	<i>odoratissimus</i>	dicot tree	1	0	2	1	0	2
Moraceae	<i>Artocarpus</i>	<i>rigidus</i>	dicot tree	1	1	2	1	1	2
Moraceae	<i>Artocarpus</i>	<i>sp. 1</i>	dicot tree	4	0	9	4	0	8

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Moraceae	<i>Artocarpus</i>	<i>sp. 11</i>	dicot tree	0	0	1	0	0	1
Moraceae	<i>Artocarpus</i>	<i>sp. 12</i>	dicot tree	3	0	0	3	0	0
Moraceae	<i>Artocarpus</i>	<i>sp. 13</i>	dicot tree	0	0	1	0	0	1
Moraceae	<i>Ficus</i>	<i>aurata</i>	dicot tree	9	54	146	5	27	58
Moraceae	<i>Ficus</i>	<i>globosa</i>	dicot liana	3	3	2	3	3	2
Moraceae	<i>Ficus</i>	<i>grossularioides</i>	dicot tree	0	20	100	0	6	31
Moraceae	<i>Ficus</i>	<i>obscura</i>	dicot tree	1	17	368	1	12	64
Moraceae	<i>Ficus</i>	<i>uncinata</i>	dicot tree	0	2	20	0	2	11
Moraceae	<i>Ficus</i>	<i>xylophylla</i>	dicot liana	1	0	1	1	0	1
Moraceae	<i>Ficus</i>	<i>sp. 1</i>	dicot tree	0	1	10	0	1	8
Moraceae	<i>Ficus</i>	<i>sp. 2</i>	dicot tree	0	1	14	0	1	11
Moraceae	<i>Ficus</i>	<i>sp. 3</i>	dicot tree	3	13	51	2	10	26
Moraceae	<i>Ficus</i>	<i>sp. 5</i>	dicot liana	48	4	9	14	1	5
Moraceae	<i>Ficus</i>	<i>sp. 7</i>	dicot tree	0	0	32	0	0	22
Moraceae	<i>Ficus</i>	<i>sp. 8</i>	dicot tree	0	0	26	0	0	15
Moraceae	<i>Ficus</i>	<i>sp. 9</i>	dicot tree	0	0	45	0	0	27
Moraceae	<i>Ficus</i>	<i>sp. 10</i>	dicot tree	0	2	5	0	2	5
Moraceae	<i>Ficus</i>	<i>sp. 13</i>	dicot tree	0	0	2	0	0	2
Moraceae	<i>Ficus</i>	<i>sp. 15</i>	dicot tree	0	0	19	0	0	12
Moraceae	<i>Ficus</i>	<i>sp. 19</i>	dicot tree	0	0	3	0	0	3
Moraceae	<i>Ficus</i>	<i>sp. 20</i>	dicot liana	0	2	11	0	2	3
Moraceae	<i>Ficus</i>	<i>sp. 23</i>	dicot tree	0	3	0	0	3	0
Moraceae	<i>Ficus</i>	<i>sp. 24</i>	dicot liana	3	1	4	3	1	4
Moraceae	<i>Parartocarpus</i>	<i>bracteatus</i>	dicot tree	1	0	0	1	0	0
Myristicaceae	<i>Gymnacranthera</i>	<i>farquhariana</i>	dicot tree	30	8	7	18	6	5
Myristicaceae	<i>Gymnacranthera</i>	<i>forbesii</i>	dicot tree	1	0	0	1	0	0
Myristicaceae	<i>Gymnacranthera</i>	<i>ocellata</i>	dicot tree	28	4	0	12	3	0
Myristicaceae	<i>Horsfieldia</i>	<i>borneensis</i>	dicot tree	15	0	0	12	0	0
Myristicaceae	<i>Horsfieldia</i>	<i>crassifolia</i>	dicot tree	2	1	0	2	1	0
Myristicaceae	<i>Horsfieldia</i>	<i>grandis</i>	dicot tree	7	2	0	7	2	0
Myristicaceae	<i>Horsfieldia</i>	<i>polyspherula</i>	dicot tree	15	9	0	12	9	0
Myristicaceae	<i>Horsfieldia</i>	<i>reticulata</i>	dicot tree	10	0	3	10	0	3
Myristicaceae	<i>Horsfieldia</i>	<i>sucosa</i>	dicot tree	12	0	0	8	0	0
Myristicaceae	<i>Horsfieldia</i>	<i>wallichii</i>	dicot tree	5	0	0	4	0	0
Myristicaceae	<i>Horsfieldia</i>	<i>sp. 1</i>	dicot tree	1	1	0	1	1	0
Myristicaceae	<i>Knema</i>	<i>conferta</i>	dicot tree	0	6	0	0	4	0
Myristicaceae	<i>Knema</i>	<i>furfuracea</i>	dicot tree	2	0	0	2	0	0
Myristicaceae	<i>Knema</i>	<i>glauca</i>	dicot tree	5	0	0	4	0	0
Myristicaceae	<i>Knema</i>	<i>hirta</i>	dicot tree	2	0	0	2	0	0
Myristicaceae	<i>Knema</i>	<i>latericia</i> var. <i>albiflora</i>	dicot tree	37	9	5	19	8	4
Myristicaceae	<i>Knema</i>	<i>latifolia</i>	dicot tree	32	0	4	22	0	2
Myristicaceae	<i>Knema</i>	<i>laurina</i>	dicot tree	23	0	2	13	0	2
Myristicaceae	<i>Knema</i>	<i>mogeana</i>	dicot tree	2	1	0	1	1	0
Myristicaceae	<i>Knema</i>	<i>pallens</i>	dicot tree	56	10	2	31	8	2
Myristicaceae	<i>Knema</i>	<i>percoriacea</i>	dicot tree	185	13	8	52	9	7
Myristicaceae	<i>Knema</i>	<i>psilantha</i>	dicot tree	66	12	3	34	7	3
Myristicaceae	<i>Knema</i>	<i>pubiflora</i>	dicot tree	34	2	2	17	2	1
Myristicaceae	<i>Knema</i>	<i>stenophylla</i>	dicot tree	35	0	0	23	0	0
Myristicaceae	<i>Myristica</i>	<i>elliptica</i>	dicot tree	0	1	0	0	1	0
Myristicaceae	<i>Myristica</i>	<i>gigantea</i>	dicot tree	7	0	0	3	0	0
Myristicaceae	<i>Myristica</i>	<i>iners</i>	dicot tree	9	0	4	9	0	3
Myristicaceae	<i>Myristica</i>	<i>malaccensis</i>	dicot tree	1	0	0	1	0	0
Myristicaceae	<i>Myristica</i>	<i>maxima</i>	dicot tree	0	1	2	0	1	2
Myristicaceae	<i>Myristica</i>	<i>villosa</i>	dicot tree	15	4	0	11	4	0
Myrsinaceae	<i>Ardisia</i>	<i>korthalsiana</i>	dicot tree	165	5	0	49	5	0

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Myrsinaceae	<i>Ardisia</i>	<i>megistosepala</i>	dicot tree	2	0	0	2	0	0
Myrsinaceae	<i>Ardisia</i>	<i>sanguinolenta</i>	dicot tree	2	1	1	1	1	1
Myrsinaceae	<i>Ardisia</i>	<i>sp. 1</i>	dicot tree	9	1	0	5	1	0
Myrsinaceae	<i>Ardisia</i>	<i>sp. 2</i>	dicot tree	3	4	0	3	4	0
Myrsinaceae	<i>Ardisia</i>	<i>sp. 3</i>	dicot tree	2	1	1	2	1	1
Myrsinaceae	<i>Ardisia</i>	<i>sp. 4</i>	dicot tree	0	0	2	0	0	1
Myrsinaceae	<i>Ardisia</i>	<i>sp. 10</i>	dicot tree	0	1	0	0	1	0
Myrsinaceae	<i>Embelia</i>	<i>javanica</i>	dicot liana	2	191	33	2	50	24
Myrsinaceae	<i>Embelia</i>	<i>sp. 2</i>	dicot liana	3	4	13	3	3	8
Myrsinaceae	<i>Embelia</i>	<i>sp. 3</i>	dicot liana	1	106	43	1	39	26
Myrsinaceae	<i>Embelia</i>	<i>sp. 5</i>	dicot liana	0	0	4	0	0	4
Myrsinaceae	<i>Maesa</i>	<i>ramentacea</i>	dicot liana	2	54	31	2	35	20
Myrsinaceae	<i>Maesa</i>	<i>sp. 2</i>	dicot liana	0	0	16	0	0	7
Myrsinaceae	<i>Maesa</i>	<i>sp. 3</i>	dicot liana	3	4	0	1	3	0
Myrtaceae	<i>Acmena</i>	<i>acuminatissima</i>	dicot tree	10	0	0	7	0	0
Myrtaceae	<i>Cleistocalyx</i>	<i>cf. operculatum</i>	dicot tree	1	0	7	1	0	4
Myrtaceae	<i>Eugenia</i>	<i>acuminatissima</i>	dicot tree	7	12	5	7	4	5
Myrtaceae	<i>Eugenia</i>	<i>caudatilimba</i>	dicot tree	66	10	1	30	6	1
Myrtaceae	<i>Eugenia</i>	<i>curtisii</i>	dicot tree	42	9	2	25	8	2
Myrtaceae	<i>Eugenia</i>	<i>heteroclada</i>	dicot tree	6	0	6	6	0	6
Myrtaceae	<i>Eugenia</i>	<i>cf. ochneocarpa</i>	dicot tree	4	0	0	3	0	0
Myrtaceae	<i>Rhodamnia</i>	<i>cinerea</i>	dicot tree	31	4	5	24	4	5
Myrtaceae	<i>Syzygium</i>	<i>confertum</i>	dicot tree	3	0	1	2	0	1
Myrtaceae	<i>Syzygium</i>	<i>corymbifera</i>	dicot tree	21	3	15	6	3	4
Myrtaceae	<i>Syzygium</i>	<i>hirtum</i>	dicot tree	28	11	6	14	8	5
Myrtaceae	<i>Syzygium</i>	<i>kunstleri</i>	dicot tree	11	0	7	9	0	4
Myrtaceae	<i>Syzygium</i>	<i>leptostemon</i>	dicot tree	14	0	1	9	0	1
Myrtaceae	<i>Syzygium</i>	<i>lineatum</i>	dicot tree	10	4	1	9	3	1
Myrtaceae	<i>Syzygium</i>	<i>napiforme</i>	dicot tree	40	0	3	16	0	3
Myrtaceae	<i>Syzygium</i>	<i>nigricans</i>	dicot tree	23	63	3	11	10	2
Myrtaceae	<i>Syzygium</i>	<i>tawahense</i>	dicot tree	157	44	21	57	25	14
Myrtaceae	<i>Syzygium</i>	<i>zeylanicum</i>	dicot tree	4	2	0	3	2	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 1</i>	dicot tree	17	1	0	9	1	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 2</i>	dicot tree	21	0	0	8	0	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 5</i>	dicot tree	21	18	0	10	3	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 6</i>	dicot tree	6	1	0	3	1	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 10</i>	dicot tree	3	0	0	3	0	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 28</i>	dicot tree	0	27	0	0	5	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 51</i>	dicot tree	1	3	2	1	3	1
Myrtaceae	<i>Syzygium</i>	<i>sp. 53</i>	dicot tree	3	0	0	3	0	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 54</i>	dicot tree	0	2	1	0	2	1
Myrtaceae	<i>Syzygium</i>	<i>sp. 57</i>	dicot tree	0	13	0	0	2	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 60</i>	dicot tree	1	0	0	1	0	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 61</i>	dicot tree	0	0	1	0	0	1
Myrtaceae	<i>Syzygium</i>	<i>sp. 62</i>	dicot tree	0	0	1	0	0	1
Myrtaceae	<i>Syzygium</i>	<i>sp. 63</i>	dicot tree	0	8	0	0	2	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 64</i>	dicot tree	0	1	0	0	1	0
Nepenthaceae	<i>Nepenthes</i>	<i>ampullaria</i>	dicot liana	0	28	0	0	3	0
Nepenthaceae	<i>Nepenthes</i>	<i>reinwardtiana</i>	dicot liana	0	35	0	0	2	0
Ochnaceae	<i>Ouratea</i> ¹	<i>serrata</i>	dicot tree	17	1	2	14	1	2
Olacaceae	<i>Anacolosia</i>	<i>frutescens</i>	dicot tree	0	1	0	0	1	0
Olacaceae	<i>Ochanostachys</i>	<i>amentacea</i>	dicot tree	55	13	12	34	9	9
Olacaceae	<i>Scorodocarpus</i>	<i>borneensis</i>	dicot tree	4	3	8	3	3	7
Olacaceae	<i>Strombosia</i>	<i>ceylanica</i>	dicot tree	22	0	1	12	0	1
Oleaceae	<i>Chionantes</i>	<i>cuspidata</i>	dicot tree	2	0	0	2	0	0
Oleaceae	<i>Chionantes</i>	<i>sp. 2</i>	dicot tree	1	0	0	1	0	0

