Aspects of Regeneration in Tropical Secondary Forests of Northeast Borneo Affected by Selective Logging, El Niño-induced Drought and Fire.

Eva Romell
Faculty of Forest Sciences
Department of Forest Ecology and Management
Umeå

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Cover: *Dipterocarpus caudiferus* is planted in a created gap (left). Assorted seedlings ready for planting are carried to the forest in a rattan backpack (right). Photos: Eva Romell

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Abstract

A large proportion of the world´s tropical rainforests are today secondary forests, a term encompassing forests in various degrees of degeneration. For the main traits of old-growth forests´ structures, species composition and ecosystem functions to recover, regeneration of non-pioneer tree species is essential. In the studies this thesis is based upon I addressed various aspects of regeneration, both natural and artificial, mainly in secondary forests of northeast Borneo subjected to selective logging in the early 1980´s followed by prolonged El Niño-induced drought and forest fires in 1982-83.

The field studies underlying this thesis included one survey of natural regeneration in transects and two experiments with artificial regeneration; gap creation with under-planting nursery raised tree seedlings and direct seeding. Forest floor light conditions in created gaps were measured as photosynthetic photon flux density and proportion canopy openness. Methods applied to analyze data were ordinations (NMS and MRPP), ANCOVA and general linear model ANOVA.

Based upon these results some general conclusions and implications for forest management are addressed for secondary forests with this type of disturbance history: Forest patches with remnant potential seed trees and a more intact canopy structure had more diversified tree species recruits and are therefore less demanding of artificial regeneration. In artificial gap creation a sub-canopy reduction would be the preferable method compared to girdling or felling pioneer canopy trees since the positive effect of sub-canopy treatments is longer lasting. Under-planted dipterocarp seedlings increase height growth in high-light environments while their survival appeared unaffected by light conditions, therefore a medium shade reduction would be preferable as this leads to only moderate release of competing vegetation. Direct seeding must be evaluated further before large scale application, especially the timing and species choice merits special attention.

Keywords: artificial gaps, canopy, direct seeding, forest floor light, lowland mixed dipterocarp forests, *Macaranga* spp., *Shorea* spp., sub-canopy, tree species recruitment, under-planting

Author's address: Eva Romell, Department of Forest Ecology and Management,
SLU, SE-901 83 Umeå, Sweden
E-mail: eva.romell@slu.se

Dedication

To everyone with curiosity and engagement, please read…

Contents

List of Publications

This thesis is based on work described in the following papers, which are referred to by the corresponding Roman numerals in the text:

I Romell, E., Hofgaard, A., Wilmann, B., Ilstedt, U. Tree seedling recruitment in lowland mixed dipterocarp forests after El Niño-induced drought, fire and selective logging. *Manuscript.*

II Romell, E., Hallsby, G., Karlsson, A. (2009). Forest floor light conditions in a secondary tropical rain forest after artificial gap creation in northern Borneo. *Agricultural and Forest Meteorology* 149: 929-937.

III Romell, E., Hallsby, G., Karlsson, A., Garcia, C. (2008). Artificial canopy gaps in a *Macaranga* spp. dominated secondary tropical rain forest – effects on survival and above ground increment of four under-planted dipterocarp species. *Forest Ecology and Management* 255: 1452-1460.

IV Romell, E. Direct seeding results can be severely affected by predation: A case study of three *Shorea* species and *Intsia palembanica* in a *Macaranga*-dominated secondary forest. *Manuscript.*

Papers II and III are reproduced with the permission of the publishers. For convenience, the studies described in Paper I-IV are referred to in the following text as Studies I-IV, respectively.

1. Introduction

1.1 Tropical secondary rain forests

Estimates of tropical forest cover vary depending on sources and classification (closed forest, fragmented forest etc.) and the methods used in different countries to estimate it (e.g. Grainger et al. 2008). The FAO (Anon. 2011) estimates that this type of vegetation covered slightly more than 4000 million hectares in 2010. Of this, an estimated 214 million hectares was in South-East Asia, although forest losses here amounted to ca. 2.4 million ha in the 1990s, and 0.9 million ha in the 2000s (Anon. 2011). The main causes of tropical deforestation are logging for timber harvesting, shifting and permanent agriculture, mining and hydroelectric schemes (Brown and Lugo 1990, Grainger et al. 1992). Shifting agriculture (also known as shifting cultivation) is a non-sedentary agricultural system, in which patches of forests are cleared, burned to obtain land for food production and then left for a period to cover (Malmer et al. 2005). Continuous shifting cultivation, with insufficient recover periods leads to progressive degradation of forests and soils (Goldammer and Seibert 1990, Malmer et al. 2005). Other causes of tropical deforestation include, according to Grainger et al. (1992), socio-economic factors (e.g. population growth and economic development), physical factors such as proximity of rivers and roads, distance from urban areas, topography and soil fertility) and government policies related to agriculture and forestry.

Climatic factors may also contribute to losses in tropical forest cover. Notably, El Niño-induced dry spells (Harger 1995a, Harger 1995b, Walsh 1996) make forests more susceptible to fire (Cochrane and Barber 2009, Langner and Siegert 2009). Land areas with tropical rain forests susceptible to El Niño droughts include the northeast of South-America, South-East

Asia and the Pacifics (Enfield 1992, Holmgren et al. 2001). Selectively logged forests in particular are prone to fire due to their fragmented canopies and generally high abundance of combustible material (dead stems and branches) on their floors (Goldammer and Seibert 1990). Furthermore, even when not followed by fire, drought poses a threat to tree survival and regeneration. Seedlings and saplings (Slik et al 2002) and trees (Condit et al. 1996) on drier locations such as ridges and upper slopes are especially vulnerable during dry spells.

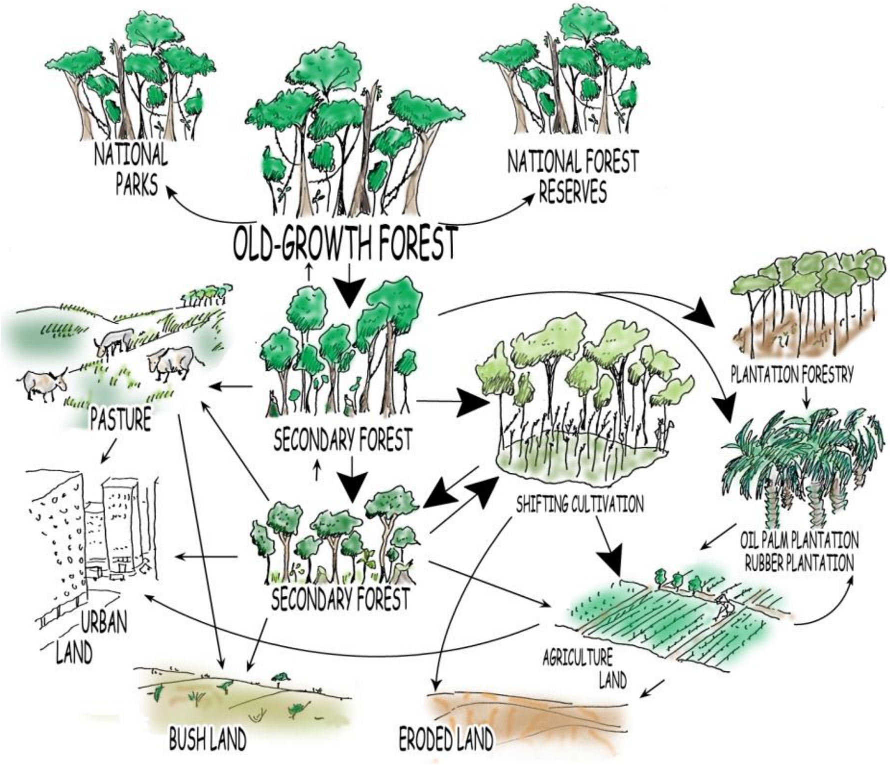

Figure 1. The landscape in many tropical countries today is a mosaic reflecting diverse land uses, some of which are leading to further land degradation and soil nutrient losses. Some arrows in the figure can be reversed, e.g. secondary forest can be converted to old-growth forest, but once the stages bush-land or eroded land have been reached forests are unlikely to recover naturally. With permission from Jan Falck (idea) and Olle Forshed (illustration).

The term tropical secondary forest is applied very broadly (Brown and Lugo 1990) to diverse kinds of vegetation, ranging (for instance) from successions in abandoned pasture (Finegan and Delgado 2000, Leopold and Salazar 2008) to forests disturbed by extracting timber of certain species or dimensions (Kammesheidt 2002). The stand structure and remaining biomass after selective logging are also highly variable, depending on original stand density and logging intensities (Tangki and Chappell 2008). Although logging techniques with reduced impact for tropical forestry have been found useful (Pinard et al. 2000, Sist et al. 2003), conventional commercial tropical forestry regimes typically include selective felling (Bruenig 1996), which causes considerable structural damage (Kartawinata 1981, Buschbacher 1990, Pinard et al. 2000). According to studies in Borneo by Cedergren (1996), the felling of a single large tree (≥60 cm in breast height diameter, dbh) destroys on average eight and damages another 13 trees of ≥ 10 cm dbh.

Tropical rainforests with high densities of merchantable timber, as found in lowlands of South-East Asia, have been intensely exploited during the last half century (Kellman and Tackaberry 1997). In contrast, tropical forests in other parts of the world have generally been harvested successively, starting with a few, highly valuable timber groups (e.g. *Swietenia mahogany* in the Neotropics), and continuing with repeated harvests of less valuable timber (Uhl and Vieria 1989). In both cases, if the logging intervals are too short, forestry will be unsustainable, leading to further degradation of the canopy structure and reductions in biological diversity (Meijard et al. 2005). Degraded secondary forests are frequently lost through transitions to other forms of land use (Whitmore 1998, Kammesheidt 2002), including shifting cultivation, tree plantations, agricultural fields or livestock husbandry (Brown and Lugo 1990; Figure 1).