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Oleaceae	<i>Chionantes</i>	<i>sp. 4</i>	dicot tree	3	0	0	3	0	0
Oleaceae	<i>Chionantes</i>	<i>sp. 5</i>	dicot tree	0	0	1	0	0	1
Oleaceae	<i>Jasminum</i>	<i>sp. 1</i>	dicot tree	0	0	1	0	0	1
Palmae	<i>Areca</i>	<i>minuta</i>	palm tree	1	0	0	1	0	0
Palmae	<i>Borassodendron</i>	<i>borneensis</i>	palm tree	14	21	19	11	11	16
Palmae	<i>Calamus</i>	<i>fimbriatus</i>	rotan	19	39	1	6	6	1
Palmae	<i>Calamus</i>	<i>flabellatus</i>	rotan	42	1	0	13	1	0
Palmae	<i>Calamus</i>	<i>javensis</i>	rotan	5	0	0	2	0	0
Palmae	<i>Calamus</i>	<i>laevigatus</i>	rotan	1	0	0	1	0	0
Palmae	<i>Calamus</i>	<i>marginatus</i>	rotan	2	0	11	2	0	8
Palmae	<i>Calamus</i>	<i>nigricans</i>	rotan	22	2	0	5	2	0
Palmae	<i>Calamus</i>	<i>ornatus</i>	rotan	3	6	8	3	1	4
Palmae	<i>Calamus</i>	<i>pandanosmus</i>	rotan	7	0	0	1	0	0
Palmae	<i>Calamus</i>	<i>paspalanthus</i>	rotan	25	0	0	1	0	0
Palmae	<i>Calamus</i>	<i>pseudoulur</i>	rotan	1	0	0	1	0	0
Palmae	<i>Calamus</i>	<i>sp. 5</i>	rotan	1	0	0	1	0	0
Palmae	<i>Calamus</i>	<i>sp. 6</i>	rotan	4	0	0	1	0	0
Palmae	<i>Calamus</i>	<i>sp. 7</i>	rotan	1	0	0	1	0	0
Palmae	<i>Calamus</i>	<i>sp. 8</i>	rotan	2	0	0	2	0	0
Palmae	<i>Calamus</i>	<i>sp. 9</i>	rotan	1	0	0	1	0	0
Palmae	<i>Calamus</i>	<i>sp. 10</i>	rotan	1	0	0	1	0	0
Palmae	<i>Calamus</i>	<i>sp. 11</i>	rotan	2	0	0	2	0	0
Palmae	<i>Calamus</i>	<i>sp. 13</i>	rotan	7	1	5	3	1	1
Palmae	<i>Calamus</i>	<i>sp. 15</i>	rotan	3	0	0	1	0	0
Palmae	<i>Calamus</i>	<i>sp. 16</i>	rotan	0	0	15	0	0	1
Palmae	<i>Calamus</i>	<i>sp. 17</i>	rotan	1	0	2	1	0	1
Palmae	<i>Calamus</i>	<i>sp. 18</i>	rotan	2	0	0	1	0	0
Palmae	<i>Ceratolobus</i>	<i>concolor</i>	rotan	13	0	46	6	0	2
Palmae	<i>Ceratolobus</i>	<i>subangulatus</i>	rotan	41	0	9	12	0	5
Palmae	<i>Daemonorops</i>	<i>sabut</i>	rotan	8	0	1	5	0	1
Palmae	<i>Korthalsia</i>	<i>cheb</i>	rotan	2	0	0	2	0	0
Palmae	<i>Korthalsia</i>	<i>echinometra</i>	rotan	32	39	16	3	6	3
Palmae	<i>Korthalsia</i>	<i>ferox</i>	rotan	51	3	8	27	3	6
Palmae	<i>Korthalsia</i>	<i>flagellaris</i>	rotan	4	0	0	1	0	0
Palmae	<i>Korthalsia</i>	<i>furtadoana</i>	rotan	17	0	4	9	0	3
Palmae	<i>Licuala</i>	<i>spinosa</i>	palm tree	1	0	1	1	0	1
Palmae	<i>Licuala</i>	<i>sp. 1</i>	palm shrub	10	0	6	7	0	6
Palmae	<i>Livistona</i>	<i>tawahensis</i>	palm tree	1	0	0	1	0	0
Palmae	<i>Oncosperma</i>	<i>horidum</i>	palm tree	11	10	2	4	6	2
Palmae	<i>Pholidocarpus</i>	<i>sp. 1</i>	palm tree	4	0	1	4	0	1
Palmae	<i>Pinanga</i>	<i>sp. 1</i>	palm shrub	4	0	0	4	0	0
Palmae	<i>Pinanga</i>	<i>sp. 2</i>	palm tree	0	0	1	0	0	1
Palmae	<i>Plectocomiopsis</i>	<i>geminiflora</i>	rotan	24	66	15	5	20	6
Palmae	<i>Plectocomiopsis</i>	<i>mira</i>	rotan	1	0	0	1	0	0
Pandaceae	<i>Galearia</i>	<i>fulva</i>	dicot tree	33	1	3	26	1	2
Pandanaceae	<i>Freycinetia</i>	<i>sp. 1</i>	monocot liana	11	1	1	8	1	1
Pandanaceae	<i>Freycinetia</i>	<i>sp. 2</i>	monocot liana	7	0	0	6	0	0
Pandanaceae	<i>Pandanus</i>	<i>sp. 2</i>	monocot tree	0	0	4	0	0	2
Passifloraceae	<i>Adenia</i>	<i>cordifolia</i>	dicot liana	0	0	1	0	0	1
Passifloraceae	<i>Adenia</i>	<i>macrophylla</i>	dicot liana	0	2	1	0	2	1
Piperaceae	<i>Piper</i>	<i>aduncum</i>	dicot tree	0	3	439	0	3	59
Piperaceae	<i>Piper</i>	<i>sp. 1</i>	dicot vine	0	23	6	0	6	3
Piperaceae	<i>Piper</i>	<i>sp. 2</i>	dicot vine	0	0	1	0	0	1
Piperaceae	<i>Piper</i>	<i>sp. 3</i>	dicot vine	0	1	1	0	1	1
Piperaceae	<i>Piper</i>	<i>sp. 4</i>	dicot vine	0	0	1	0	0	1
Podocarpaceae	<i>Nageia</i>	<i>wallichiana</i>	gymno tree	7	2	0	6	2	0

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Polygalaceae	<i>Xanthophyllum</i>	<i>affine</i>	dicot tree	72	3	3	32	3	3
Polygalaceae	<i>Xanthophyllum</i>	<i>griffithii</i>	dicot tree	7	1	0	7	1	0
Polygalaceae	<i>Xanthophyllum</i>	<i>obscurum</i>	dicot tree	2	0	0	2	0	0
Polygalaceae	<i>Xanthophyllum</i>	<i>rufum</i>	dicot tree	22	1	0	13	1	0
Polygalaceae	<i>Xanthophyllum</i>	<i>stipitatum</i>	dicot tree	7	2	2	6	2	2
Polygalaceae	<i>Xanthophyllum</i>	<i>vitellinum</i>	dicot tree	2	0	0	1	0	0
Polygalaceae	<i>Xanthophyllum</i>	<i>sp. 1</i>	dicot tree	1	0	0	1	0	0
Polygalaceae	<i>Xanthophyllum</i>	<i>sp. 2</i>	dicot tree	1	0	1	1	0	1
Polygalaceae	<i>Xanthophyllum</i>	<i>sp. 5</i>	dicot tree	0	0	2	0	0	2
Polygalaceae	<i>Xanthophyllum</i>	<i>sp. 7</i>	dicot tree	0	1	0	0	1	0
Polygalaceae	<i>Xanthophyllum</i>	<i>sp. 8</i>	dicot tree	0	0	3	0	0	3
Proteaceae	<i>Helicia</i>	<i>sp. 1</i>	dicot tree	0	0	1	0	0	1
Proteaceae	<i>Helicia</i>	<i>sp. 2</i>	dicot liana	2	0	0	2	0	0
Rhamnaceae	<i>Ziziphus</i>	<i>sp. 1</i>	dicot liana	17	2	2	12	1	2
Rhamnaceae	<i>Ziziphus</i>	<i>sp. 2</i>	dicot liana	28	6	0	20	5	0
Rhamnaceae	<i>Ziziphus</i>	<i>sp. 3</i>	dicot liana	3	0	3	3	0	2
Rhamnaceae	<i>Ziziphus</i>	<i>sp. 4</i>	dicot liana	0	0	2	0	0	1
Rhamnaceae	<i>Ziziphus</i>	<i>sp. 5</i>	dicot liana	0	0	2	0	0	1
Rhamnaceae	<i>Indet</i>	<i>sp. 1</i>	dicot liana	0	0	6	0	0	2
Rhizophoraceae	<i>Carallia</i>	<i>branchiata</i>	dicot tree	0	0	1	0	0	1
Rhizophoraceae	<i>Pellacalyx</i>	<i>axillaris</i>	dicot tree	0	3	5	0	2	2
Rhizophoraceae	<i>Pellacalyx</i>	<i>lobbii</i>	dicot tree	0	0	4	0	0	3
Rosaceae	<i>Prunus</i>	<i>sp. 1</i>	dicot tree	15	1	3	13	1	3
Rosaceae	<i>Rubus</i>	<i>moluccanus</i>	dicot liana	0	1	0	0	1	0
Rubiaceae	<i>Canthium</i>	<i>confertum</i>	dicot tree	1	0	0	1	0	0
Rubiaceae	<i>Coptosapelta</i>	<i>tomentosa</i>	dicot liana	10	0	3	6	0	2
Rubiaceae	<i>Gaertnera</i>	<i>vaginas</i>	dicot tree	1	0	0	1	0	0
Rubiaceae	<i>Gardenia</i>	<i>tubiflora</i>	dicot tree	3	0	4	3	0	2
Rubiaceae	<i>Gynochtodes</i>	<i>sp. 1</i>	dicot tree	2	1	0	2	1	0
Rubiaceae	<i>Hedyotis</i>	<i>congesta</i>	dicot herb	15	12	116	5	10	20
Rubiaceae	<i>Hypobathrum</i>	<i>microcarpum</i>	dicot tree	2	3	3	2	3	3
Rubiaceae	<i>Ixora</i>	<i>fluminaus</i>	dicot tree	1	0	1	1	0	1
Rubiaceae	<i>Ixora</i>	<i>sp. 1</i>	dicot tree	85	5	0	36	4	0
Rubiaceae	<i>Ixora</i>	<i>sp. 2</i>	dicot tree	1	0	0	1	0	0
Rubiaceae	<i>Ixora</i>	<i>sp. 4</i>	dicot shrub	2	0	0	2	0	0
Rubiaceae	<i>Ixora</i>	<i>sp. 6</i>	dicot tree	12	0	0	1	0	0
Rubiaceae	<i>Ixora</i>	<i>sp. 7</i>	dicot shrub	2	0	0	2	0	0
Rubiaceae	<i>Jackiopsis</i>	<i>ornata</i>	dicot tree	0	6	0	0	3	0
Rubiaceae	<i>Lasianthus</i>	<i>borneensis</i>	dicot tree	9	0	2	7	0	2
Rubiaceae	<i>Lasianthus</i>	<i>chryseus</i>	dicot shrub	1	0	0	1	0	0
Rubiaceae	<i>Lasianthus</i>	<i>constrictus</i>	dicot shrub	1	1	0	1	1	0
Rubiaceae	<i>Lasianthus</i>	<i>pterospermus</i>	dicot tree	17	0	0	7	0	0
Rubiaceae	<i>Lasianthus</i>	<i>reticulatus</i>	dicot shrub	3	0	0	3	0	0
Rubiaceae	<i>Mussaenda</i>	<i>lanuginosa</i>	dicot liana	0	15	36	0	12	27
Rubiaceae	<i>Nauclea</i>	<i>officinalis</i>	dicot tree	0	1	4	0	1	3
Rubiaceae	<i>Nauclea</i>	<i>subdita</i>	dicot tree	1	16	10	1	15	5
Rubiaceae	<i>Neolamarckia</i>	<i>cadamba</i> ²	dicot tree	0	2	9	0	2	6
Rubiaceae	<i>Neonauclea</i>	<i>gigantea</i>	dicot tree	0	0	1	0	0	1
Rubiaceae	<i>Ochreinauclea</i>	<i>maingayi</i>	dicot tree	0	0	13	0	0	2
Rubiaceae	<i>Oxyceros</i>	<i>longifera</i>	dicot liana	0	0	1	0	0	1
Rubiaceae	<i>Paederia</i>	<i>foetida</i>	dicot liana	4	11	3	4	7	3
Rubiaceae	<i>Paederia</i>	<i>verticillata</i>	dicot liana	0	3	2	0	3	2
Rubiaceae	<i>Paederia</i>	<i>sp. 1</i>	dicot liana	0	0	1	0	0	1
Rubiaceae	<i>Pavetta</i>	<i>indica</i>	dicot tree	3	0	0	3	0	0
Rubiaceae	<i>Pertusadina</i>	<i>eurhyncha</i>	dicot tree	5	1	114	4	1	34
Rubiaceae	<i>Pleiocarpidia</i>	<i>polyneura</i>	dicot tree	6	2	8	5	2	6

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Rubiaceae	<i>Porterandia</i>	<i>anisophylla</i>	dicot tree	15	2	6	10	2	6
Rubiaceae	<i>Prismatomeris</i>	<i>beccariana</i>	dicot tree	23	0	2	18	0	2
Rubiaceae	<i>Psychotria</i>	<i>viridiflora</i>	dicot shrub	26	30	27	21	15	14
Rubiaceae	<i>Rothmannia</i>	<i>schoemani</i>	dicot tree	5	0	6	4	0	5
Rubiaceae	<i>Saprosma</i>	<i>glomerulata</i>	dicot liana	1	0	0	1	0	0
Rubiaceae	<i>Tarenna</i>	<i>cumingiana</i>	dicot tree	4	14	7	4	10	7
Rubiaceae	<i>Tarenna</i>	<i>winkleri</i>	dicot tree	0	4	0	0	4	0
Rubiaceae	<i>Timonius</i>	<i>lasiantoides</i>	dicot tree	4	1	11	3	1	9
Rubiaceae	<i>Timonius</i>	<i>mutabilis</i>	dicot tree	5	9	1	4	5	1
Rubiaceae	<i>Uncaria</i>	<i>barbata</i>	dicot liana	8	227	26	5	58	10
Rubiaceae	<i>Uncaria</i>	<i>borneensis</i>	dicot liana	3	26	78	1	20	37
Rubiaceae	<i>Uncaria</i>	<i>canescens</i>	dicot liana	0	5	84	0	4	36
Rubiaceae	<i>Uncaria</i>	<i>cordata</i>	dicot liana	6	97	72	5	41	38
Rubiaceae	<i>Uncaria</i>	<i>kunstleri</i>	dicot liana	24	20	3	10	15	3
Rubiaceae	<i>Uncaria</i>	<i>longiflora</i>	dicot liana	2	0	4	2	0	2
Rubiaceae	<i>Uncaria</i>	<i>cf. elliptica</i>	dicot liana	3	38	19	1	27	13
Rubiaceae	<i>Uncaria</i>	<i>cf. lanosa</i> var. <i>ferrea</i>	dicot liana	0	1	6	0	1	6
Rubiaceae	<i>Uncaria</i>	<i>sp. 16</i>	dicot liana	7	0	6	3	0	3
Rubiaceae	<i>Uncaria</i>	<i>sp. 18</i>	dicot liana	0	0	1	0	0	1
Rubiaceae	<i>Urophyllum</i>	<i>arborescens</i>	dicot tree	151	27	42	60	11	14
Rubiaceae	<i>Urophyllum</i>	<i>sp. 11</i>	dicot tree	0	0	5	0	0	3
Rubiaceae	<i>cf. Hedyotis</i>	<i>sp. 1</i>	dicot tree	0	0	1	0	0	1
Rubiaceae	<i>Indet</i>	<i>sp. 8</i>	dicot liana	1	0	0	1	0	0
Rubiaceae	<i>Indet</i>	<i>sp. 11</i>	dicot liana	2	1	1	2	1	1
Rubiaceae	<i>Indet</i>	<i>sp. 23</i>	dicot tree	4	0	4	4	0	3
Rubiaceae	<i>Indet</i>	<i>sp. 24</i>	dicot tree	0	0	1	0	0	1
Rubiaceae	<i>Indet</i>	<i>sp. 31</i>	dicot liana	0	0	1	0	0	1
Rubiaceae	<i>Indet</i>	<i>sp. 35</i>	dicot liana	1	0	0	1	0	0
Rubiaceae	<i>Indet</i>	<i>sp. 44</i>	dicot liana	3	1	1	3	1	1
Rutaceae	<i>Luvunga</i>	<i>sp. 1</i>	dicot liana	18	1	0	8	1	0
Rutaceae	<i>Luvunga</i>	<i>sp. 2</i>	dicot liana	3	0	0	3	0	0
Rutaceae	<i>Luvunga</i>	<i>sp. 5</i>	dicot liana	3	0	1	2	0	1
Rutaceae	<i>Melicope</i>	<i>glabra</i>	dicot tree	0	1	198	0	1	48
Rutaceae	<i>Paramignya</i>	<i>scandens</i>	dicot liana	38	1	0	23	1	0
Sabiaceae	<i>Meliosma</i>	<i>sumatrana</i>	dicot tree	1	0	3	1	0	1
Sapindaceae	<i>Dimocarpus</i>	<i>longan</i>	dicot tree	12	0	5	10	0	5
Sapindaceae	<i>Guioa</i>	<i>bijuga</i>	dicot tree	2	0	1	1	0	1
Sapindaceae	<i>Guioa</i>	<i>diplopetala</i>	dicot tree	5	1	0	5	1	0
Sapindaceae	<i>Guioa</i>	<i>pterorachis</i>	dicot tree	4	0	0	2	0	0
Sapindaceae	<i>Lepisanthes</i>	<i>amoena</i>	dicot tree	12	1	6	6	1	6
Sapindaceae	<i>Lepisanthes</i>	<i>senegalensis</i>	dicot tree	121	4	0	48	4	0
Sapindaceae	<i>Nephelium</i>	<i>cuspidatum</i>	dicot tree	29	1	15	19	1	9
Sapindaceae	<i>Nephelium</i>	<i>lappaceum</i>	dicot tree	14	12	2	10	7	2
Sapindaceae	<i>Nephelium</i>	<i>ramboutan-ake</i>	dicot tree	0	0	1	0	0	1
Sapindaceae	<i>Nephelium</i>	<i>reticulatum</i>	dicot tree	0	2	0	0	1	0
Sapindaceae	<i>Paranephelium</i>	<i>xestophyllum</i>	dicot tree	1	0	0	1	0	0
Sapindaceae	<i>Pometia</i>	<i>pinnata</i>	dicot tree	0	1	1	0	1	1
Sapindaceae	<i>Rhysotoechia</i>	<i>acuminata</i>	dicot tree	1	0	0	1	0	0
Sapindaceae	<i>Xerospermum</i>	<i>noronhianum</i>	dicot tree	4	0	0	4	0	0
Sapotaceae	<i>Madhuca</i>	<i>kingiana</i>	dicot tree	1107	34	0	73	15	0
Sapotaceae	<i>Madhuca</i>	<i>palembanica</i>	dicot tree	31	4	0	8	4	0
Sapotaceae	<i>Madhuca</i>	<i>pallida</i>	dicot tree	8	2	1	2	2	1
Sapotaceae	<i>Madhuca</i>	<i>sericea</i>	dicot tree	13	4	13	13	3	10
Sapotaceae	<i>Palaquium</i>	<i>beccarianum</i>	dicot tree	4	1	0	1	1	0
Sapotaceae	<i>Palaquium</i>	<i>calophyllum</i>	dicot tree	0	1	0	0	1	0

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Sapotaceae	<i>Palaquium</i>	<i>leiocarpum</i>	dicot tree	0	0	1	0	0	1
Sapotaceae	<i>Palaquium</i>	<i>quercifolium</i>	dicot tree	4	6	2	4	6	2
Sapotaceae	<i>Palaquium</i>	<i>rostratum</i>	dicot tree	1	0	0	1	0	0
Sapotaceae	<i>Palaquium</i>	<i>sericeum</i>	dicot tree	0	0	1	0	0	1
Sapotaceae	<i>Palaquium</i>	<i>stenophyllum</i>	dicot tree	2	0	4	2	0	4
Sapotaceae	<i>Payena</i>	<i>lowiana</i>	dicot tree	1	0	1	1	0	1
Sapotaceae	<i>Payena</i>	<i>lucida</i>	dicot tree	26	2	0	17	2	0
Sapotaceae	<i>Pouteria</i>	<i>obovata</i>	dicot tree	1	0	1	1	0	1
Schizaeaceae	<i>Lygodium</i>	<i>cincinatum</i>	fern vine	0	0	9	0	0	5
Schizaeaceae	<i>Lygodium</i>	<i>flexuosum</i>	fern vine	0	19	9	0	2	4
Schizaeaceae	<i>Lygodium</i>	<i>microphyllum</i>	fern vine	0	57	191	0	24	44
Schizaeaceae	<i>Lygodium</i>	<i>salicifolium</i>	fern vine	0	0	13	0	0	9
Scrophulariaceae	<i>Brookea</i>	<i>sp. 1</i>	dicot tree	0	0	1	0	0	1
Simaroubaceae	<i>Eurycoma</i>	<i>longifolia</i>	dicot tree	54	2	0	29	2	0
Simaroubaceae	<i>Quassia</i>	<i>indica</i>	dicot tree	11	4	1	9	3	1
Smilacaceae	<i>Smilax</i>	<i>barbata</i>	monocot liana	3	1	12	3	1	9
Smilacaceae	<i>Smilax</i>	<i>odoratissima</i>	monocot liana	6	2	22	4	2	13
Solanaceae	<i>Solanum</i>	<i>jamaicense</i>	dicot shrub	0	8	618	0	1	65
Sonneratiaceae	<i>Duabanga</i>	<i>moluccana</i>	dicot tree	0	0	1	0	0	1
Sterculiaceae	<i>Heritiera</i>	<i>elata</i>	dicot tree	3	1	1	3	1	1
Sterculiaceae	<i>Heritiera</i>	<i>littoralis</i>	dicot tree	1	0	0	1	0	0
Sterculiaceae	<i>Heritiera</i>	<i>sumatrana</i>	dicot tree	17	2	0	11	2	0
Sterculiaceae	<i>Pterospermum</i>	<i>javanicum</i>	dicot tree	2	0	0	1	0	0
Sterculiaceae	<i>Scaphium</i>	<i>macropodium</i>	dicot tree	39	7	12	25	5	5
Sterculiaceae	<i>Sterculia</i>	<i>oblongata</i>	dicot tree	3	0	0	3	0	0
Sterculiaceae	<i>Sterculia</i>	<i>parviflora</i>	dicot tree	0	0	1	0	0	1
Sterculiaceae	<i>Sterculia</i>	<i>rubiginosa</i>	dicot tree	36	9	0	27	7	0
Sterculiaceae	<i>Sterculia</i>	<i>stipulata</i>	dicot tree	4	4	3	2	4	3
Sterculiaceae	<i>Sterculia</i>	<i>sp. 1</i>	dicot tree	4	0	2	3	0	2
Sterculiaceae	<i>Sterculia</i>	<i>sp. 2</i>	dicot tree	0	0	3	0	0	3
Strychnaceae	<i>Strychnos</i>	<i>sp. 1</i>	dicot liana	15	0	0	5	0	0
Strychnaceae	<i>Strychnos</i>	<i>sp. 2</i>	dicot liana	19	1	2	13	1	2
Strychnaceae	<i>Strychnos</i>	<i>sp. 3</i>	dicot liana	6	0	2	6	0	2
Symplocaceae	<i>Symplocos</i>	<i>sp. 1</i>	dicot tree	2	0	0	2	0	0
Tetrameristaceae	<i>Tetramerista</i>	<i>glabra</i>	dicot tree	0	2	2	0	2	2
Theaceae	<i>Eurya</i>	<i>acuminata</i>	dicot tree	0	0	11	0	0	7
Theaceae	<i>Gordonia</i>	<i>borneensis</i>	dicot tree	6	1	1	4	1	1
Theaceae	<i>Schima</i>	<i>wallichii</i>	dicot tree	3	28	13	1	12	7
Thymelaeaceae	<i>Aquilaria</i>	<i>beccariana</i>	dicot tree	1	0	1	1	0	1
Thymelaeaceae	<i>Aquilaria</i>	<i>malaccensis</i>	dicot tree	14	2	6	13	2	5
Thymelaeaceae	<i>Enkleia</i>	<i>malaccensis</i>	dicot liana	6	2	0	6	2	0
Thymelaeaceae	<i>Gonystylus</i>	<i>affinis</i>	dicot tree	152	15	1	46	10	1
Thymelaeaceae	<i>Gonystylus</i>	<i>consanguineus</i>	dicot tree	0	0	1	0	0	1
Trigonatiaceae	<i>Trigoniatrum</i>	<i>hypoleucum</i>	dicot tree	69	0	0	26	0	0
Ulmaceae s.l.	<i>Gironniera</i>	<i>nervosa</i>	dicot tree	242	50	45	71	25	28
Ulmaceae s.l.	<i>Trema</i>	<i>cannabina</i>	dicot tree	0	1	39	0	1	14
Ulmaceae s.l.	<i>Trema</i>	<i>tomentosa</i>	dicot tree	0	1	85	0	1	26
Urticaceae	<i>Astrothalamus</i>	<i>reticulatus</i>	dicot tree	0	0	1	0	0	1
Violaceae	<i>Rinorea</i>	<i>sp. 1</i>	dicot tree	120	1	0	15	1	0
Vitaceae	<i>Ampelocissus</i>	<i>imperialis</i>	dicot liana	2	12	23	1	11	12
Vitaceae	<i>Ampelocissus</i>	<i>rubiginosa</i>	dicot liana	1	4	0	1	4	0
Vitaceae	<i>Ampelocissus</i>	<i>winkleri</i>	dicot liana	16	8	8	10	7	6
Vitaceae	<i>Ampelocissus</i>	<i>sp. 1</i>	dicot liana	0	0	11	0	0	2
Vitaceae	<i>Cayratia</i>	<i>japonica</i>	dicot liana	0	3	57	0	3	17
Vitaceae	<i>Leea</i>	<i>indica</i>	dicot tree	0	0	226	0	0	54
Vitaceae	<i>Pterisanthes</i>	<i>cissoides</i>	dicot liana	1	9	12	1	5	7