Repeated logging and fire-based land utilization systems (shifting cultivation) can result in the transformation of former forest land to grasslands (Otsamo 2000a). In South East Asia, for example, the grass *Imperata cylindrica* has become very abundant due to its vegetative dispersal via fire-resistant rhizomes (Brook 1989). The natural transformation of grassland back to secondary forest is slow and often interrupted by new disturbances (Otsamo 2000b).

In this thesis, I use the terms old-growth and secondary forests. In old-growth forests no commercial logging has taken place, but small-scale slash-and-burn traces might have occurred. Other terms are pristine or virgin forest but strictly these terms refer to forests that have not been affected by any human activity at all, which is misleading since very few forest lands are really free from human influence (e.g. Josefsson 2009).

Forest disturbances such as logging and fire changes the tree species composition in tropical forests in several ways. For instance, the proportion of long-lived, slow-growing trees (non-pioneers) decreases (Curran et al. 1999, Ashton et al. 2001). In contrast, short-lived, fast-growing trees (here referred to as pioneers) are favored by high light intensities at the forest floor and thus rapidly colonize new open areas, and increase in abundance in them (Fox 1972, Whitmore 1998).

Non-pioneers are also called shade-tolerants since they are capable of persisting for long periods of dark suppression in seedling or sapling growth stages (Delissio et al. 2002). Pioneers, on the other hand, require high light environments, often with a canopy openness of at least 15% (Slik 2005) for establishment in new sites. Pioneers can also rapidly colonize tree fall gaps in old-growth forests (Manokaran and Swaine 1994, Bischoff et al. 2005) and are thus also found in old-growth forests, although less abundantly (Whitmore 1998).

In tropical Asia and parts of Africa pioneers of the genus *Macaranga* are common or even dominant in secondary forests (Goldammer 1996, Hjerpe et al. 2001, Slik et al. 2002), especially after repeated fires (Slik and Eichorn 2003). This is in large part due to their growth strategies as early, often very dominant colonizers, which frequently allows them to form young, even-aged stands with homogenous canopies rapidly (Guarigata and Ostertag 2002, Finegan 1996). *Cecropia* spp. (Urticaceae) display similar growth strategies and are similarly abundant in disturbed forests in the Neotropics, i.e. tropical parts of Central and South America (Finegan 1992). Furthermore, pioneers in tropical south-east Asia (and elsewhere) produce seeds substantially more frequently, and in much greater numbers, than non-pioneers (Whitmore 1998).

Conceptual models of secondary successions have been presented by several authors, e.g. Buschbacher (1990), Finegan (1996) and Ashton et al. (2001). According to these models, four major phases can be distinguished: 1) initial colonization by herbs, shrubs and climbers; 2) the growth of, and formation of a main canopy by, pioneer trees; 3) replacement of short lived-pioneers by long-lived pioneers and non-pioneers; 4) gradual replacement of the canopy by non-pioneers. The time required for a secondary forest to recover its original structure and species composition may reflect previous disturbance (Brown and Lugo 1990, Kammesheidt 2002). Other important factors for forest recovery are residual trees (seed sources), seedling banks, soil seed banks, the presence of sprouting trees or stumps, and the proximity of old-growth or species-rich secondary forests in the surrounding landscape from which species can spread (Aide et al. 2000, Sayer et al. 2004, Arroyo-Mora et al. 2005). Both species initiation (see, for instance, Guarigata and Ostertag 2002) and primary production (e.g. Bischoff et al. 2005) are usually high during the initial 5-20 years after disturbance. For example, Tang et al. 2010 found the annual mean litterfall to be 52% higher in a secondary forest than in old-growth forest in Xishuangbanna, a sub-tropical region of China.

Sayer et al. (2004) and Lamb et al. (2005) claim that secondary forests can recover through natural succession if protected and not repeatedly disturbed by events such as logging and fire. However, according to studies in tropical America the return of tree species characterizing native old-growth forests can be relatively slow (Aide et al. 2000, Leopold and Salazar 2008). There may also be marked variations in regeneration capacity, depending on severity and timing of disturbances, in particular if disturbances are repeated within relatively short time-span (e.g. Slik et al. 2002, Slik and Eichorn 2003).

Forest fires in the under-storey and sub-canopy layers generally destroy nearly all seedlings, saplings and small trees, together with dormant seeds in the topsoil layer (van Nieuwstadt et al. 2001), while selective logging affects single trees, which may be of either rare or common species (e.g. Forshed 2006). In addition, fire may more strongly promote the rapid establishment and high dominance of a single species or genus, resulting in relatively uniform, even-aged stands (e.g. Hjerpe et al. 2001), and according to Lamb et al. (2005), the most common absentees in tropical secondary forests are large-fruited species due to the absence of seed vectors.

As pointed out by Finegan and Delgado (2000), few studies have described tropical secondary forests beyond the initial stages of pioneer successions, possibly because tropical secondary forests are often subjected to continuous degradation (see Figure 1), which reduces possibilities for long-term monitoring of their successions. In addition, conservation interests have mainly focused on old-growth forests (Meijard et al. 2005) and, according to Arroyo-Mora et al. (2005), in studies of forest fragmentation more attention has been paid to analyzing deforestation processes than to describing secondary successions.

1.2 Restoration of secondary forests

Secondary forests may recover naturally if forest soils, canopy structure and the surrounding landscape are not too degraded. Examples of recovery through natural regeneration have been documented in Brazil (Buschbacher and Serrao 1988) and Costa Rica (Arroyo-Mora et al. 2005). Silvicultural treatments, for example stem and weed reduction may be beneficial for naturally recruited seedlings and saplings since this improves under-storey light conditions and reduces competition (e.g. Wyatt-Smith 1995). Methods that can improve seedling establishment after seed fall could be mild soil scarification (e.g. Kennedy and Swaine 1992).

Trees retained after selective logging are important seed sources for regeneration of all species which can not be stored in soil seed banks. In lowland mixed dipterocarp forests these species are mainly non-pioneers (e.g. Chin 1975). In addition, many of these species have irregular seed production (Richards 1996, Whitmore 1998), in particular forests of south-east Asia host many tree species which synchronize reproduction into mast fruit spells (Fox 1972, Ashton 1998), often induced by pro-longed El Niño-induced droughts (Curran et al. 1999, Curran and Webb 2000).

The irregular occurrence of mast seed production, which contributes to an important part of non-pioneer tree recruits, thus results in cohorts with different abundance and species composition between years. As many non-pioneer tree species have the ability to persist shade for ten years or even more (Ashton 1998, Delissio 2002) the seedling stock (in forests with natural dynamics) can remain until next heavy seed rain, even if individuals gradually die-off (Ashton et al. 2001). In forests with high disturbance-related seedling and sapling mortality, remnant trees of species with short-distance seed dispersal are hypothesized to be important for new trees to recruit.

If the natural regeneration is limited, active restoration efforts can accelerate forest recovery (Kammesheidt 2002, Lamb et al. 2005). Such efforts improve the value of degraded forest lands, which may indirectly prevent transition to other kinds of land use (agriculture, plantations etc.) in regions where forest cover is strongly pushed behind by agriculture or industrial demands (Buschbacher 1990).

In tropical forestry, methods used to increase the populations of important timber trees include *enrichment planting* (Appanah and Weinland 1993, Wyatt-Smith 1995), in which absent commercial tree species are raised in nurseries and subsequently planted in secondary forests. The two main techniques for this are *gap planting* (Anderson 1951, 1953, Ramos and del Amo 1992) in existing or created gaps and *line planting* in cleared strips (Lamb 1969, Montagini 1997). Enrichment planting can also be applied to enhance tree species diversity by planting "old-growth forest species" (non-pioneers) that do not readily regenerate naturally (Lamb 1998, Lamb et al. 2005). While line-planting is an established method (Lamb 1969, Montagini 1997, Bebber et al. 2002, Appanah and Weinland 1993), gap-planting is still at an experimental stage, but it provides much greater resemblance to natural gap dynamics than planting in regularly spaced lines (Denslow 1987). Gap creation techniques could also be applied to stimulate the natural regeneration of non-pioneer species by reducing above-ground competition from herbs, climbers and trees. Successful applications of enrichment planting for restoring tropical secondary forests in both Brazil (Peña-Claros et al. 2002) and Vietnam (van Kuijk 2008), by line-planting in both cases, have been documented.

Another method that is used to restore degraded forest lands is direct seeding (e.g. Florentine and Westbrooke 2004). Direct seeding has not been very frequently used in tropical forest restoration programmes (e.g. Appanah and Weinland 1993). Although, a few studies are mentioned here; Sun et al. (1995) and Pinard et al. (1996) performed trials with direct seeding of pioneer tree species in heavily degraded sites in attempts to establish a canopy under which non-pioneers can gradually establish, see also Engel and Parotta (2001).

Curran and Leighton (2000) distributed seeds of non-pioneer species to germinate underneath a canopy and found that predation losses were higher in secondary compared to old-growth forests.

A potential problem in regeneration measures is the fact that many non-pioneer tree species produce recalcitrant seeds (e.g. Meijer and Wood 1964, Cockburn 1975) which cannot be stored. Direct seeding could be an alternative to planting in periods of heavy seed rains to use the seed surplus when seed supplies exceed the capacity of tree seedling nurseries. However, heavy seed rain usually attract seed predators but according to Janzen (1970) and Conell (1971) heavy and synchronized mast fruiting will satiate predators allowing at least parts of the tree species populations to germinate and establish.

1.3 Regeneration and forest floor light climate

Forest floor light is an important limiting factor for establishment, growth and survival of tree seedlings (Denslow 1987, Rijkers 2000b), unregarded whether these are naturally regenerated (Whitmore 1998) or planted (Ådjers et al. 1995). However, planted seedlings fostered in more high-light environments in plant nurseries may be less resistant to persist long periods of shade (Ashton and de Zoysa 1989) whereas many naturally regenerated non-pioneer species can persist long periods of low-light levels (e.g. Delissio et al. 2002). One obstacle with creating high-light environments to improve plant growth in tropical humid habitats is that this will also improve recuperation of shrubs, ferns, ginger, grasses and climbers, which can inhibit tree seedling regeneration (Appanah and Weinland 1993, Wyatt-Smith 1995). If forest canopies are dense, on the other hand, shade may retard seedling growth.

Non-pioneer trees adapted to survive long periods of suppression in their seedling stage must not necessarily be shade demanders, rather their capacity to persist shade give them a competitive benefit in old-growth tropical forests where light levels under closed canopies can be very low; as little as 2% of the total incoming light may reach the floor according to measurements by Raich (1989) and Rich et al. (1993). However, according to Montgomery and Chazdon (2001), the availability of light at the forest floor level is even lower in secondary forests due to their higher densities of sub-canopy and under storey vegetation. It would be logical to assume that a more permeable main canopy in single-storied early succession forests with high abundance of pioneer trees allow sub-canopy vegetation to thrive and therefore increase in densities. But, as emphazised by Montgomery and Chazdon (2001) light climate is complicated, both to predict and relate to different height strata, and even if the diurnal average light transmission is relatively low at the forest floor level, sun flecks - brief, intense light influxes through small openings in the canopy and sub-canopies (Chazdon and Fetcher 1984) can provide substantial photosynthetic inputs for individual seedlings and saplings (Chazdon and Pearcy 1991, Rijkers et al. 2000b, Leakey et al. 2005).

In artificial regeneration by planting nursery-raised seedlings, creating canopy- and/or sub-canopy gaps has similarities to natural gaps dynamics (e.g. see Richards 1996, Whitmore 1998) where seedlings establish under canopies and height growth is induced after a tree fall. There are two lines of reasoning here; i) sub-canopy could be dense in secondary forests and a reduction of stems and foliage would improve the light climate and reduce above- and belowground competition for the planted seedlings and ii) a canopy reduction, possibly in combination with sub-canopy thinning may improve light and growth and survival of under-planted seedlings. Thus, canopy reduction may also reduce competition for light, water and nutrients but if the clearing is too big, it is very likely to be rapidly infested by competing weeds.

The main challenge when developing management operations to improve the establishment of under-planted seedlings concerns how to avoid uncontrolled release of competing vegetation. For the reduction of main canopy foliage there are two main strategies: gradual or immediate shade reduction. A gradual reduction of the canopy foliage by girdling pioneer canopy trees may be beneficial to non-pioneer seedlings as they can slowly adapt and utilize the increased light transmitted to the forest floor. An immediate reduction of shading by canopy trees, on the other hand, causes a sharp, immediate increase in light intensity, but such "gaps" in the foliage may contribute to the release of weeds (herbs, climbers, ferns and ginger) and new pioneers that can hinder the development of non-pioneer seedlings. Since canopy cover and forest floor light reception in secondary tropical rain forests are complex, dynamic variables (Jennings et al. 1999, Montgomery and Chazdon 2001), any gap creation strategy that may be applied in order to improve the survival and growth of seedlings (planted or naturally established) has to be carefully considered. Separate tree species may also react in different ways after such treatments - if artificial regeneration with a mixture of (native) trees should be successful, i.e. allow planted seedlings to survive, establish and grow into trees, methods which fulfill requirements of a wide range of non-pioneer tree species would be necessary.

2. Objectives

The overall aims of the studies this thesis is based upon were: to analyze regeneration in secondary tropical rain forests after selective logging, drought and fire; increase understanding of secondary forest succession; and elucidate the interactive effects of canopy and sub-canopy growth and dynamics on seedlings at the forest floor. The specific objectives of the four studies (I-IV) were:

- to increase knowledge of natural regeneration patterns in tropical secondary forests of lowland mixed dipterocarp forest type, after disturbance from selective logging, drought and forest fires and to examine if tree seedling recruitment and species composition among seedlings were related to previous disturbances, present canopy structure and/or remnant potential seed trees (Paper I);
- to improve understanding of growth and mortality patterns in the sub-canopy and canopy of *Macaranga*-dominated secondary forests, and to elucidate the effects of shade-reducing canopy and sub-canopy treatments on forest floor light intensities as well as their efficacy for promoting seedling establishment (Paper II)
- to improve knowledge of how well under-planted non-pioneer tree species thrive under different combinations of shade-reducing canopy and sub-canopy treatments in *Macaranga*-dominated secondary forest (Paper III).
- to evaluate the results of applying direct seeding methods in *Macaranga*-dominated secondary forest and their potential utility, during mast fruiting spells, as alternatives to artificial regeneration through planting (Paper IV).

3. Material and methods

3.1 Study sites

The studies underlying this thesis were based on experiments and descriptive surveys of tropical secondary forests in various succession stages, ranging from selectively logged forests with a confirmed fire history to old-growth forests. All field studies were conducted in north-east Borneo in three areas located between 116-117°E latitude at 4°N longitude in the state of Sabah, Malaysia (Figure 2). These areas were: Kalabakan Forest Reserve, covering 18 400 ha (Papers I-IV), and Tibau Forest Area, covering ca. 100 ha (Paper I), both in the Tawau district; and Danum Valley Conservation Area sized 43 800 ha (Paper I), in Lahad Datu district.

The main study area was Kalabakan Forest Reserve, which has been dominated by secondary forest in various stages of succession following selective logging in 1975-85, drought and fires in 1982-83 (e.g. Woods 1989). At present and since 1998, a restoration programme aiming to refrain tree species diversity and forest recovery is conducted within the area (for further description, see Appendix 5). Tibau Forest Area has been selectively logged, probably in the 1970s, but Danum Valley Conservation Area has never been commercially logged and has been set aside as a reserve for research, education and tourism (Marsh 1995).

As the main human populations of Sabah are concentrated in the coastal areas and western districts, the eastern parts further inland than Tawau are relatively uninhabited (Marsh 1995). Approximately 25 km east of Kalabakan Forest Reserve, a village (Luasong) has grown at the site of a logging camp, around Luasong Forestry Centre, and the municipality now has ca. 1000 residents, many of whom obtain part of their livelihood from forestry (David Alloysius pers. comm) In Danum Valley a research station is located at the end of the road leading into the valley, which also marks the eastern boundary of the old-growth forest. The landscape further east hosts secondary forest that has been selectively logged, but not ravaged by fire (Yap Sau Wai, pers comm.)

The climate is tropical humid and non-seasonal (Fox 1972), with high precipitation year-round (Walsh 1996, 1999) but with two periods of slightly drier climate since the rainfall patterns in northeastern Borneo are influenced by two monsoons, one from the north-east in November-March (which is the wettest) and one from the south-west in May-August and the inter-monsoon period tends to be drier, but the onset of both monsoons is variable (Marsh 1995). Strong dry spells occur irregularly as a consequence of El Niño southern oscillation (Harger 1995a, Harger 1995b, Walsh 1996), both in Sabah and East Kalimantan while Sarawak and West Kalimantan are not affected to the same extent (MacKinnon et al. 1996).

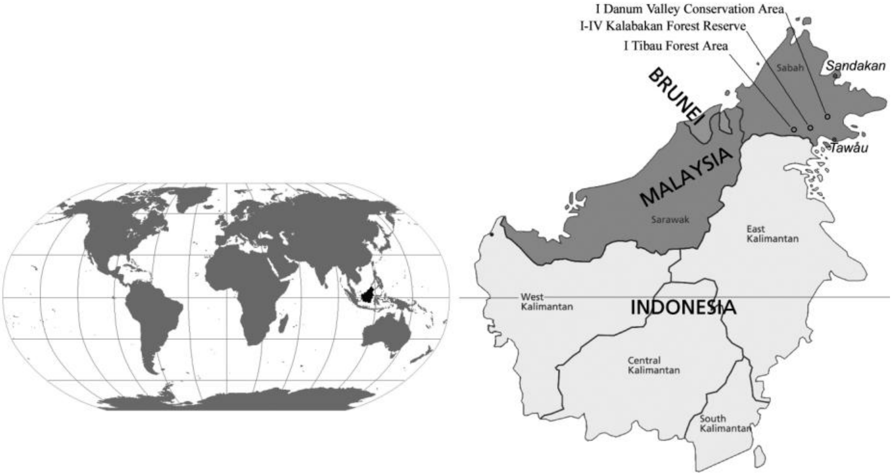

Figure 2. Map showing locations of Borneo and the three study sites: Kalabakan, Danum and Tibau. Kalabakan is the main study site at which the field studies reported in Papers I-IV were conducted, while sites at Danum and Tibau were considered in Paper I. Graphics by Göran Hallsby.