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
Vitaceae	<i>Pterisanthes</i>	<i>sp. 1</i>	dicot liana	9	6	6	5	4	5
Vitaceae	<i>Pterisanthes</i>	<i>sp. 2</i>	dicot liana	0	0	6	0	0	4
Vitaceae	<i>Tetrastigma</i>	<i>pedunculare</i>	dicot liana	0	0	10	0	0	8
Vitaceae	<i>Indet</i>	<i>sp. 1</i>	dicot liana	3	21	0	3	17	0
Vitaceae	<i>Indet</i>	<i>sp. 2</i>	dicot liana	0	3	0	0	1	0
Vitaceae	<i>Indet</i>	<i>sp. 3</i>	dicot liana	0	1	0	0	1	0
Vitaceae	<i>Indet</i>	<i>sp. 4</i>	dicot liana	0	0	16	0	0	16
Vitaceae	<i>Indet</i>	<i>sp. 5</i>	dicot liana	0	0	5	0	0	3
Vitaceae	<i>Indet</i>	<i>sp. 6</i>	dicot liana	0	0	1	0	0	1
Vitaceae	<i>Indet</i>	<i>sp. 7</i>	dicot liana	0	0	4	0	0	1
Vitaceae	<i>Indet</i>	<i>sp. 8</i>	dicot liana	0	0	3	0	0	3
Vitaceae	<i>Indet</i>	<i>sp. 9</i>	dicot liana	0	0	2	0	0	1
Vitaceae	<i>Indet</i>	<i>sp. 10</i>	dicot liana	0	0	2	0	0	2
Zingiberaceae s.l.	<i>Alpinia</i>	<i>ligulata</i>	monocot herb	3	0	11	1	0	2
Zingiberaceae s.l.	<i>Ammomum</i>	<i>sp. 18</i>	monocot herb	10	0	30	2	0	6
Zingiberaceae s.l.	<i>Costus</i>	<i>globosus</i>	monocot herb	0	0	10	0	0	2
Zingiberaceae s.l.	<i>Costus</i>	<i>speciosus</i>	monocot herb	0	0	231	0	0	26
Zingiberaceae s.l.	<i>Elettaria</i>	<i>sp. 17</i>	monocot herb	0	2	73	0	1	15
Zingiberaceae s.l.	<i>Elettaria</i>	<i>sp. 32</i>	monocot herb	38	52	16	9	6	1
Zingiberaceae s.l.	<i>Elettaria</i>	<i>sp. 36</i>	monocot herb	0	0	6	0	0	1
Zingiberaceae s.l.	<i>Etlingera</i>	<i>fimbriobracteata</i>	monocot herb	0	28	448	0	1	42
Zingiberaceae s.l.	<i>Etlingera</i>	<i>sp. 3</i>	monocot herb	102	64	24	16	5	3
Zingiberaceae s.l.	<i>Etlingera</i>	<i>sp. 31</i>	monocot herb	20	149	190	5	15	36
Zingiberaceae s.l.	<i>cf. reticulata</i>		monocot herb	22	1467	127	5	62	26
Zingiberaceae s.l.	<i>Hornstedtia</i>	<i>sp. 2</i>	monocot herb	0	115	1676	0	14	70
Zingiberaceae s.l.	<i>Plagiostachys</i>	<i>sp. 22</i>	monocot herb	0	0	29	0	0	5
Zingiberaceae s.l.	<i>Plagiostachys</i>	<i>sp. 35</i>	monocot herb	5	36	23	1	9	6
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 4</i>	monocot herb	22	0	8	4	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 5</i>	monocot herb	13	0	0	2	0	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 21</i>	monocot herb	0	4	0	0	1	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 23</i>	monocot herb	1	24	0	1	4	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 26</i>	monocot herb	13	4	7	2	1	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 27</i>	monocot herb	0	0	6	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 33</i>	monocot herb	0	0	7	0	0	2
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 43</i>	monocot herb	0	0	62	0	0	8
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 45</i>	monocot herb	0	0	33	0	0	9
cf. Anacardiaceae	<i>cf. Mangifera</i>	<i>sp. 11</i>	dicot tree	1	0	0	1	0	0
cf. Anacardiaceae	<i>cf. Mangifera</i>	<i>sp. 13</i>	dicot tree	0	0	1	0	0	1
cf. Anacardiaceae	<i>cf. Mangifera</i>	<i>sp. 14</i>	dicot tree	0	0	1	0	0	1
cf. Anacardiaceae	<i>Indet</i>	<i>sp. 1</i>	dicot tree	1	0	0	1	0	0
cf. Anacardiaceae	<i>Indet</i>	<i>sp. 12</i>	dicot tree	0	0	1	0	0	1
cf. Anacardiaceae	<i>Indet</i>	<i>sp. 15</i>	dicot tree	1	0	0	1	0	0
cf. Annonaceae	<i>Indet</i>	<i>sp. 5</i>	dicot tree	1	0	1	1	0	1
cf. Apocynaceae	<i>Indet</i>	<i>sp. 1</i>	dicot liana	0	0	2	0	0	1
cf. Apocynaceae	<i>Indet</i>	<i>sp. 15</i>	dicot liana	0	2	0	0	1	0
cf. Apocynaceae	<i>Indet</i>	<i>sp. 16</i>	dicot liana	0	0	1	0	0	1
cf. Caprifoliaceae	<i>Indet</i>	<i>sp. 5</i>	dicot liana	1	0	0	1	0	0
cf. Celastraceae	<i>cf. Eonymus</i>	<i>sp. 1</i>	dicot tree	0	0	2	0	0	2
cf. Celastraceae	<i>cf. Microtropis</i>	<i>sp. 1</i>	dicot tree	0	0	3	0	0	2
cf. Celastraceae	<i>cf. Microtropis</i>	<i>sp. 2</i>	dicot tree	0	0	1	0	0	1
cf. Celastraceae	<i>cf. Salacia</i>	<i>sp. 20</i>	dicot liana	0	0	2	0	0	2
cf. Crypteroniaceae	<i>cf. Crypteronia</i>	<i>sp. 3</i>	dicot tree	1	0	0	1	0	0
cf. Dichapetalaceae	<i>cf. Dichapetalum</i>	<i>sp. 1</i>	dicot tree	1	0	1	1	0	1
cf. Euphorbiaceae	<i>cf. Glochidion</i>	<i>sp. 11</i>	dicot tree	2	0	5	1	0	2
cf. Fagaceae	<i>Indet</i>	<i>sp. 10</i>	dicot tree	0	1	0	0	1	0
cf. Icacinaceae	<i>cf. Gonocaryum</i>	<i>sp. 1</i>	dicot tree	0	1	0	0	1	0

Appendix 1. Continued.

Family	Genus	Species	Plant type	N0	N1	N2	S0	S1	S2
cf. Lauraceae	<i>Indet</i>	<i>sp. 10</i>	dicot tree	3	1	3	3	1	3
cf. Lauraceae	<i>Indet</i>	<i>sp. 20</i>	dicot tree	0	0	1	0	0	1
cf. Lauraceae	<i>Indet</i>	<i>sp. 21</i>	dicot tree	0	2	0	0	2	0
cf. Melastomataceae	<i>cf. Memecylon</i>	<i>sp. 10</i>	dicot tree	0	0	2	0	0	1
cf. Melastomataceae	<i>cf. Memecylon</i>	<i>sp. 11</i>	dicot tree	0	2	0	0	1	0
cf. Myrtaceae	<i>cf. Syzygium</i>	<i>sp. 65</i>	dicot tree	0	1	0	0	1	0
cf. Myrtaceae	<i>cf. Syzygium</i>	<i>sp. 66</i>	dicot tree	1	0	0	1	0	0
cf. Myrtaceae	<i>cf. Syzygium</i>	<i>sp. 67</i>	dicot tree	0	0	6	0	0	1
cf. Olacaceae	<i>cf. Scorodocarpus</i>	<i>sp. 1</i>	dicot tree	0	0	1	0	0	1
cf. Oxalidaceae	<i>Indet</i>	<i>sp. 1</i>	dicot liana	0	0	3	0	0	1
cf. Sapotaceae	<i>cf. Palaquium</i>	<i>sp. 12</i>	dicot tree	0	0	1	0	0	1
<i>Indet</i>	<i>Indet</i>	<i>sp. 504</i>	dicot tree	0	0	1	0	0	1
<i>Indet</i>	<i>Indet</i>	<i>sp. 506</i>	dicot liana	0	4	0	0	2	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 508</i>	dicot tree	1	0	0	1	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 511</i>	dicot tree	1	0	0	1	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 513</i>	dicot liana	0	4	0	0	2	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 514</i>	dicot tree	1	0	0	1	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 518</i>	dicot liana	0	0	1	0	0	1
<i>Indet</i>	<i>Indet</i>	<i>sp. 524</i>	dicot tree	1	0	0	1	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 525</i>	dicot tree	1	0	0	1	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 531</i>	dicot tree	0	1	25	0	1	12
<i>Indet</i>	<i>Indet</i>	<i>sp. 532</i>	dicot tree	0	0	1	0	0	1
<i>Indet</i>	<i>Indet</i>	<i>sp. 536</i>	dicot tree	2	0	0	1	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 537</i>	dicot tree	0	0	1	0	0	1
<i>Indet</i>	<i>Indet</i>	<i>sp. 542</i>	dicot tree	0	1	1	0	1	1
<i>Indet</i>	<i>Indet</i>	<i>sp. 546</i>	dicot tree	1	0	0	1	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 550</i>	dicot tree	0	0	1	0	0	1
<i>Indet</i>	<i>Indet</i>	<i>sp. 551</i>	dicot tree	0	0	1	0	0	1
<i>Indet</i>	<i>Indet</i>	<i>sp. 553</i>	dicot tree	1	0	0	1	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 557</i>	dicot tree	0	0	2	0	0	2
<i>Indet</i>	<i>Indet</i>	<i>sp. 559</i>	dicot tree	2	0	0	2	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 562</i>	dicot liana	2	0	0	2	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 563</i>	dicot liana	0	1	0	0	1	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 567</i>	dicot tree	0	0	1	0	0	1
<i>Indet</i>	<i>Indet</i>	<i>sp. 569</i>	dicot liana	1	0	0	1	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 573</i>	dicot liana	0	1	0	0	1	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 615</i>	dicot liana	0	0	4	0	0	1
<i>Indet</i>	<i>Indet</i>	<i>sp. 623</i>	dicot liana	1	0	0	1	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 633</i>	dicot liana	0	1	2	0	1	2
<i>Indet</i>	<i>Indet</i>	<i>sp. 703</i>	dicot tree	0	0	1	0	0	1
<i>Indet</i>	<i>Indet</i>	<i>sp. 716</i>	dicot tree	1	0	0	1	0	0
<i>Indet</i>	<i>Indet</i>	<i>sp. 723</i>	dicot tree	0	0	1	0	0	1

Appendix 2

List of all small species recorded in the 2 × 4 m subplots. After each family, genus and species name respectively plant type and number of subplots having at least one individual of this species per forest disturbance type (S0 = unburnt, S1 = once-burnt, S2 = twice-burnt, n = 80).

Family	Genus	Species	Plant type	S0	S1	S2
Acanthaceae	<i>Indet</i>	<i>sp. 1</i>	dicot herb	0	0	2
Acanthaceae	<i>Indet</i>	<i>sp. 2</i>	dicot herb	0	0	2
Araceae	<i>cf. Alocasia</i>	<i>sp. 1</i>	monocot herb	0	1	5
Araceae	<i>Indet</i>	<i>sp. 15</i>	monocot herb	0	0	2
Aristolochiaceae	<i>Thottea</i>	<i>sp. 1</i>	dicot herb	4	3	2
Aspleniaceae	<i>cf. Asplenium</i>	<i>sp. 1</i>	fern herb	0	3	0
Blechnaceae	<i>Blechnum</i>	<i>sp. 1</i>	fern herb	0	7	18
Blechnaceae	<i>Blechnum</i>	<i>sp. 5</i>	fern herb	1	0	0
Compositae	<i>Chromolaena</i>	<i>odorata</i>	dicot shrub	0	0	3
Compositae	<i>Mikania</i>	<i>scandens</i>	dicot vine	0	28	44
Cyatheaceae	<i>Cyathea</i>	<i>mohuccana</i>	fern treelet	0	0	1
Cyperaceae	<i>Hypolytrum</i>	<i>nemorum</i>	monocot grass	1	1	4
Cyperaceae	<i>Mapania</i>	<i>cuspidata</i>	monocot herb	1	9	12
Cyperaceae	<i>Mapania</i>	<i>sp. 1</i>	monocot grass	39	28	27
Cyperaceae	<i>Mapania</i>	<i>sp. 2</i>	monocot grass	9	7	12
Cyperaceae	<i>Mapania</i>	<i>sp. 3</i>	monocot grass	0	0	1
Cyperaceae	<i>Mapania</i>	<i>sp. 4</i>	monocot grass	6	12	7
Cyperaceae	<i>Mapania</i>	<i>sp. 5</i>	monocot grass	2	1	0
Cyperaceae	<i>Mapania</i>	<i>sp. 6</i>	monocot grass	0	1	0
Cyperaceae	<i>Mapania</i>	<i>sp. 10</i>	monocot grass	0	1	0
Cyperaceae	<i>Scleria</i>	<i>terrestris</i>	monocot grass	14	15	8
Cyperaceae	<i>Scleria</i>	<i>sp. 1</i>	monocot grass	0	0	14
Davalliaceae	<i>Davallia</i>	<i>solida</i>	fern herb	1	1	0
Dennstaedtiaceae	<i>Lindsaea</i>	<i>sp. 1</i>	fern herb	3	1	0
Dennstaedtiaceae	<i>Microlepia</i>	<i>speluncaea</i>	fern herb	3	62	61
Dennstaedtiaceae	<i>Pteridium</i>	<i>aquilinum</i> ³	fern herb	0	36	17
Dryopteridaceae	<i>Diplazium</i>	<i>sp. 2</i>	fern herb	1	0	0
Dryopteridaceae	<i>Diplazium</i>	<i>sp. 3</i>	fern herb	0	0	1
Dryopteridaceae	<i>Diplazium</i>	<i>sp. 4</i>	fern herb	3	0	0
Dryopteridaceae	<i>Diplazium</i>	<i>sp. 5</i>	fern herb	2	0	0
Dryopteridaceae	<i>Diplazium</i>	<i>sp. 6</i>	fern herb	0	1	0
Dryopteridaceae	<i>Diplazium</i>	<i>sp. 7</i>	fern herb	1	0	0
Dryopteridaceae	<i>Pleocnemia</i>	<i>irregularis</i>	fern herb	0	0	1
Dryopteridaceae	<i>Tectaria</i>	<i>sp. 1</i>	fern herb	1	0	0
Dryopteridaceae	<i>Tectaria</i>	<i>sp. 2</i>	fern herb	1	1	0
Dryopteridaceae	<i>Tectaria</i>	<i>sp. 3</i>	fern herb	2	0	2
Gesneriaceae	<i>Cyrtandra</i>	<i>sp. 1</i>	dicot herb	2	0	3
Gesneriaceae	<i>Cyrtandra</i>	<i>sp. 2</i>	dicot herb	0	0	2
Gramineae	<i>Centotheca</i>	<i>lappacea</i>	monocot grass	0	0	1
Gramineae	<i>Cyrtococcum</i>	<i>acrescens</i>	monocot grass	0	0	3
Gramineae	<i>Cyrtococcum</i>	<i>oxyphyllum</i>	monocot grass	0	1	0
Gramineae	<i>Imperata</i>	<i>cylindrica</i>	monocot grass	0	41	15
Gramineae	<i>Leptaspis</i>	<i>urceolata</i>	monocot herb	1	0	0
Gramineae	<i>Lophatherum</i>	<i>gracile</i>	monocot grass	0	0	4