According to reconstructions of climatic data by Walsh (1996) several El Niño induced droughts have occurred throughout the last hundred years in the North-East of Borneo (records are from Tawau and Sandakan, see

Figure 2). Except from occasional dry spells, climate is hot and humid with a yearly precipitation of ca 2.7 m in Danum Valley (Marsh 1995, data from 1961-1990) and ca 2.9 m in Luasong (unpubl. data from 2002-2004). The diurnal temperature averages 27°C (Marsh 1995).

The terrain in all three study areas is undulating with convexo-concave slopes (see Malmer 1996), formed from eroded sedimentary bedrock (Acres 1975), mainly originating from the Cretaceous and Tertiary eras (Marsh 1995). The altitude in the areas (Paper 1-IV) varies between 300-600m a.s.l. Both Kalabakan Forest Reserve and Danum Valley Conservation Area have rifts at elevations of 600-1000m, but these areas were not included in the studies. The terrain north of the Tibau Forest Area also has forest at altitudes exceeding 600m. The soils are mixtures of acrisols, alisols and plinthosols (Acres et al. 1975). Weathering processes and local variations in substrate, drainage and exposure make major contributions to the floristic composition in different forest stands (Jakobs 1981).

The vegetation type in all three study areas is classified as lowland mixed dipterocarp forest, of *Parashorea malanonaan* type (Fox 1972). Among dipterocarp trees, certain species are restricted to specific habitats (such as riparian or alluvial zones, hill slopes or rifts) or to limited geographical areas, while other species are distributed more extensively throughout the island (Newman et al. 1996, Newman et al. 1998). The Dipterocarpaceae family (here referred to as dipterocarps) represent 278 tree species in Borneo (Meijer and Wood, 1964) whereas the most abundant genera are *Shorea*, *Parashorea*, *Dryobalanops, Dipterocarpus* and *Hopea* (Fox 1972). Other important tree families in lowland mixed dipterocarp forests are the Euphorbiaceae, Annonaceae, Lauraceae, Meliaceae, Myrtaceae, Leguminosae, and Rubiaceae (Fox 1972, Newbery et al. 1992). In terms of numbers of individuals, Euphorbiaceae is often the most abundant tree family (Newbery et al 1992). According to Goldammer (2007) dipterocarps are suppressed by disturbance from fire while many species representing Euphorbiaceae are favored by fire.

3.2 Experimental designs

The seedlings in the forests were surveyed to estimate their species frequencies and abundance (Paper I), and completely randomized split plot block designs (Stehman and Meredith 1995) were applied in field experiments in which gaps were created artificially (Papers II and III) and direct seeding was evaluated (Paper IV).

The survey had the following design: First, sites representing five forest disturbance categories were selected: selectively logged and heavily degraded (designated Early-sec 1); selectively logged and burned (Early-sec 2); selectively logged, partly burned and less degraded (Early-sec 3); selectively logged and more lightly degraded (Late-sec); and never commercially logged, with no recent fire history (Old-growth). Three 1-ha sites were selected in each study area except Late-sec (Tibau Forest Area), where only one 1-ha area was selected due to geographical restrictions. At each of these sites three 50-m long and two meter wide parallel transects were established, and large trees above 40cm in dbh were recorded within 10 m distance from each transect mid-line.

In the gap study based upon a 3-step hierarchal design three main canopy treatments (in which pioneer trees were selectively girdled, selectively felled or neither girdled nor felled) were randomly assigned to plots within each block, and two sub-canopy treatments (slashing/not slashing saplings and small trees) were randomly assigned to subplots (Figure 1, Paper II), planting four dipterocarp tree species randomized for position within each sub-plot was the last, supplementary treatment (Figure 2, Paper III).

In the direct seeding trial three pre-seeding site preparation treatments (in which leaves were removed, leaves were removed and the soil was scarified, or leaves were not removed and the soil was not scarified), were randomly assigned to plots within each block. Four different species were seeded as additional treatments, and each species was randomly applied to one seeding line within each main plot (Figure 2, Paper IV). In Studies II and IV four blocks were included, respectively, and seven in Study III.

3.3 Gap creation and under-planting of dipterocarp seedlings

To create artificial gaps, each subplot assigned to a canopy treatment was considered as one gap unit, in which that treatment was applied in a circle with a 5 m radius and the sub-canopy treatment (if applied) in a smaller, inner circle with a 2.5 m radius. For canopy treatments, all stems of Macaranga and other pioneer tree species exceeding 10 cm in dbh were selected for `treatment´ or `leaving´ according to a constructed function (Figure 2, Paper II), in which the stem dbh and distance from gap centre of each individual tree were used as coordinates. Basically, the aim was to develop a selection system that could be applied to all plots, regardless of tree positions in the specific subplots, and to create centre-weighted gaps that had high basal areas of stems 3-5m from their respective centers (Figure 2, Paper II). Trees allocated to "treatment" according to the function were marked with plastic tape in all plots. Non-pioneer species were excluded from treatment.

Trees were felled with a chainsaw at the bases of their stems, while girdling involved stripping the outer and inner bark from stems 50-100 cm above ground using a *parang* (long, sharp jungle-knife), and control plots were left untreated. Trees selected for felling and girdling accounted for, on average, approximately 30 % (10.4 m^2 ha^{-1}) to 33 % (11.6 m^2 ha^{-1}) of the initial basal area (ca. 35 m^2 ha^{-1}), respectively. The sub-canopy treatments, each of which were randomly assigned to half of the subplots in each plot, involved slashing seedlings, saplings and small trees, identified as pioneer species, with a dbh $\leq$10 cm or no slashing (control). The sites were prepared during the week before planting, by removing non-woody forest floor vegetation (mainly ginger, ferns and climbers) in the central part (r = 2.0 m) of each sub-plot (Paper III). This treatment was also repeated after six months. The seedlings of the four planted dipterocarp species were randomly planted in each subplot, at positions in a grid, 1.25 – 1.50 m from the subplot centre, with slight modifications of specific planting spots to avoid the seedlings being too close to big roots, stumps, stones etc.

3.4 Tree species

In the survey (Paper I), tree seedlings/saplings (up to 2m height) were identified to family, and if possible, to genus and species levels. Samples of seedlings that could not be determined to species level in the field were tagged and identified later by a forest botanist at Sabah Forestry Department (Leopold Madani). Adult trees were determined using a battery of characters, including outer and inner bark, resin and leaf traits. Often a piece of stem bark was slashed to obtain supplementary information about the outer and inner stem bark, and resins, to aid species identification (see Meijer and Wood 1964).

A mast fruiting spell occurred six months before the gap planting experiment commenced, which supplied sufficient seeds of seven species for the required numbers of seedlings. Four dipterocarp species were selected for the experiment (Paper III): *Dipterocarpus applanatus*, *D. caudiferus*, *Shorea argentifolia* and *S. pauciflora*, in accordance with the concept of ecological species groups in tropical rain forests (Swaine and Whitmore 1988). The two *Dipterocarpus* species are considered medium hardwood trees (Newman et al. 1998), while the *Shorea* species are regarded as light hardwoods (Newman et al. 1996), hence seedlings of these genera planted in constructed gaps or under shaded conditions may display different growth strategies (e.g. Rijkers 2000a).

Only a few tree species synchronistically fruited in sufficient amounts (nine months after the end of the mast fruiting period) to include in the direct seeding experiment (Paper IV): *Shorea gibbosa*, *S. platyclados* and *Shorea* sp. (not determined to species level, but clearly distinguishable from the two other *Shorea* species). The tendency for seeds of *Shorea* spp. and many other tropical trees to germinate immediately (Appanah and Weinland 1993) limited the species selection. Therefore, in order to include the desired number of four species, *Intsia palembanica*, a legume that produces storable seeds, was also included. The seed collection procedure is described further in Papers III and IV, while a more detailed overview of the seedling production and out-planting procedures is presented in Paper III.

3.5 Plants and seeds in nursery and forest

Seedlings for the gap experiments were raised in the Luasong nursery which is an open shade-house (Figure 3) with three layers of black polyurethane plastics nets to provide a balance between light and shade. The dipterocarp seedlings in Study II were raised in plastic bags filled with a mixture of river-bed sand and soil with NPK fertilizer added. Seeds in the germination trial parallel with the direct seeding (Study IV) were also raised in the Luasong nursery (but without fertilizer). In both cases, all individuals were provided with water daily.

Gap-experiment seedlings were tagged and planted out (at the start of gap experiments) in two early mornings to avoid plant heat stress and this was done after three days of regular rainfall. Seeding in the forest and initiating of the parallel nursery germination were done after collection of mature seeds; at that time forest soil conditions were moisture enough to alleviate germination.

Figure 3. The nursery at Luasong Forestry Centre is an open shade-house. Three layers of black polyurethane plastic nets provide sufficient shade to avoid drought stress in seeds and seedlings. Water was provided daily for the experiment seeds and seedlings raised here. Photo: Eva Romell.

3.6 Measurements of canopy openness and light transmission

In Study II canopy openness was measured by image analyses (Winscanopy software, Anon. 2005) of a time series of fisheye photos taken before the shade reduction treatments, just after the treatments, and every six months during the following 2.5 years.

Picture image analyses (Paper II) do not distinguish between canopy closure by one or several leaves covering a single spot of the recorded hemisphere, although this influences the shade effect. Therefore, in addition, light levels (photosynthetic photon flux density, PPFD) were directly measured at the forest floor concurrently with the photos, using calibrated LICOR LI-190 (www.licor.com) sensors measuring the photosynthetic active radiation (PAR), which for most plants is within the range of 400-700 nm wavelengths (Raven et al. 1992). Light (PPFD) levels were recorded simultaneously just above forest floor and on an above-canopy platform (Figure 4), then the proportions of incoming forest floor light (relative PPFD) were calculated from the parallel recordings.

Figure 4. One of the above-canopy tree platforms used for reference light recordings. Two platforms were used to limit the distance between reference and forest floor recordings in plots. If small clouds covered the platform but no the plot, recordings might be unreliable, therefore distance in between should preferably be short. Photo: Eva Romell

Relative PPFD values exceeding 0.8 (caused by very local changes in sky conditions, i.e. small clouds) were considered unrealistic and excluded from the calculation of mean values for each treatment combination and block. In addition, single fish-eye photos showing the sun "burning" through the foliage were discarded and taken again since image analysis of such photos exaggerates canopy openness proportions. Fish-eye photos were preferably taken during the morning, when the sky was overcast to reduce sun reflections in the photos, and PPFD recordings were taken under clear conditions according to a fixed measurement schedule at around mid-day.

3.7 Survival, height and biomass increments

Survival rates of gap-planted seedlings were monitored at pre-determined, 3-monthly intervals (Paper III) while the development of directly seeded plants was monitored weekly (Paper IV) and numbers of survivors were counted after 30 months and 8 weeks respectively (Paper III and Paper IV). In Study III seedling heights were measured directly after planting and every six months during the following 2.5 years. The relative height growth, RGR_H, of the seedlings under each treatment combination was calculated for each half-year period during the course of the study. Fresh and dry weights of sets of 20 seedlings of each species were determined at the time of planting, and of 13 individuals representing each treatment and species combination (three canopy treatments, two sub-canopy treatments and four species; in total 312 individuals) at the final assessments (Paper III). In addition, a series of *in situ* measurements (height, height up to the lowest living branch, diameter at stump level, and dbh of individuals at or above that height) were taken for all seedlings 2.5 years after planting. Using multiple logistic regressions, functions were constructed to estimate fresh weights of non-destructively measured seedlings of each species (Swanberg 2005) and calculate their dry matter contents (see Paper III). Relative biomass increments, RGR_B (cf. Portsmuth and Niinemets 2006), could then be calculated from the estimated final and initial dry weights.

3.8 Statistical analyses

Ordination (Non-metric Multidimensional scaling, NMS and Multi-Response Permutation Procedure MRPP; McCune & Grace 2002) were used to analyse seedling and sapling species composition, if the variation were positively correlated to trees ≥40 cm in dbh and if forest disturbance categories had different species composition. ANCOCA/ANOVA was applied to analyse and compare number of individual seedlings and saplings in different forest categories where trees ≥40 cm in dbh was included as a covariate. Species rarefaction analyses with Jack-knife estimations was performed on the number of species/taxa in each forest succession category.

Analyses of Variance (ANOVA) with General Linear Models (GLMs) was used to evaluate effects of the treatments in the artificial gap experiments on canopy openness and relative PPFD (Paper II) and seedling survival, relative height and biomass increment (RGR_H and RGR_B) (Paper III). The relative PPFD-data were log transformed to meet ANOVA requirements for normality of data distributions (see Sabin and Stafford

1990). Tukey´s Studentized range test (Zar 1999), with the significance level set to 5% was applied to determine differences between treatments.

SAS 8.1 software (SAS Institute, Inc., Anon 1999) was used for the GLM-ANOVAs in Study II-III. The ANCOVA, ANOVA Spearman rank correlation, rarefaction and regression analyses were conducted using the statistical package R 2.2.1 and the additional package "vegan" (Ihaka & Gentleman 1996), while the NMS and MRPP analyses were conducted using the statistical program Pcord4 (McCune & Mefford 1999).

Due to the extremely low survival rates of the seedlings in the direct seeding experiment (Paper IV), the data did not fulfill ANOVA assumptions of normal distribution and constant variance. Further, there were too few data to apply a probability test (S. Holm pers. comm.) to assess whether the pre-seeding treatments and/or species choice significantly influenced seed germination and seedling survival. Thus, only descriptive statistics regarding their survival rates were calculated and presented.

4. Results

Seedlings and saplings were recruited in all forest categories, the highest average abundance of seedlings and saplings had old-growth forest but the least disturbed secondary forests scored the highest abundance in one single measurement unit, although tree recruits were highly variable within this category. The most degraded secondary forest was significantly separated from the old-growth when number of individuals was analyzed. Ordination results indicated high variation in species composition, all forest categories and all seedlings/saplings included. NMS-analyses indicated significant, positive correlation to proximity to remnant trees and variation in seedling and sapling species composition.

Before gap creation treatments were performed, forest floor light levels were low; $PPFD_R$ and canopy openness ranged from 1.8-2.3% and 8.8-10.7%, respectively, before initial treatments (and no significant differences in these variables were detected either between or within blocks). Immediately after the treatments canopy openness averaged 14.6% in plots treated by felling pioneer canopy trees, and somewhat lower in the girdling and control plots (11.8 and 11.7%, respectively; Figure 3, Paper II). $PPFD_R$-levels increased dramatically to 11.4% immediately after felling, but remained relatively unaffected immediately after the girdling and control treatments. Eighteen months after the treatments, gaps created by girdling had similar light conditions (canopy openness) to those of gaps created by felling, and there were no longer any significant differences in this respect between treatment combinations. At the end of the study period, 2.5 years after the initial treatments, mean $PPFD_R$-levels were highest (but non-significantly) in gaps created by girdling (Paper II, Figure 3). The average canopy openness proportions were very similar (ca. 12%) following the felling, girdling and control treatments at the final assessment, and there were no significant between-treatment differences in this respect at that time. The proportion of the basal area of the trees selected for felling/girdling in the respective plots varied from 23 to 51%, and was on average 31 %. According to estimates six months after the initial treatments, 13 % of the residual trees were estimated to have been unintentionally damaged by the felling treatment, either by direct mechanical damage or secondary effects, e.g. one tree falling on another.

Slashing sub-canopy seedlings, saplings and trees resulted in higher forest floor light ($PPFD_R$) and canopy openness, compared to the control throughout the whole 30-month period. However, while this was significant for canopy openness at all recordings after the treatments, it was only significant after 18 and 30 months for $PPFD_R$. Intriguingly, Canopy openness and $PPFD_R$ values also increased after the treatments in the control plots, from directly after the treatments until the final assessments 30 months later (Figure 3, Paper II).

Canopy treatments did not have any statistically significant effects on seedling survival rates (Figure 2a, Paper III), and there were no significant interactions between canopy and sub-canopy treatments on seedling survival, RGR_H or RGR_B. However, seedlings displayed significant responses to the canopy treatments (felling, girdling and no felling or girdling) in terms of relative height increment (RGR_H) during the first six months following the treatments. The mean RGR_H values of seedlings in the felling, girdling and control plots for the 0-6 months period all significantly differed (1.32, 0.77 and 0.34m m^{-1} $year^{-1}$, respectively; Figure 2d, Paper III). In the following period (6-12 months), RGR_H declined in the felling and girdling plots to 0.83 and 0.50m m^{-1} $year^{-1}$, respectively, while it increased in the control plots to 0.46m m^{-1} $year^{-1}$, and significantly differed from the corresponding values for the girdling and control plots. In months 12-18 the mean RGR_H in girdling plots again increased (to 0.6m m^{-1} $year^{-1}$) and was significantly different from the RGR_H in the control plots (0.42m m^{-1} $year^{-1}$), but not the felling plots (0.70 m m^{-1} $year^{-1}$) (Figure 2d, Paper III).

Canopy treatments had significant effects on relative biomass growth during the 30-month post-treatment period. Felling resulted in the highest growth rate (1.37 g g^{-1} $year^{-1}$), followed by girdling (1.03 g g^{-1} $year^{-1}$) and the control (0.64 g g^{-1} $year^{-1}$); all these between-treatment differences were significant ($p<0.05$) (Paper III).

Sub-canopy treatments and species had significant interactive effects on seedling survival rates, 12 and 18-30 months after the treatments. The survival rates of *D. applanatus*, *D. caudiferus* and *S. argentifolia* seedlings were significantly higher after sub-canopy slashing, but those of *S. pauciflora* seedlings were higher after no slashing (Figure 2b, Paper III).

The sub-canopy treatment also had a significant effect on RGR_H except in the 6-12 month post-treatment period (Figure 2e, Paper III). Sub-canopy slashing resulted in higher RGR_H-values than the control treatment in each of the five six-month study periods. For RGR_B, there was a significant interaction between the effects of sub-canopy treatment and species. This parameter was much higher in the slashed plots than in the control plots for all species, but the difference in RGR_B values between the slashed and control plots differed significantly between species. The difference was highest for *S. argentifolia* seedlings and significantly higher for *S. argentifolia* than for *S. pauciflora* seedlings. When only main effects were analyzed, RGR_B was found to be significantly higher after slashing (1.31 g g^{-1} $year^{-1}$) than after not slashing (0.72 g g^{-1} $year^{-1}$).

Seedling mortality of all species was observed throughout the whole study period. The final survival percentages averaged 72.6-86.0 % and *S. pauciflora*, the species with the highest survival rate in the absence of sub-canopy slashing, displayed the highest survival rates throughout the study period (Figure 2c, Paper III). *S. pauciflora* also displayed the highest initial RGR_H (0-6 months, 0.98 m m^{-1} $year^{-1}$), although *S. argentifolia* seedlings grew most strongly over the 30-month period (Figure 2f, Paper III). The RGR_B during the entire 30-month period was 1.00-1.10 g g^{-1} $year^{-1}$ for *D. applanatus*, *S. argentifolia* and *S. pauciflora*, and significantly lower for *D. caudiferus* seedlings (0.86 g g^{-1} $year^{-1}$).