Appendix 2. Continued.

Family	Genus	Species	Plant type	S0	S1	S2
Gramineae	<i>Ottochloa</i>	<i>nodosa</i>	monocot grass	0	0	1
Gramineae	<i>Saccharum</i>	<i>spontaneum</i>	monocot grass	0	0	2
Hanguanaceae	<i>Hanguana</i>	<i>malayana</i>	monocot herb	0	3	0
Hymenophyllaceae	<i>Trichomanes</i>	<i>javanica</i>	fern herb	1	0	0
Hymenophyllaceae	<i>Trichomanes</i>	<i>cf. obscurum</i>	fern herb	3	0	0
Hypoxidaceae	<i>Curculigo</i>	<i>sp. 1</i>	monocot herb	4	3	19
Lycopodiaceae	<i>Lycopodium</i>	<i>cernuum</i>	fern herb	0	0	7
Marantaceae	<i>Phrynium</i>	<i>cf. jagoreanum</i>	monocot herb	53	48	55
Marantaceae	<i>Phrynium</i>	<i>sp. 2</i>	monocot herb	1	8	4
Marantaceae	<i>Indet</i>	<i>sp. 4</i>	monocot herb	1	0	0
Marantaceae	<i>Indet</i>	<i>sp. 5</i>	monocot herb	0	0	4
Melastomataceae	<i>Clidemia</i>	<i>hirta</i>	dicot herb	0	0	54
Myrsinaceae	<i>Labisia</i>	<i>pumila</i>	dicot herb	1	0	0
Myrsinaceae	<i>cf. Labisia</i>	<i>sp. 1</i>	dicot shrub	1	0	0
Nephrolepidaceae	<i>Nephrolepis</i>	<i>cf. biserrata</i>	fern herb	1	75	62
Orchidaceae	<i>Indet</i>	<i>sp. 1</i>	monocot herb	0	2	1
Palmae	<i>Licuala</i>	<i>sp. 1</i>	palm shrub	31	4	3
Palmae	<i>Pinanga</i>	<i>sp. 1</i>	palm shrub	5	0	0
Pandanaceae	<i>Pandanus</i>	<i>sp. 3</i>	monocot herb	4	2	3
Polypodiaceae	<i>cf. Goniophlebium</i>	<i>sp. 1</i>	fern herb	1	0	0
Pteridaceae	<i>Pityrogramma</i>	<i>calomelanes</i>	fern herb	0	0	1
Pteridaceae	<i>Pteris</i>	<i>tripartita</i>	fern herb	0	1	2
Pteridaceae	<i>Taenitis</i>	<i>blechnoides</i>	fern herb	1	1	1
Pterydophyta	<i>Indet</i>	<i>sp. 2</i>	fern herb	1	0	0
Rubiaceae	<i>Geophila</i>	<i>sp. 3</i>	dicot herb	2	2	0
Rubiaceae	<i>Hedyotis</i>	<i>congesta</i>	dicot herb	19	20	25
Rubiaceae	<i>Ixora</i>	<i>sp. 4</i>	dicot shrub	1	0	0
Rubiaceae	<i>Ixora</i>	<i>sp. 7</i>	dicot shrub	1	0	0
Rubiaceae	<i>Lasianthus</i>	<i>attenuata</i>	dicot shrub	2	0	0
Rubiaceae	<i>Lasianthus</i>	<i>constrictus</i>	dicot shrub	1	0	0
Rubiaceae	<i>Lasianthus</i>	<i>oblongatus</i>	dicot shrub	4	1	1
Rubiaceae	<i>Psychotria</i>	<i>sp. 1</i>	dicot shrub	1	3	1
Rubiaceae	<i>Psychotria</i>	<i>sp. 5</i>	dicot herb	0	0	2
Rubiaceae	<i>Indet</i>	<i>sp. 26</i>	dicot shrub	0	2	0
Rubiaceae	<i>Indet</i>	<i>sp. 28</i>	dicot shrub	0	1	0
Schizaeaceae	<i>Lygodium</i>	<i>cincinatum</i>	fern vine	0	4	10
Schizaeaceae	<i>Lygodium</i>	<i>microphyllum</i>	fern vine	2	41	52
Schizaeaceae	<i>Lygodium</i>	<i>salicifolium</i>	fern vine	1	0	4
Selaginellaceae	<i>Selaginella</i>	<i>sp. 1</i>	fern herb	1	1	5
Selaginellaceae	<i>Selaginella</i>	<i>sp. 2</i>	fern herb	0	1	0
Selaginellaceae	<i>Selaginella</i>	<i>sp. 3</i>	fern herb	0	0	1
Selaginellaceae	<i>Selaginella</i>	<i>sp. 4</i>	fern herb	0	1	0
Solanaceae	<i>Solanum</i>	<i>jamaicense</i>	dicot shrub	0	0	44
Thelypteridaceae	<i>cf. Cyclosorus</i>	<i>sp. 1</i>	fern herb	2	2	1
Thelypteridaceae	<i>Indet</i>	<i>sp. 1</i>	fern herb	0	0	1
Thelypteridaceae	<i>Indet</i>	<i>sp. 2</i>	fern herb	0	0	1
Thelypteridaceae	<i>Indet</i>	<i>sp. 3</i>	fern herb	0	0	1
Zingiberaceae s.l.	<i>Alpinia</i>	<i>ligulata</i>	monocot herb	0	1	0
Zingiberaceae s.l.	<i>Amomum</i>	<i>sp. 18</i>	monocot herb	0	1	6
Zingiberaceae s.l.	<i>Costus</i>	<i>globosus</i>	monocot herb	0	0	1

Appendix 2. Continued.

Family	Genus	Species	Plant type	S0	S1	S2
Zingiberaceae s.l.	<i>Costus</i>	<i>speciosa</i>	monocot herb	0	0	37
Zingiberaceae s.l.	<i>Elettaria</i>	<i>sp. 17</i>	monocot herb	1	0	17
Zingiberaceae s.l.	<i>Elettaria</i>	<i>sp. 32</i>	monocot herb	3	2	1
Zingiberaceae s.l.	<i>Etlingera</i>	<i>fimbriobracteata</i>	monocot herb	0	0	8
Zingiberaceae s.l.	<i>Etlingera</i>	<i>sp. 3</i>	monocot herb	3	3	0
Zingiberaceae s.l.	<i>Etlingera</i>	<i>sp. 31</i>	monocot herb	0	3	6
Zingiberaceae s.l.	<i>Globba</i>	<i>sp. 24</i>	monocot herb	0	0	2
Zingiberaceae s.l.	<i>Globba</i>	<i>sp. 34</i>	monocot herb	1	2	0
Zingiberaceae s.l.	<i>Hornstedtia</i>	<i>cf. reticulata</i>	monocot herb	7	38	35
Zingiberaceae s.l.	<i>Hornstedtia</i>	<i>sp. 2</i>	monocot herb	0	4	41
Zingiberaceae s.l.	<i>Plagiostachys</i>	<i>sp. 35</i>	monocot herb	2	4	28
Zingiberaceae s.l.	<i>Zingiber</i>	<i>sp. 56</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 4</i>	monocot herb	0	1	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 6</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 7</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 8</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 9</i>	monocot herb	1	0	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 10</i>	monocot herb	1	0	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 14</i>	monocot herb	0	1	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 15</i>	monocot herb	0	1	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 19</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 21</i>	monocot herb	0	0	3
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 23</i>	monocot herb	1	3	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 27</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 29</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 37</i>	monocot herb	0	1	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 39</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 40</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 41</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 42</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 43</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 44</i>	monocot herb	0	1	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 45</i>	monocot herb	0	0	6
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 46</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 47</i>	monocot herb	2	0	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 48</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 49</i>	monocot herb	2	0	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 50</i>	monocot herb	0	1	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 52</i>	monocot herb	0	0	1
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 53</i>	monocot herb	0	1	0
cf. Joinvilleaceae	<i>cf. Joinvillea</i>	<i>borneensis</i>	monocot herb	0	0	1

Appendix 3

List of all species identified during the soil seed bank analysis of the 10 × 20 m subplots. After each family, genus and species name respectively plant type and number of germinated seeds per forest disturbance type (N0 = unburnt, N1 = once-burnt, N2 = twice-burnt, n = 80).

Family	Genus	Species	Plant type	N0	N1	N2
Commelinaceae	<i>Amischotolype</i>	<i>mollissima</i>	monocot liana	0	0	2
Compositae	<i>Chromolaena</i>	<i>odorata</i>	dicot shrub	0	2	9
Compositae	<i>Mikania</i>	<i>scandens</i>	dicot vine	2	18	24
Compositae	<i>Vernonia</i>	<i>arborea</i>	dicot tree	6	6	0
Cyperaceae	<i>Mapania</i>	<i>sp. 2</i>	monocot grass	1	0	0
Dilleniaceae	<i>Tetracera</i>	<i>scandens</i>	dicot liana	0	1	0
Euphorbiaceae	<i>Homalanthus</i>	<i>populneus</i>	dicot tree	0	0	18
Euphorbiaceae	<i>Macaranga</i>	<i>hypoleuca</i>	dicot tree	0	0	1
Euphorbiaceae	<i>Macaranga</i>	<i>lowii</i>	dicot tree	0	1	0
Euphorbiaceae	<i>Macaranga</i>	<i>trichocarpa</i>	dicot tree	1	0	0
Gentianaceae	<i>Fagraea</i>	<i>racemosa</i>	dicot tree	13	2	1
Gramineae	<i>Indet</i>	<i>sp. 1</i>	monocot grass	0	0	4
Gramineae	<i>Indet</i>	<i>sp. 2</i>	monocot grass	0	0	1
Gramineae	<i>Indet</i>	<i>sp. 3</i>	monocot grass	0	2	5
Gramineae	<i>Indet</i>	<i>sp. 4</i>	monocot grass	0	0	1
Gramineae	<i>Indet</i>	<i>sp. 5</i>	monocot grass	1	0	0
Gramineae	<i>Indet</i>	<i>sp. 6</i>	monocot grass	0	2	1
Gramineae	<i>Indet</i>	<i>sp. 7</i>	monocot grass	1	0	1
Gramineae	<i>Indet</i>	<i>sp. 8</i>	monocot grass	1	0	1
Gramineae	<i>Indet</i>	<i>sp. 9</i>	monocot grass	1	1	0
Guttiferae	<i>Cratoxylum</i>	<i>arborescens</i>	dicot tree	1	0	0
Guttiferae	<i>Cratoxylum</i>	<i>formosum</i>	dicot tree	1	3	0
Guttiferae	<i>Cratoxylum</i>	<i>sumatranum</i>	dicot tree	1	1	1
Hypoxidaceae	<i>Curculigo</i>	<i>sp. 1</i>	monocot herb	1	0	0
Labiatae	<i>Callicarpa</i>	<i>pentandra</i>	dicot tree	0	1	24
Melastomataceae	<i>Clidemia</i>	<i>hirta</i>	dicot herb	1	1	27
Melastomataceae	<i>Dissochaeta</i>	<i>gracilis</i>	dicot liana	21	13	9
Melastomataceae	<i>Macrolenes</i>	<i>sp. 2</i>	dicot liana	8	2	0
Melastomataceae	<i>Melastoma</i>	<i>malabathricum</i>	dicot tree	4	8	17
Melastomataceae	<i>Pternandra</i>	<i>coerulescens</i>	dicot tree	34	21	9
Melastomataceae	<i>Pternandra</i>	<i>rostrata</i>	dicot tree	1	0	0
Melastomataceae	<i>Indet</i>	<i>sp. 1</i>	dicot shrub	1	0	0
Moraceae	<i>Ficus</i>	<i>aurata</i>	dicot tree	8	1	10
Moraceae	<i>Ficus</i>	<i>grossularioides</i>	dicot tree	0	0	5
Moraceae	<i>Ficus</i>	<i>uncinata</i>	dicot tree	1	0	0
Moraceae	<i>Ficus</i>	<i>sp. 3</i>	dicot tree	3	1	0
Moraceae	<i>Ficus</i>	<i>sp. 7</i>	dicot tree	2	0	1
Moraceae	<i>Ficus</i>	<i>sp. 10</i>	dicot tree	1	0	0
Moraceae	<i>Ficus</i>	<i>sp. 20</i>	dicot liana	1	0	0
Moraceae	<i>Ficus</i>	<i>sp. 24</i>	dicot liana	3	0	0
Myrsinaceae	<i>Embelia</i>	<i>javanica</i>	dicot liana	5	1	0
Myrsinaceae	<i>Embelia</i>	<i>sp. 2</i>	dicot liana	0	0	1
Myrsinaceae	<i>Embelia</i>	<i>sp. 3</i>	dicot liana	1	0	0
Piperaceae	<i>Piper</i>	<i>aduncum</i>	dicot tree	0	0	1

Appendix 3. Continued.