Direct seeding in *Macaranga*-dominated secondary forests resulted, overall, in 99% mortality of the four directly seeded species (*I. plamembanica*, *Shorea gibbosa*, *S. platyclados* and *Shorea* sp.) Destructed parts of seeds and seedlings at the sowing spots indicated high predation by evertebrates. At the final assessments, eight weeks after sowing all *Shorea* seeds/seedlings were dead or had disappeared, while only 3% of *I. palembanica* seeds had developed into healthy seedlings. The proportions of viable (germinative) seeds of the abovementioned species were 21, 61, 61 and 91%, respectively, according to the germination test in the seedling nursery. The significance of pre-seeding treatment effects could not be evaluated due to the lack of sufficient data.

5. Discussion

Macaranga-dominated secondary forests in Eastern Borneo have expanded in recent decades as a result of repeated logging, fire and El Niño-induced dry spells (Woods 1989, Slik et al. 2002, Slik and Eichhorn 2003). *Macaranga* stands in the area in which the artificial gaps were created were typically dense (see Figure 4) with 35 m^2 ha^{-1} basal area, on average, in the seven experimental blocks considered in Papers II and III) and single-storied, forming fairly high canopies that restricted forest floor light availability to levels previously found in old-growth forests in North Borneo (Whitmore 1998). Even the 20 year-old secondary forests described in Paper I had dominance by *Macaranga* trees, though very variable between forest patches.

As indicated by Slik et al. (2002), the dominance of *Macaranga* in prevailing stages of stand development may be closely related to the previous fire history in the area. Fire scars on remaining old-growth stems and charcoal were encountered within the research areas, supporting local testimonies of fire incidents dating back to about 20 years before the experiment was initiated. Slik and Eichhorn (2003) compared unburned mixed dipterocarp forest in Kalimantan (Indonesian Borneo) with fire-ravaged forests in 1982-83 and/or 1997-98, and found that the number of trees of non-pioneer species in the size classes 0-5 and 5-10 cm dbh was ca. 80% lower in burnt than in unburned forest sites.

Figure 5. This is a typical *Macaranga*-dominated forest stand within the main study area. The grey-blue uniform canopy is *Macaranga* spp. trees, the open area is an abandoned logging road and the remnant trees on top of the ridge are dipterocarps and other non-pioneer trees. Photo: Eva Romell

Critical issues to resolve for forest restoration/management are if, and when, non-pioneer trees are recruited, and if *Macaranga* spp. and other dominant pioneer trees are gradually reduced, releasing light and other resources to non-pioneer trees present before disturbances (see for instance, Ashton et al. 2001). Under-planting of non-pioneer species may help to accelerate forest recovery, but seedling establishment and survival rates must be sufficient if such a measure is to be successful. If seedlings of non-pioneer tree species establish by natural regeneration, on the other hand, sub-canopy or canopy treatments may improve seedling (and sapling) height growth. However, if the current main canopy of *Macaranga* and other pioneer trees gradually die off by self-thinning, resources may become available for new tree recruits of long-lived, non-pioneer species. Golddammer and Seibert (1990) observed recruited dipterocarp seedlings ca. 1 year after the `Borneo fire´ in 1982-83 following mast-fruiting, but there are few records of long-term successional development after disturbances from both logging and fire. Verburg and van Eijk-Bos (2003) concluded that there are no pre-determined successional pathways whereby the tree species composition in selectively logged forest will shift with time after disturbance. According to the studies underlying this thesis (mainly Paper I-II) it seems that the current circumstances on the local site determines the succession rather than temporal pre-determined succession pathways. Remnant trees and other intact forest structures which was there before disturbances occurred may determine the succession with interference from climatic conditions, i.e. if mast fruit spells are induced (see Curran and Webb 2000) and if conditions after seed falls are moist enough to alleviate substantial seed germination. It is also very likely - although not investigated in the studies underlying this thesis - that soil conditions and eventual soil degradation caused by logging are an important factor for seedling recruitment and survival (see for example Ilstedt 2002).

5.1 Tree species recruits and secondary successions

The findings of the survey of seedling recruits in secondary forests ca. 20 years after disturbance by selective logging, drought and forest fire indicated that there was a marked difference in seedling species composition between the most degraded early secondary and old-growth forests, but within the secondary forest of Kalabakan Forest Reserve patches were highly heterogene. The least degraded forest within the Kalabakan area, Early-secondary 3 had a relatively high seedling and sapling recruitment and high abundance of dipterocarps (see Figure 2, Paper III). From this survey, it is not possible to model future tree composition but according to one of few studies of late secondary forest (Brearley et al. 2004) tree composition was still altered as long as 55 years after disturbances from selective logging, including trees of all dimensions, in a 55-year old succession in Kalimantan, Borneo; Melastomataceae and Hypericaceae trees dominated the secondary forest while Dipterocarpaceae dominated the old-growth forest.

Over-all species composition (analysed with ordination) displayed high variation in seedling and sapling recruits. The heterogeneity in secondary forests may be partly due to differences in intermediate disturbance-related successional patterns (e.g. Shiel 1999), fostering the establishment of disturbance-thriving species and the initiation of late-seral (non-pioneer) species to varying degrees. However, high variation also seems to be a natural, inherent feature of these forests. For instance, Slik et al. (2003) found high variations in tree species composition between different parts of

Borneo and, according to Gunatilleke et al. (2006) topographical patterns strongly influence local species patterns.

In forest patches with a confirmed fire history and high abundance of even-aged *Macaranga* trees (referred to as Late-sec 2 in Study I), seedling and sapling abundance was lower compared to other disturbance categories (Paper I). One theory I had before attending these studies was that *Macaranga* spp. canopy trees could provide a shelter under which non-pioneer tree species could recruit. But it seems that, for at least within 0-200cm height level, tree recruitment still after 20 years are low in fire-raved forests, which confirm findings found by Slik et al. (2002).

Another issue related to forest succession is whether a second generation of *Macaranga* spp. could establish under the first, but according to the findings in Study I there were relatively few *Macaranga* seedlings and saplings in all forest disturbance categories (Figure 2, Paper I). It might be too dark for seeds of *Macaranga* species to germinate, as several are truly pioneers. According to Slik (2005) the common species *M. beccariana*, *M. hypoleuca* and *M. gigantea* require 13-25% canopy openness for successful establishment. In the pre-treatment recordings in the pioneer dominated forest stands where gap experiments were condition (Paper II) canopy openness were ca 10%.

5.2 Light supply in the artificial gaps in *Macaranga*-dominated secondary forests

When planning enrichment planting in secondary forests such as the Macaranga-dominated secondary forests described in Papers II-III and in Paper I (categorized as Late-sec 2) a key issue to consider is the best method for ensuring prolonged alleviation of the competition for light at the seedling level. There is substantial support for the conclusion (proposed in the review by Turner 2001) that the survival and growth of seedlings of tropical tree species are nearly always promoted by increased light intensities since light, or PPFD, is required for photosynthesis. Measurements of light availability indicated that gap-centered felling or girdling of trees could treble $\mathrm{PPFD_R}$ values compared to control treatments after six months. The visual impact of canopy treatments was dramatic, but the maximum average PPFD corresponded to slightly below 13% of above-canopy values (Paper II, Figure 3). In fact, over the entire study period the estimated average PPFD for felling and girdling plots was closer to 10 % of above-canopy values. Below the *Macaranga* canopy, ca. 90 % of the hemispherical images acquired did not contain open sky. During the study period felling caused the highest increases in mean canopy openness values, of 4-5 %, compared to the control treatment (Paper II, Figure 3), but there were no significant differences in this respect between the girdling and control treatments.

In general, felling resulted in an instant improvement in light availability, but this effect did not persist throughout the study period. Using $PPFD_R$ values to compare effects of the felling and girdling treatments revealed a weak (non-significant) tendency for $PPFD_R$ to be higher in the girdling plots. A possible explanation for the observed tendencies is that the growth of forest floor vegetation may be stimulated more by the felling treatment, while the gradual demise of girdled trees retards the growth and development of forest floor competitors.

Results reported in Paper II indicate that light availability also tended to increase below the *Macaranga* canopy in the untreated control plots. The estimated age of the *Macaranga* trees, based on local reports concerning the dates of logging and wild fires in the Kalabakan Forest Reserve, was in the range 20-30 years (Garcia pers. comm.). According to Ashton et al. (2001), dominance of pioneer *Macaranga* spp. persists for about 30 years in secondary forest successions of Sri Lanka. Davies et al. (2001) also reported high mortality rates in established *Macaranga* stands. If the *Macaranga*-dominated secondary forest examined in our studies is close to its maximum age and has entered a phase of self-thinning this could explain the observed increases in light availability with time in the control plots.

Creating circular gaps with 2.5 m radii in the sub-canopy by slashing all forest floor vegetation provided a more consistent improvement in light than the canopy treatments (Paper II, Figure 3). An increase in $PPFD_R$ of 3-6% was registered throughout the study period and canopy openness remained 2-3% higher in slashed plots compared to the untreated control plots. Judging solely from the observed treatment effects on light conditions close to the forest floor, sub-canopy slashing in a concentrated gap would be the most reliable pre-planting treatment to alleviate competition for light and favor the introduction of non-pioneer species in mature *Macaranga*-dominated secondary forests similar to those investigated in these studies (Paper II).

5.3 Treatment effects and establishment of under-planted seedlings

Canopy treatments did not appear to affect overall seedling survival rates after 30 months. Sub-canopy slashing, in contrast, generally improved seedling survival compared to the no sub-canopy treatment. Of the four studied species *S. pauciflora* seedlings tended to have the highest survival rates, regardless of canopy and sub-canopy treatments.