Family	Genus	Species	Plant type	N0	N1	N2
Rubiaceae	<i>Hedyotis</i>	<i>congesta</i>	dicot herb	15	2	0
Rubiaceae	<i>Ochreinauclea</i>	<i>maingayi</i>	dicot tree	0	1	0
Rubiaceae	<i>Pertusadina</i>	<i>eurhyncha</i>	dicot tree	6	0	1
Rubiaceae	<i>Uncaria</i>	<i>barbata</i>	dicot liana	29	18	5
Rubiaceae	<i>Uncaria</i>	<i>borneensis</i>	dicot liana	13	2	12
Rubiaceae	<i>Uncaria</i>	<i>canescens</i>	dicot liana	5	4	15
Rubiaceae	<i>Uncaria</i>	<i>cordata</i>	dicot liana	30	12	9
Rubiaceae	<i>Uncaria</i>	<i>kunstleri</i>	dicot liana	19	3	4
Rubiaceae	<i>Uncaria</i>	<i>cf. elliptica</i>	dicot liana	1	0	0
Rubiaceae	<i>Uncaria</i>	<i>cf. lanosa var. ferrea</i>	dicot liana	0	0	1
Rubiaceae	<i>Uncaria</i>	<i>sp. 16</i>	dicot liana	5	1	1
Rubiaceae	<i>Urophyllum</i>	<i>arborescens</i>	dicot tree	11	2	0
Solanaceae	<i>Solanum</i>	<i>jamaicense</i>	dicot shrub	0	10	33
Ulmaceae s.l.	<i>Trema</i>	<i>cannabina</i>	dicot tree	0	1	1
Ulmaceae s.l.	<i>Trema</i>	<i>tomentosa</i>	dicot tree	0	1	20
Vitaceae	<i>Cayratia</i>	<i>japonica</i>	dicot liana	0	0	3
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 1</i>	monocot herb	1	0	1

Appendix 4

List of all species having five stems exceeding 1.3 m in height in at least one 10 × 20 m subplot of the unburnt forest in Sungai Wain (this subplot either randomly located or in canopy gaps within the 450 ha plot). After each family, genus and species name respectively number of random subplots (N0, n = 40) and subplots in canopy gaps (NG, n = 25) having at least five stems exceeding 1.3 m in height of the corresponding species.

Family	Genus	Species	N0	NG
Alangiaceae	<i>Alangium</i>	<i>ridleyi</i>	1	0
Anacardiaceae	<i>Gluta</i>	<i>wallichii</i>	2	0
Anacardiaceae	<i>Melanochyla</i>	<i>fulvinervis</i>	0	2
Ancistrocladaceae	<i>Ancistrocladus</i>	<i>tectorius</i>	0	2
Annonaceae	<i>Cyathostemma</i>	<i>excelsum</i>	1	0
Annonaceae	<i>Polyalthia</i>	<i>sumatrana</i>	2	0
Apocynaceae	<i>Parameria</i>	<i>laevigata</i>	5	0
Bombacaceae	<i>Durio</i>	<i>acutifolius</i>	5	1
Bombacaceae	<i>Durio</i>	<i>oxleyanus</i>	1	0
Burseraceae	<i>Dacryodes</i>	<i>rostrata</i>	14	3
Celastraceae	<i>Salacia</i>	<i>sp. 1</i>	1	0
Compositae	<i>Vernonia</i>	<i>arborea</i>	0	6
Connaraceae	<i>Agelaea</i>	<i>trinervis</i>	1	0
Connaraceae	<i>Ellipanthus</i>	<i>beccarii</i> var. <i>peltatus</i>	1	0
Connaraceae	<i>Rourea</i>	<i>sp. 12</i>	1	0
Convolvulaceae	<i>Erycibe</i>	<i>sp. 13</i>	1	0
Cucurbitaceae	<i>Trichosanthes</i>	<i>borneensis</i>	0	2
Cyperaceae	<i>Scleria</i>	<i>terrestris</i>	3	8
Dilleniaceae	<i>Dillenia</i>	<i>borneensis</i>	0	3
Dilleniaceae	<i>Tetracera</i>	<i>scandens</i>	0	4
Dilleniaceae	<i>Tetracera</i>	<i>sp. 10</i>	0	2
Dilleniaceae	<i>Tetracera</i>	<i>sp. 12</i>	1	0
Dipterocarpaceae	<i>Cotylelobium</i>	<i>melanoxylum</i>	5	0
Dipterocarpaceae	<i>Dipterocarpus</i>	<i>confertus</i>	17	1
Dipterocarpaceae	<i>Dipterocarpus</i>	<i>cornutus</i>	1	0
Dipterocarpaceae	<i>Hopea</i>	<i>mengerawan</i>	1	0
Dipterocarpaceae	<i>Hopea</i>	<i>rudiformis</i>	1	0
Dipterocarpaceae	<i>Shorea</i>	<i>laevis</i>	16	11
Dipterocarpaceae	<i>Shorea</i>	<i>lamellata</i>	1	0
Dipterocarpaceae	<i>Shorea</i>	<i>ovalis</i>	4	3
Dipterocarpaceae	<i>Shorea</i>	<i>parvifolia</i>	1	0
Dipterocarpaceae	<i>Shorea</i>	<i>smithiana</i>	4	0
Dipterocarpaceae	<i>Vatica</i>	<i>odorata</i> ssp. <i>odorata</i>	1	0
Dipterocarpaceae	<i>Vatica</i>	<i>umbonata</i>	8	0
Euphorbiaceae	<i>Antidesma</i>	<i>neurocarpum</i>	1	0
Euphorbiaceae	<i>Aporosa</i>	<i>lunata</i>	3	0
Euphorbiaceae	<i>Aporosa</i>	<i>nitida</i>	1	0
Euphorbiaceae	<i>Aporosa</i>	<i>subcaudata</i>	4	0
Euphorbiaceae	<i>Baccaurea</i>	cf. <i>tetrandra</i>	5	0
Euphorbiaceae	<i>Baccaurea</i>	<i>minor</i>	1	0
Euphorbiaceae	<i>Cleistanthus</i>	<i>erycibifolius</i>	3	0
Euphorbiaceae	<i>Cleistanthus</i>	<i>myrianthus</i>	1	0
Euphorbiaceae	<i>Drypetes</i>	<i>kikir</i>	6	0

Appendix 4. Continued.

Family	Genus	Species	N0	NG
Euphorbiaceae	<i>Endospermum</i>	<i>diadenum</i>	0	1
Euphorbiaceae	<i>Fahrenheitia</i>	<i>pendula</i>	3	0
Euphorbiaceae	<i>Macaranga</i>	<i>bancana</i> (syn. <i>triloba</i>)	0	6
Euphorbiaceae	<i>Macaranga</i>	<i>conifera</i>	0	8
Euphorbiaceae	<i>Macaranga</i>	<i>gigantea</i>	0	10
Euphorbiaceae	<i>Macaranga</i>	<i>hypoleuca</i>	0	3
Euphorbiaceae	<i>Macaranga</i>	<i>lowii</i>	29	13
Euphorbiaceae	<i>Macaranga</i>	<i>motleyana</i>	0	1
Euphorbiaceae	<i>Macaranga</i>	<i>pearsonii</i>	0	1
Euphorbiaceae	<i>Macaranga</i>	<i>trichocarpa</i>	0	5
Euphorbiaceae	<i>Omphalea</i>	<i>bracteata</i>	3	0
Guttiferae	<i>Cratoxylum</i>	<i>formosum</i>	0	1
Labiatae	<i>Teijsmanniodendron</i>	<i>coriaceum</i>	1	0
Lauraceae	<i>Eusideroxylon</i>	<i>zwageri</i>	1	0
Lecythidaceae	<i>Barringtonia</i>	<i>macrostachya</i>	2	0
Leguminosae	<i>Crudia</i>	<i>reticulata</i>	2	0
Leguminosae	<i>Fordia</i>	<i>splendidissima</i>	22	10
Leguminosae	<i>Spatholobus</i>	<i>ferrugineus</i>	0	3
Leguminosae	<i>Spatholobus</i>	<i>sp. 1</i>	13	0
Leguminosae	<i>Spatholobus</i>	<i>sp. 3</i>	1	0
Leguminosae	<i>Spatholobus</i>	<i>sp. 4</i>	1	1
Melastomataceae	<i>Dissochaeta</i>	<i>gracilis</i>	0	4
Melastomataceae	<i>Macrolenes</i>	<i>sp. 1</i>	0	1
Melastomataceae	<i>Pternandra</i>	<i>azurea</i>	1	0
Melastomataceae	<i>Pternandra</i>	<i>coerulescens</i>	1	3
Melastomataceae	<i>Pternandra</i>	<i>rostrata</i>	4	0
Meliaceae	<i>Aglaia</i>	<i>forbesii</i>	4	0
Meliaceae	<i>Aglaia</i>	<i>simplicifolia</i>	3	0
Meliaceae	<i>Aglaia</i>	<i>tomentosa</i>	3	0
Meliaceae	<i>Reinwardtiodendron</i>	<i>humile</i>	1	0
Moraceae	<i>Ficus</i>	<i>aurata</i>	0	1
Moraceae	<i>Ficus</i>	<i>sp. 5</i>	1	0
Myristicaceae	<i>Knema</i>	<i>pallens</i>	1	0
Myristicaceae	<i>Knema</i>	<i>percoriacea</i>	3	3
Myristicaceae	<i>Knema</i>	<i>psilantha</i>	2	0
Myristicaceae	<i>Knema</i>	<i>pubiflora</i>	1	0
Myristicaceae	<i>Myristica</i>	<i>gigantea</i>	1	0
Myrsinaceae	<i>Ardisia</i>	<i>korthalsiana</i>	7	0
Myrsinaceae	<i>Embelia</i>	<i>javanica</i>	0	1
Myrsinaceae	<i>Embelia</i>	<i>sp. 2</i>	0	3
Myrsinaceae	<i>Embelia</i>	<i>sp. 3</i>	0	4
Myrsinaceae	<i>Maesa</i>	<i>ramentacea</i>	0	5
Myrtaceae	<i>Eugenia</i>	<i>caudatilimba</i>	1	0
Myrtaceae	<i>Syzygium</i>	<i>napiforme</i>	2	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 1</i>	1	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 2</i>	1	0
Myrtaceae	<i>Syzygium</i>	<i>sp. 5</i>	1	0
Myrtaceae	<i>Syzygium</i>	<i>tawahense</i>	3	0
Olacaceae	<i>Strombosia</i>	<i>ceylanica</i>	1	0
Palmae	<i>Calamus</i>	<i>fimbriatus</i>	1	0
Palmae	<i>Calamus</i>	<i>flabellatus</i>	0	1

Appendix 4. Continued.