The height rankings of the species included in the studies described in Paper III were the same after 30 months as they were initially, but in relation to height at out-planting the height growth of *D. caudiferus* appeared to be somewhat stronger than that of *S. pauciflora. S. argentifolia* seedlings displayed the highest relative growth rates during the study period, while those of *D. applanatus* seedlings were relatively low. The overall survival and growth rates found in the studies (Paper II) were comparable to results found in other planting studies with dipterocarp species (Ådjers 1995, Otsamo 2000, Vincent and Davies 2003). However, it should be noted that the declining growth rates and canopy treatment effects on light availability observed, together with the continuing seedling mortality, indicate that additional tending of the gaps may be needed to ensure the continued survival of the planted seedlings. Unless the current mortality trend is interrupted less than 10 % of the planted seedlings will still remain 15 years after planting.

5.4 Correlation between forest floor light conditions and plant height growth

The ranges of $PPFD_R$ and canopy openness observed in the artificial gaps indicated that the seedlings grew under relatively shaded conditions (Figure 6-7). Double layers of shade cloth, as used in local forest nurseries, provide an approximate 50 % reduction of full sunlight (Yasman and Hernawan 2002) without negative effects on the average rates of dipterocarp seedling growth. The correlation between observed light availability and seedling height was positive, but weak on all recording occasions except six months after planting, when it was strong (Figure 6-7). It should be noted that several other factors, in addition to the light availability and gap properties considered in Study III (Figs. 6-7; Figure 2, Paper III) such as colonization by mycorrhiza and competition (above- and below-ground), are also likely to have influenced the height growth of the under-planted seedlings.

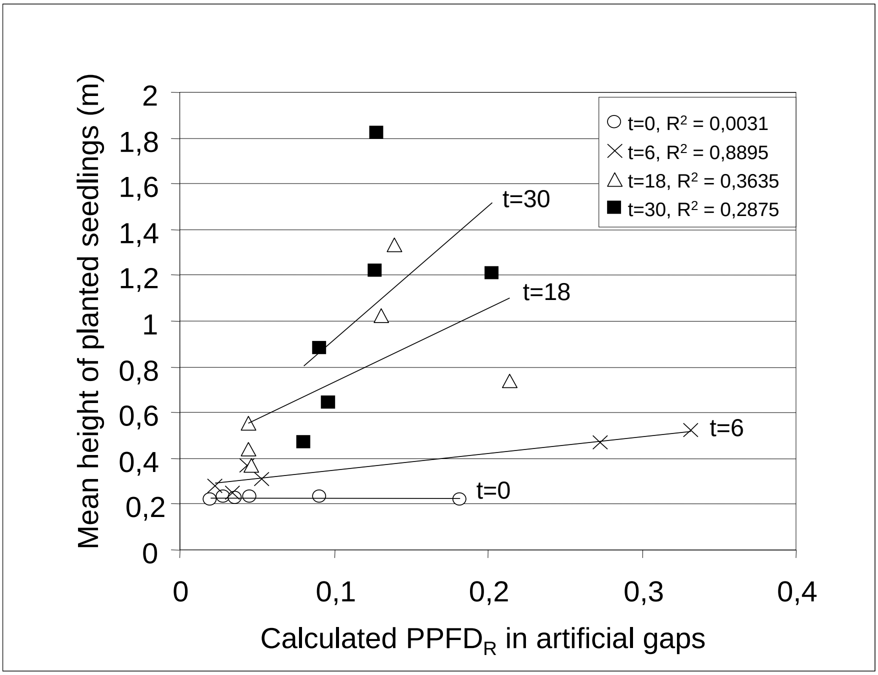

Figure 6. Correlation of relative PPFD and mean height of under-planted seedlings in six different treatment combinations (canopy x sub-canopy treatments). Linear correlation coefficients (r^2) are displayed for the separate recordings; 0, 6, 18 and 30 months.

The PPFD values should theoretically be directly related to the seedlings' photosynthetic performance (Norisada and Kojima 2005) and, therefore, strongly correlated to their height and biomass increments. These experiments indicated that seedlings of the four dipterocarp species used in the studies (*D. applanatus*, *D. caudiferus*, *S. argentifolia* and *S. pauciflora*) all grew better with increases in canopy openness and relative PPFD levels (Figure 6-7). In contrast, some previous studies have found that partially shaded environments favor the photosynthesis and growth of dipterocarp seedlings (Nicholson 1960, Ashton 1995, Tennakoon 2005). However, the Macaranga-canopy and surrounding vegetation still remained after the treatments in the experiments reported here, which seemed to provide sufficient shade for the seedlings. A *Macaranga*-canopy may both provide shelter and allow light to reach sub-canopy levels since the crown density of Macaranga species is low (Davies et al. 1998). Thus, partial reduction of sub-canopy vegetation may provide sufficient light for adequate seedling survival rates. Sub-canopy slashing may also reduce root competition and thus stimulate height growth of the seedlings (cf. Putz and Canham 1992).

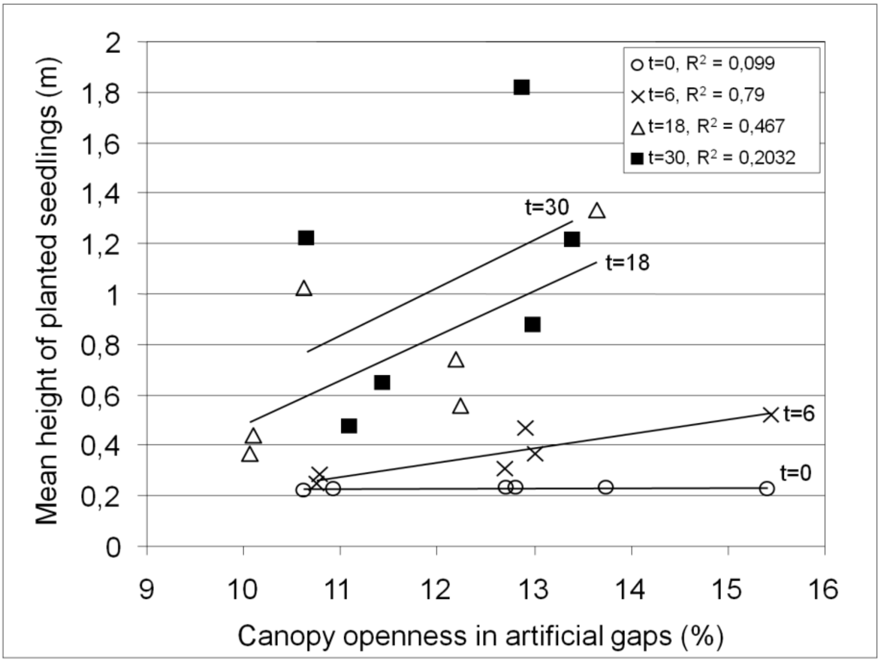

Figure 7. Correlation of canopy openness and mean height of under-planted seedlings in six different treatment combinations (canopy x sub-canopy treatments). Linear correlation coefficients (r^2) are displayed for the separate recordings; 0, 6, 18 and 30 months.

5.5 Germination and survival in direct seeding trials

The effects of the pre-seeding treatments could not be statistically evaluated, due to the high predation losses; within a week over 95% of the *Shorea* seeds had been lost and nearly 30% of *I. palembanica* seeds. At the final census, eight weeks after sowing, only nine individuals of *I. palembanica* had developed into seedlings and none of the *Shorea* species remained. When observed after two days the seeds in untreated control plots seemed to have established better than those in other plots, possibly because leaves (litter) protected the seeds from predation, or at least made it more difficult for the predators to locate presumptive food (seeds) and delayed the seed losses while seeds placed in sites with no leaves and scarified soils seemed to be more exposed. Other trials with direct seeding in tropical secondary forests have also observed high seed/seedling losses due to herbivory (Curran and Leighton 2000, Lyal and Curran 2000).

However, it should be noted that climatic factors can also influence direct seeding results. For example, drought after seeding affected germination success in an experiment in Brazil reported by Engel and Parotta (2001). In addition, the opposite problem (heavy tropical rain) can flush seeds away from planting sites, as indicated by a simulation presented by Pinard et al. (1996) of the fate of small pioneer seeds distributed on abandoned logging skid trails and landings, in which 80% of the seeds were either washed away or carried away by animals.

A possible strategy to avoid, or at least minimize, such problems, is to bury the seeds, as illustrated by Doust et al. (2008), who found that >20% of seeds buried in the soil at a site in tropical Australia successfully developed into seedlings, compared to just 2% of seeds placed on the topsoil. However, this alternative may not be realistic for *Shorea* and other dipterocarp species in Borneo since the radicle of these species develops early, often when seeds are still in the parental tree, and it is sensitive to mechanical damage after the initiation of germination. Direct seeding could be a feasible approach in forest restoration as it is markedly cheaper than enrichment planting (Engel and Parotta 2001, Hooper et al. 2002) and it may be a viable alternative if nursery capacity is limited. However, in situations such as that reported in Study IV, in which mortality is close to 100%, other methods such as under-planting or relying on natural regeneration would clearly be preferable. Thus, before attempting its application on a larger scale, further evaluation of direct seeding in this type of forests is required.