Family	Genus	Species	N0	NG
Palmae	<i>Calamus</i>	<i>marginatus</i>	0	1
Palmae	<i>Calamus</i>	<i>nigricans</i>	1	0
Palmae	<i>Ceratolobus</i>	<i>concolor</i>	1	0
Palmae	<i>Ceratolobus</i>	<i>subangulatus</i>	1	0
Palmae	<i>Daemonorops</i>	<i>sabut</i>	0	2
Palmae	<i>Korthalsia</i>	<i>echinometra</i>	1	0
Palmae	<i>Korthalsia</i>	<i>furtadoana</i>	0	1
Polygalaceae	<i>Xanthophyllum</i>	<i>affine</i>	2	0
Rubiaceae	<i>Hedyotis</i>	<i>congesta</i>	1	8
Rubiaceae	<i>Ixora</i>	<i>sp. 6</i>	1	0
Rubiaceae	<i>Ixora</i>	<i>sp. 1</i>	4	0
Rubiaceae	<i>Lasianthus</i>	<i>pterospermus</i>	1	0
Rubiaceae	<i>Ochreinauclea</i>	<i>maingayi</i>	0	2
Rubiaceae	<i>Porterandia</i>	<i>anisophylla</i>	0	2
Rubiaceae	<i>Psychotria</i>	<i>viridiflora</i>	0	1
Rubiaceae	<i>Tarenna</i>	<i>cumingiana</i>	0	1
Rubiaceae	<i>Uncaria</i>	<i>barbata</i>	0	9
Rubiaceae	<i>Uncaria</i>	<i>borneensis</i>	0	3
Rubiaceae	<i>Uncaria</i>	<i>canescens</i>	0	2
Rubiaceae	<i>Uncaria</i>	<i>cf. elliptica</i>	0	2
Rubiaceae	<i>Uncaria</i>	<i>cordata</i>	0	5
Rubiaceae	<i>Uncaria</i>	<i>kunstleri</i>	0	3
Rubiaceae	<i>Uncaria</i>	<i>longiflora</i>	0	1
Rubiaceae	<i>Uncaria</i>	<i>sp. 16</i>	1	0
Rubiaceae	<i>Urophyllum</i>	<i>arborescens</i>	2	2
Rutaceae	<i>Luvunga</i>	<i>sp. 1</i>	1	0
Rutaceae	<i>Melicope</i>	<i>glabra</i>	0	1
Sapindaceae	<i>Lepisanthes</i>	<i>amoena</i>	1	0
Sapindaceae	<i>Lepisanthes</i>	<i>senegalensis</i>	6	0
Sapotaceae	<i>Madhuca</i>	<i>kingiana</i>	23	2
Sapotaceae	<i>Madhuca</i>	<i>palembanica</i>	2	0
Sapotaceae	<i>Madhuca</i>	<i>pallida</i>	1	0
Sapotaceae	<i>Payena</i>	<i>lucida</i>	1	0
Sterculiaceae	<i>Heritiera</i>	<i>sumatrana</i>	1	0
Thymelaeaceae	<i>Gonystylus</i>	<i>affinis</i>	5	0
Malvaceae	<i>Pentace</i>	<i>laxiflora</i>	2	0
Trigoniaceae	<i>Trigonistrum</i>	<i>hypoleucum</i>	1	0
Ulmaceae s.l.	<i>Gironniera</i>	<i>nervosa</i>	9	5
Violaceae	<i>Rinorea</i>	<i>sp. 1</i>	1	0
Vitaceae	<i>Ampelocissus</i>	<i>rubiginosa</i>	0	2
Vitaceae	<i>Ampelocissus</i>	<i>winkleri</i>	0	4
Vitaceae	<i>Pterisanthes</i>	<i>sp. 1</i>	1	0
Zingiberaceae s.l.	<i>Amomum</i>	<i>sp. 18</i>	1	0
Zingiberaceae s.l.	<i>Elettaria</i>	<i>sp. 32</i>	2	0
Zingiberaceae s.l.	<i>Etlingera</i>	<i>sp. 3</i>	6	0
Zingiberaceae s.l.	<i>Etlingera</i>	<i>sp. 31</i>	1	0
Zingiberaceae s.l.	<i>Hornstedtia</i>	<i>cf. reticulata</i>	1	2
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 4</i>	1	0
Zingiberaceae s.l.	<i>Indet</i>	<i>sp. 5</i>	2	0
Zingiberaceae s.l.	<i>Plagiostachys</i>	<i>sp. 35</i>	1	0

RINGKASAN

Meningkatnya pengrusakan hutan yang dramatis di kawasan tropis diakibatkan oleh perpaduan dari aktivitas manusia dan kebakaran hutan. Selama peristiwa osilasi selatan El-Niño, area yang luas telah dimusnahkan oleh kebakaran hutan. Telah dipertunjukkan bahwa kebakaran api yang paling luas sudah terjadi di Indonesia di propinsi Kalimantan Timur, di mana 3.5 juta hektar tumbuh-tumbuhan mengalami kerusakan di tahun 1982–1983, dan 5.2 juta hektar di tahun 1998, yang mencakup 2.6 juta ha hutan. Sesuai dengan konsesi hutan dan perkebunan, taman nasional dan banyak lagi hutan penelitian lainnya juga sebagian besar atau seluruhnya musnah. Pertanyaan yang sekarang muncul adalah apakah area hutan yang pernah terbakar masih mempunyai cukup keanekaragaman hayati untuk mengukuhkan pemeliharaan status konservasi hutan yang pernah terbakar. Sejauh ini, data pada dampak dari kebakaran api pada keanekaragaman jenis telah menjadi langka. Saya telah meneliti dua tipe hutan yang pernah terbakar secara detil dan membandingkannya dengan salah satu minoritas hutan tidak terbakar dataran rendah di Kalimantan Timur. Penekanan tertentu ditempatkan pada keanekaragaman dan struktur hutan di skala bentang alam.

Studi lapangan dilaksanakan di dua cadangan hutan dibagian utara kota Balikpapan.

Keanekaragaman tumbuhan yang sudah dipelajari di hutan yang tidak terbakar dan hutan penelitian Sungai Wain yang pernah sekali terbakar, dan pada hutan penelitian Wanariset yang dua kali terbakar. Dari Januari sampai Mei tahun 2000, ketiga hutan ini dicatat menggunakan metode yang sama: semua tumbuhan terestrial diambil sampelnya dan diidentifikasi di dalam dua tempat 40 petak-petak kecil diletakkan secara acak yang ditempatkan dalam 18 plot dan di dalam 450 hektar. Selain dari pada survei lapangan, sampel tanah juga diteliti sebagai kandungan benih perkecambahan.

Kepadatan pohon-pohon kecil tiga kali lebih besar di hutan yang dua kali terbakar di areal penelitian Wanariset di bandingkan dengan areal hutan penelitian Sungai Wain yang terbakar hanya satu kali. Penemuan antara kedua hutan yang pernah terbakar ini akan mencerminkan kepadatan pohon penabur benih di dalam tanah penyimpanan bibit benih sebelum kebakaran tahun 1998. Di areal penelitian Wanariset kemudian di dominasi oleh tumbuhan pionir sebagai hasil kebakaran di awal tahun 1982–1983, sedang tumbuhan seperti itu jarang ditemukan di hutan yang tidak terbakar di Sungai Wain. Karena jenis pionir membentuk lahan penyimpanan benih dengan baik, sehingga banyak tumbuhan kecil kemungkinan telah ada di atas lapisan tanah di areal penelitian Wanariset. Pada kedua hutan tersebut, kebakaran belum menunjukkan kerusakan hutan secara permanen.

Kekayaan jenis ditaksir pada skala petak-petak kecil (0.02 ha) dan di skala bentang alam (450 ha). Pada skala petak-petak kecil, kekayaan jenis lebih rendah di kedua hutan yang pernah terbakar dibandingkan pada hutan tidak terbakar, sedang pada skala bentang

alam, perbedaan di antara kedua lokasi jauh lebih kecil. Hasil penelitian menunjukkan bahwa skala penilaian betul-betul menentukan perbedaan dalam kekayaan jenis di antara ke tiga hutan. Usaha untuk menyediakan bukti lebih lanjut tentang dampak dari peristiwa gangguan pada skala lebih besar kebakaran api seperti tahun 1997–1998 perlu memusatkan perhatian pada skala besar dalam penilaian biodiversitas dibandingkan dengan replikasi penelitian pada skala kecil, karena hanya studi pada skala besar yang dapat menggambarkan keseluruhan. Jumlah angka-angka jenis tidak jauh lebih rendah di hutan yang pernah terbakar dan perbedaan yang utama bahwa jenis mayoritas terjadi pada kepadatan yang lebih rendah dibandingkan pada hutan tidak terbakar.

Sisa-sisa dari hutan yang tidak terbakar sering diamati di area hutan yang pernah terbakar dan telah dipertanyakan sampai sejauh mana tingkat integritas biotiknya dirawat selama rangkaian kebakaran. Pada lokasi studi hutan yang pernah terbakar, area yang tidak terkena api masih dengan mudah dapat dikenali dan mencakupi kurang lebih 10% keseluruhan area. Hampir semua yang ditemukan berada di pinggiran sungai kecil dan daerah curahan air hujan. Akibat dari arus yang membentuk suatu hubungan yang terintegrasi di bentang alam hutan yang terbakar, maka sisa hutan yang tidak terbakar tidak meliputi fragmen terisolasi, namun merupakan tambalan yang secara efektif saling menghubungkan petak-petak kecil. Komposisi dari jaringan hutan tidak terbakar dipelajari dengan penggolongan semua jenis sebagai berlimpah atau jarang. Kedua kelas ini nampak mencerminkan tingkatan yang tinggi tentang dua jenis ekologi tumbuhan, sebagai paling berlimpahnya jenis sering dikenal sebagai jenis pionir, sementara jarang terjadi pada yang sedikit jenisnya. Di kedua hutan yang pernah terbakar, suatu perbandingan menyangkut hubungan hutan tidak terbakar dengan hutan terbakar dengan menggunakan data matriks menunjukkan bahwa mayoritas dari semua jenis tampak di dalamnya dan itu banyak jenis yang langka, bahkan terbatas. Jaringan hutan yang tidak terbakar menjadi suatu kontribusi penting bagi keseluruhan keanekaragaman tumbuhan di hutan yang pernah terbakar. Pada hutan penelitian Wanariset terbakar dua kali setelah 18 tahun, jaringan masih terlihat setelah awal kebakaran tahun 1982–1983. Ini memperlihatkan bahwa hutan dapat bertahan setelah kebakaran ulang dan komposisinya telah menjadi rangkain yang terus menerus selama kebakaran api. Karena banyak jenis yang berkurang secara kritis, maka dengan mencegah kebakaran yang lebih besar dalam jaringan ini, mungkin akan dapat memfasilitasi dengan baik di pemulihan masa depan pada matriks kawasan yang terbakar.

Pengamatan kekuatan regenerasi yang tinggi pada hutan yang terbakar nampaknya bertentangan dengan penemuan di dalam dokumen yang menggambarkan kebakaran ulang yang menjadi terus meningkat bersifat merusak dan mengakibatkan pengundulan hutan yang permanen. Faktor utama yang menjelaskan penemuan yang berbeda ini adalah frekuensi kebakaran. Jika kebakaran api terjadi pada frekuensi yang tinggi, tumbuhan pionir ini akan punah sebelum masa reproduksi. Tempat penyimpanan bibit benih berkurang dengan terjadinya kebakaran ulang dan titik api yang berikut akan mempunyai struktur yang lebih terbuka. Selama musim kemarau, semakin banyak lahan yang terbuka menjadi lebih peka terhadap kebakaran yang berikut. Kebakaran juga akan lebih sering dan bahkan dapat menghancurkan pohon-pohon besar dan sisa-sisa hutan tidak terbakar. Umpan balik positif ini dalam dinamika kebakaran akhirnya

akan mendorong kearah penggundulan hutan secara permanen. Bagaimanapun, jika kebakaran terjadi pada frekuensi yang lebih rendah, tumbuhan pionir menjadi reproduktif dan mengisi penyimpanan bibit benih sebelum kebakaran berikutnya. Tumbuhan pionir yang tertinggal berikut tidak akan mempunyai suatu struktur yang lebih terbuka dan penggundulan hutan tidak akan terjadi. Nampaknya posisi titik api yang tertinggal kemudian akan tetap lembab selama musim kemarau untuk mencegah kebakaran yang berkepanjangan yang memusnahkan pohon-pohon tinggi dan sisa-sisa hutan yang tidak terbakar. Gambaran pengindraan jauh dan tambahan studi lapangan dapat menyediakan bukti bahwa kebakaran hutan lainnya di Kalimantan Timur juga masih mempunyai suatu keanekaragaman tumbuhan yang tinggi. Hubungan hutan tidak terbakar, sisa-sisa pohon yang tinggi dan kecambah pohon, kembali banyak terlihat di hutan yang pernah terbakar di sekitar teluk Balikpapan, di PT.ITCI, Bukit Bankirai, Bukit Soeharto, Taman Nasional Kutai dan sampai ke utara kawasan kebakaran dekat Sangkulirang. Ini merupakan suatu indikasi yang kuat bahwa kebanyakan dari keanekaragaman tumbuhan juga dikonservasi di kawasan tersebut dan mungkin pada banyak lokasi-lokasi kebakaran lainnya di Kalimantan Timur.

Di dalam ketidakhadiran gangguan lebih lanjut kebakaran di hutan hujan tropis di Kalimantan Timur, sepertinya dapat memelihara kebanyakan dari kesempurnaan keanekaragaman jenis tumbuhan tinggi. Pendapat saya, ini betul-betul mendukung perlindungan spesies dari aktivitas manusia yang bersifat merusak. Aktivitas seperti itu nampak telah sangat meningkat sejak kebakaran api tahun 1997–1998 di Kalimantan Timur. Penebangan liar, pengambilan kayu mati yang bersifat komersil, sangat dipengaruhi oleh peraturan pemerintah dan sekarang telah menjadi suatu ancaman untuk memperbaharui hutan yang pernah terbakar sebagai akibat dari penggunaan mesin berat dan pemotongan pohon hidup secara tidak sah. Sering terjadinya kebakaran hutan berhubungan dengan reklamasi daratan, juga telah meningkat dan ini mempunyai potensi menjadikan penggundulan hutan secara permanen. Tetapi, saya bermaksud untuk menekan pandangan yang terlalu pesimistis hanya akan merangsang aktivitas manusia bersifat merusak yang lebih jauh karena akan menguatkan pendapat bahwa hutan yang telah rusak tidak perlu mendapat konservasi biodiversitas. Hasil studi ini menunjukkan bahkan setelah kerusakan yang diakibatkan oleh kebakaran, hutan hujan tropis masih dapat mempunyai keanekaragaman tumbuhan yang tinggi, tetapi harus disadari bahwa ancaman yang utama untuk keanekaragaman itu akan datang dari aktivitas manusia yang bersifat merusak.

SAMENVATTING

De combinatie van menselijke activiteiten en bosbranden heeft geleid tot een dramatische vernietiging van regenwoud in de tropen. Met name tijdens aan El Niño gerelateerde droogteperiodes zijn enorme oppervlaktes bos aangetast door vuur. De grootste bosbranden uit de menselijke geschiedenis hebben plaatsgevonden in Oost-Kalimantan, waar 3,5 miljoen ha vegetatie is verbrand in 1982–1983 en 5,2 miljoen in 1997–1998, waarvan 2,6 miljoen ha bos. Behalve bosconcessies en plantages zijn ook nationale parken en andere reservaten geheel of grotendeels aangetast. De vraag dient zich aan of verbrande regenwouden nog een voldoende hoge biodiversiteit herbergen om hun beschermde status te rechtvaardigen. Tot op heden zijn weinig gegevens verzameld over het effect van de branden op de biodiversiteit. Voor het in dit proefschrift gepresenteerde onderzoek zijn twee verbrande regenwouden in detail bestudeerd en vergeleken met één van de laatste laagland regenwouden in Oost-Kalimantan die nog niet zijn aangetast door branden of houtkap. Daarbij is vooral aandacht besteed aan de botanische diversiteit en de structuur van het bos op proefvlak- en landschapsniveau.

De veldstudie is uitgevoerd in twee bosreservaten ten noorden van de stad Balikpapan. In het Sungai Wain-reservaat werd de botanische diversiteit bestudeerd in onverbrand en eenmaal verbrand regenwoud, in het Wanariset-reservaat in tweemaal verbrand regenwoud. Van januari tot mei 2000 zijn deze drie bossen op exact gelijke wijze bestudeerd: alle terrestrische vaatplanten zijn bemonsterd en gedetermineerd in twee sets van veertig proefvlakken (10 × 20 m) die waren gelokaliseerd in gebieden van 18 ha en 450 ha. Daarnaast zijn bodemon monsters verzameld en op de abundantie van kiemkrachtige zaden onderzocht.

Voor beide verbrande bossen geldt dat de branden van 1998 nog niet tot een definitieve ontbossing hebben geleid. Ondanks dat er vrijwel geen kleine bomen het vuur overleefd hebben, bleken zich sindsdien toch weer jonge bomen te hebben gevestigd door de kieming van zaden en door het herspruiten van de wortelstelsels van bovengronds afgestorven bomen. Opvallend is dat de dichtheid van jonge bomen drie keer hoger was in het tweemaal verbrande bos van Wanariset dan in het eenmaal verbrande bos van Sungai Wain. Dit verschil lijkt het gevolg te zijn van de beschikbaarheid van zaden in de bodem voordat de branden van 1998 plaatsvonden. Toen werd het Wanariset bos namelijk gedomineerd door pionierbomen als gevolg van de branden in 1982–1983, terwijl zulke bomen maar weinig voorkwamen in Sungai Wain. Aangezien pionierbomen een grote zaadvoorraad in de bodem hebben, is het aannemelijk dat er veel meer zaden van bomen beschikbaar waren in het Wanariset bos dan in Sungai Wain.

De soortenrijkdom is gekwantificeerd op de schaal van proefvlakken (0.02 ha) en op de schaal van het landschap (450 ha). Op de schaal van proefvlakken bleek de botanische diversiteit in de verbrande bossen beduidend lager dan in het onverbrande bos, maar op de schaal van het landschap waren de verschillen tussen de bossen veel kleiner. De

resultaten laten zien dat de schaal waarop de soortenrijkdom wordt bestudeerd van grote invloed is op de verschillen die worden gevonden tussen de drie bossen. Om de effecten te kwantificeren van een verstoring die op grote schaal plaatsvindt, zoals de bosbranden in Oost-Kalimantan, hebben studies op een grote schaal de voorkeur boven meer gedetailleerde studies op een kleinere schaal, aangezien alleen studies op een grote schaal het juiste totaalbeeld laten zien. De verbrande bossen hadden niet zozeer veel minder soorten dan de onverbrande bossen, maar het overgrote deel van de soorten was in veel kleinere dichtheden aanwezig.

Onverbrande bosrestanten zijn al vaker waargenomen in verbrande bossen maar tot op heden was nog niet bekend in hoeverre de botanische diversiteit hierin gehandhaaft blijft. In de verbrande bossen van deze studie bedekten zij ca. 10% van het onderzoeksgebied. Vrijwel alle onverbrande bosrestanten waren gelokaliseerd in de stroomvlakten van beken en rivieren. Aangezien deze waterlopen een geïntegreerd netwerk in het landschap vormen, zijn ook de onverbrande bosrestanten onderling goed met elkaar verbonden. De samenstelling van dit netwerk van onverbrande bosrestanten is bestudeerd door per onderzoekslokatie alle soorten in te delen in algemene en zeldzame soorten. Deze indeling lijkt in hoge mate een indeling in twee contrasterende ecologische typen te weerspiegelen, aangezien de meeste algemene soorten als pioniers worden beschouwd, terwijl dit maar voor weinig zeldzame soorten geldt. In beide verbrande bossen bleek het overgrote deel van de soorten in het onverbrande netwerk voor te komen terwijl veel van de zeldzame soorten zelfs helemaal beperkt waren tot dit netwerk. Hierdoor leveren de onverbrande bosrestanten een belangrijke bijdrage aan de totale botanische diversiteit van verbrande bossen. In het Wanariset bos heeft dit onverbrande netwerk al sinds de branden van 1982–1983 kunnen voortbestaan. Dit toont aan dat het netwerk meerdere branden kan overleven en dat de samenstelling onaangetast is gebleven tijdens de afgelopen 18 jaar. Aangezien de door de branden getroffen soorten hierin nog relatief veel voorkomen, is het goed mogelijk dat zij zich vanuit dit onverbrande netwerk opnieuw zullen vestigen in de verbrande delen van het landschap.

Het hier waargenomen grote herstelvermogen is oppervlakkig gezien in tegenspraak met diverse andere publicaties, waarin wordt geconstateerd dat opeenvolgende bosbranden steeds destructiever worden en uiteindelijk leiden tot definitieve ontbossing. De verklaring voor dit verschil lijkt in de frequentie van de bosbranden te zitten. Als bosbranden in hoge frequentie optreden, dan worden pionierbomen vernietigd voordat zij tot reproductie kunnen komen. Hierdoor neemt het aantal zaden van pionierbomen af met elke volgende brand en krijgen de opeenvolgende bosopstanden een steeds ijlere structuur. Tijdens perioden van droogte drogen deze opstanden dan steeds sterker uit en worden zij steeds kwetsbaarder voor nieuwe branden. De opeenvolgende branden zijn daardoor ook steeds intenser en vernietigen ook steeds vaker de onverbrande bosrestanten. Deze positieve terugkoppeling leidt uiteindelijk tot definitieve ontbossing. Echter, als bosbranden in lagere frequenties voorkomen, dan krijgen de pionierbomen de kans om hun zaadvoorraad weer aan te vullen voordat een volgende brand optreedt. Hierdoor zullen de bosopstanden na opeenvolgende branden niet steeds ijler worden en treedt er geen definitieve ontbossing op. Tijdens droge perioden blijven zulke opstanden bovendien vochtig genoeg om de vernietiging van het onverbrande bosnetwerk en zijn hoge diversiteit te voorkomen.

‘Remote sensing’-radarbeelden en aanvullende veldstudies geven een indicatie dat ook andere verbrande bossen in Oost-Kalimantan nog steeds een hoge botanische diversiteit herbergen. Netwerken van onverbrande bosrestanten, grote bomen die de branden overleefd hebben en herspruitende bomen bleken algemeen voor te komen in verbrande bossen rond de baai van Balikpapan, in de ITCI-concessie, Bukit Bankirai, Bukit Soeharto, Nationaal Park Kutai en tot in het noorden van de verbrande regio bij Sankulirang. Dit is een sterke aanwijzing dat ook in deze bossen het grootste deel van de botanische diversiteit nog behouden is gebleven. Mogelijk geldt dit ook voor veel andere verbrande bossen in Oost-Kalimantan.

Het lijkt aannemelijk dat de verbrande bossen van Oost-Kalimantan in staat zijn om het grootste deel van hun botanische rijkdom te behouden indien verdere verstoring uitblijft. Naar mijn mening dienen deze bossen dan ook beschermd te worden tegen vernietiging door menselijke activiteiten. Zulke activiteiten zijn sterk toegenomen sinds de branden van 1997–1998. Het oogsten van dode bomen wordt gestimuleerd door de overheid en is een bedreiging geworden voor het bosherstel door het gebruik van zware machines en het illegaal oogsten van levende bomen. Hoog-frequente branden die samengaan met ontginning zijn toegenomen en dreigen tot permanente ontbossing te leiden. Echter, een te negatief beeld leidt alleen maar tot verdere vernietiging van het regenwoud omdat het de indruk versterkt dat verstoorde bossen het niet waard zijn om te beschermen. De resultaten van deze studie tonen aan dat, zelfs na herhaalde verstoring door branden, tropische regenwouden een grote rijkdom aan planten kunnen herbergen. De grootste bedreiging voor deze botanische diversiteit komt niet zozeer van grootschalige branden als in 1997–1998, maar van de aanhoudende destructieve activiteiten die daarna plaatsvinden.

CURRICULUM VITAE

Karl August Otto Eichhorn werd op 9 augustus 1967 geboren te Zeist. In 1987 behaalde hij zijn Atheneum-diploma aan de Scholengemeenschap Schoonoord te Zeist, waarna hij begon met zijn Biologiestudie aan de Rijksuniversiteit Utrecht. Tijdens zijn studie heeft hij twee doctoraalstages gedaan. Onder begeleiding van dr. Jo Willems en dr. Roland Bobbink heeft hij onderzoek verricht naar de overlevingsstrategieën van kiemplanten in twee Zuid-Limburgse kalkgraslanden, samen met studiegenoot Rob de Jong. Daarna heeft hij onder begeleiding van dr. Renske Ek en dr. Marjon Jansen-Jacobs onderzoek verricht naar de biodiversiteit van kruiden en andere kleine groeivormen in de ondergroei van een tropisch regenwoud in Guyana. Naast deze stages heeft hij drie literatuurscripties geschreven, over de plantengeografische positie van het Ducke-reservaat in Brazilië, over het computerprogramma Linnaeus II en over hakhoutbossen in Engeland en Zuid-Limburg. Verder heeft hij in de periode van 1989 tot 1995 in totaal 13 assistentschappen gedaan in het universitair onderwijs, bij cursussen over flora, vegetatie, taxonomie, ecologie en landschap. Zijn doctoraal-diploma behaalde hij in februari 1996.

Sinds 1996 verricht hij voor de Vereniging Natuurmonumenten onderzoek naar de effecten van hakhoutbeheer op de flora van twee Zuid-Limburgse hellingbossen, vanaf 1997 samen met zijn vrouw Lia. Daarnaast heeft hij in 1996 aan de Universiteit Utrecht als gastmedewerker taxonomisch onderzoek verricht aan het geslacht *Crematosperma* van de Zuurzakfamilie (Annonaceae), onder begeleiding van Prof. dr. P.J.M. Maas.

In september 1997 begon hij aan zijn promotie-onderzoek bij het Rijksherbarium/Hortus Botanicus te Leiden, inmiddels de Leidse vestiging van het Nationaal Herbarium Nederland. Het onderzoek werd uitgevoerd in het kader van het NWO prioriteiten-programma 'Biodiversity in disturbed ecosystems'. Het onderzoek richtte zich eerst op het geslacht *Pipturus* van de Brandnetelfamilie (Urticaceae). Nadat een taxonomisch onderzoek was afgerond zou aansluitend populatiegenetisch onderzoek plaatsvinden in de Indonesische provincie Oost-Kalimantan. Dit onderzoek bleek echter onuitvoerbaar doordat de onderzoeksplanten te schaars voorkwamen in het door de branden van 1998 verwoeste landschap. Daarop besloot hij om het in dit proefschrift gepubliceerde onderzoek uit te voeren naar de botanische diversiteit van verbrand en onverbrand regenwoud. Bijzondere aandacht werd in dit onderzoek besteed aan diversiteitspatronen op landschapsniveau en het belang van netwerken van onverbrande bosrestanten voor het behoud van de diversiteit tijdens grootschalige branden.

Na afloop van zijn aanstelling in juli 2003, heeft hij het ecologisch adviesburo Eichhorn Ecologie opgericht. Sindsdien verricht hij in opdracht diensten als floristische inventarisatie, vegetatiekartering, ecologisch onderzoek, advies bij inrichting en beheer van natuurterreinen, visie-, plan- en beleidsondersteuning.

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