Important ecological features of this type of forest that predators have adapted to, and must be considered, are the intense mast fruiting spells (see Curran and Webb 2000). For instance, seeding before or during a mast spell may promote survival as predators are less abundant and/or feeding-satiated at these times (e.g. Janzen 1971). It could also be worth trying to seed other tree species than dipterocarps. Bagchi et al. (2010) claim that dominant tree taxa such as Dipterocarpaceae (with similar phylogentic pathways) are affected more by seedling herbivores. In rain forests of New Guinea trees of large genera were shown to be more predated by specialists compared to smaller genera (Novotny et al. 2002).

5.6 Experimental designs and methodological considerations

The over all aim of measuring seedlings in 1ha-areas including parallel transects was to get an overview of natural regeneration present at that moment. To register seedlings in transects was faster than establishing permanent sampling plots including all growth stages from seedlings to adult trees and could therefore include more replicates. However, the study does not answer whether there are (non-pioneer) tree species established earlier which may have grown out of the measurement range. Species determination of seedlings and saplings can be challenging since leaf morphology can be different compared to adult trees (see Turner 2001). In some studies instead morpho-species were used (e.g. Verburg and van Eijk-Bois 2003). I have used species to but some taxa could not be determined to species level, instead to genera or, in a few cases to family. This means the total number of taxa in Study I is slightly under-estimated. One major reason for working with species was to get an overview of what species, genera and families are recruited naturally which could be important information to be implemented in practical restoration work (see further Appendix 5). For this, families and genera would be the most important and management efforts could be focused on enriching the forest with taxa which not seems to recover naturally.

The rationale for using the split-plot completely randomized block design applied was that it increased the number of comparable observations and limited variations in site conditions (soil, topography and stand structure), facilitating the construction of a powerful ANOVA-model, and this goal was largely fulfilled. However, some edge-effects between the treatments may have occurred, e.g. unintentional damage to trees and sub-canopy vegetation in felling and girdling plots, and the minimum distance between sub-canopy treatment circles was 5 m, which may have been sub-optimal, eventually creating some `egde-effect´ into the control sub-plots. All walking through the plots, except for performing measurements, was restricted, but even this limited disturbance may also have influenced the initial canopy openness at the forest floor level.

The aim of using the two techniques for measuring light intensities was to allow a more complete appraisal of the effects of artificially created gaps on light conditions close to the forest floor over time. The results obtained by the two techniques were not perfectly correlated and PPFD-levels fluctuated more than canopy openness. Image analyses from hemispherical photos do not account for variations in foliage density, since multiple layers of leaves in one location of the hemisphere cannot be distinguished from a single leaf with the same projected area (Engelbrecht and Herz 2001). In contrast, quantum sensors register both direct and diffuse light (which can make a substantial contribution to the light received below closed or semi-closed canopies; Canham et al. 1990), and thus take account of leaf permeability and crown density. However, quantum sensors provide instantaneous measurements of the gap light quality that are sensitive to weather fluctuations and intermittent sun flecks, even for simultaneous relative recordings (Canham et al. 1990, Chazdon and Pearcy 1991).

The measurements of light conditions could have been carried out more frequently, in order to determine when $PPFD_R$ and canopy openness values peaked, which cannot be determined from the registered data. Using systems with continuous monitoring of data could have answered the question of when values peaked for the separate treatments but such equipment is expensive and can be sensitive to disturbances of animals (feeding on cables etc.) and would not allow measurements in so many plots. Recorded $PPFD_R$ averaged highest values six months after the felling treatment and after 30 months for girdling (Paper II, Figure 3). This could partly be described by a delayed effect of felling (some of the 20-35m tall pioneer trees hooked into other crowns and did not reach the ground immediately) and a delayed effect of girdling. When comparing canopy openness and $PPFD_R$ these peaks are not really synchronised. The PPFD recordings were more sensitive to weather fluctuations and in several single observations the PPFD-values 1.5 m above the forest floor exceeded the values recorded in the reference station above canopy. Disturbances of small Cumulus clouds are supposed to be the main reason for lower above-canopy PPFD. Such values had to be considered un-realistic, a limit of 0.8 was set to be the highest proportional value of forest floor-PPFD because a canopy at heights >20m would not allow more light to reach the PAR-sensor (e.g. Jennings et al. 1999). To limit the problem with different local weather situations two canopy platforms for reference PPFD-measurements were used.

In the direct seeding experiment the fast predation rate was unexpected and if an experiement like this should be repeated, more intense measurements the first days after seeding would be preferable as this would provide better understanding of seed/seedling losses. The seeds originated from a few tree individuals, more diversified genetic populations originated from several tree species might give a better protection to pests and predation (e.g. Wyatt-Smith 1995).

5.7 Natural or artificial regeneration?

There was substantial natural regeneration in all surveyed transects (Paper I) of secondary forest patches 20 years after disturbances by El Niño-induced drought, fire and/or selective logging. If this is sufficient for recovering the main traits of old-growth forests´ structure and ecosystem functions to recover can only be hypothesized from the current data and current knowledge. As mentioned in the introduction, we still lack models describing the long-term development of these types of disturbed forests. Luc (2010) found seedling/sapling diversity to be similar in patches of secondary forests not yet subjected to gap- or line-planting versus planted spots (within the Kalabakan forest reserve), but the forest patches subjected to enrichment planting had higher total numbers of naturally and artificially regenerated dipterocarp seedlings/saplings.

According to the results presented in Paper III, a very low proportion of under-planted seedlings would grow into trees, but seedling mortality may be at its highest during the initial years. Sayer et al. (2004) argue that natural recovery should be relied upon, claiming that management efforts such as line-planting open up the canopy and make secondary forests more drought-prone and therefore more susceptible to fire.

However, there are other than ecological aspects to consider, (i.e. socio-economical) notably as the pressures on forest lands for agriculture or industrial activities remain high (Anon. 2011, see also Figure 1) management efforts may highlight the importance of secondary forests and protect such areas from further degradation.

Secondary forests today comprise an important proportion of remaining tropical forest cover in the world and, as demonstrated by Kammesheidt (2002), less effort (time, manpower, costs etc.) is required to restore forests of original structure and function from secondary forest than from forests that have been further degraded or converted to plantations etc. It is, however, important to preserve intact old-growth forest in the landscape from which tree species can disperse (e.g. see Guarigata and Ostertag 2002, Meijard et al. 2005).

5.8 Conclusions and implications for forest management

5.8.1 General conclusions

Tree seedlings were recruited in forests of all disturbance categories and displayed high variations in species composition. Less disturbed forests had higher accumulations of seedling taxa than the most disturbed forest patches. The latter also displayed lower abundance of potential seed trees.

Artificial gap creation in *Macaranga*-dominated secondary tropical rain forests, by canopy and sub-canopy treatments, had positive effects on both light conditions above the forest floor and the establishment of under-planted dipterocarp seedlings.

Sub-canopy slashing of pioneer saplings and trees with diameters (dbh) less than 10cm improved the light availability near the ground (in terms of both canopy openness and PPFD_R although not significant for relative PPFD at 0 and 6 months after treatments), seedling survival (for three of the four tested species), and relative height and biomass increments of the seedlings. These positive sub-canopy treatment effects persisted throughout the 30-month study period.

Canopy treatments (felling or girdling of selected canopy trees) also had positive effects on light conditions and relative growth rates of the seedlings, but did not affect seedling survival rates. Among canopy treatments, felling caused immediate, strong positive effects on light conditions and seedling height growth, but these effects gradually disappeared, while the effects of girdling were weaker but more persistent.

After two years, no significant effects of canopy treatments on light conditions and relative height growth rates of the seedlings were detected. Felling canopy trees, and sub-canopy slashing, resulted in the highest relative biomass increments during the study period. After 30 months seedling survival rates averaged 73-86 %, for the four dipterocarp species. There were also significant between-species differences in the seedlings' survival and growth rates. Direct seeding of four species (*Shorea gibbosa*, *S. palembanica*, *Shorea* sp. and *Intsia palembanica*) resulted in almost 100% mortality, possibly due to high densities of seed predators in the area at the time.

5.8.2 Implications for forest management

Based upon these results, the following general suggestions for managing 20 year-old secondary successions in forests after selective logging, drought and fire can be made:

1. Forest height structure variables and the presence of remnant non-pioneer trees can, to some extent, be used as guidelines in assessments of whether or not artificial regeneration measures are required.
2. Sub-canopy treatments had a more durable effect than girdling or felling pioneer canopy trees. Therefore, sub-canopy slashing can be recommended rather than girdling or felling to increase forest floor light for under-planted seedlings.
3. Under-planted seedlings grow better with more light, but intense management is likely to be needed if the canopy openness exceeds ca. 15%, as this will probably stimulate competing weeds. Since survival rates of seedlings were not affected by the shade-reduction treatments, a treatment that results in a slightly slower initial growth but less above- and below-ground competition for light, water and nutrients might be more effective.
4. Further evaluation of direct seeding is required before attempting larger scale applications and, according to these results, it is not a reliable regeneration method.

5.8.3 Future research

As the pressure on tropical forest areas is still increasing, the management and conservation of secondary forests remain important research issues. In south-east Asia areas of Macaranga-dominated forests expand following El Niño-induced dry spells, fire and logging (Uhl 1998, Slik et al. 2002, Slik and Eichhorn 2003). Future climate changes may also contribute to shifts in forest composition and changes in human land use (Anon. 2001, Holmgren et al. 2001). In this context, both generally and specifically in the ongoing enrichment planting program in Kalabakan Forest Reserve, aspects that warrant further attention include the following:

To obtain long-term studies tree species initiation and the dynamics and interactions of canopy and sub-canopy strata in *Macaranga*-dominated secondary forests over longer timeframes (30 years or more) after logging and fire, eventually in permanent plots to allow repeated measurements.

To study site and light requirements in tree species of other taxa than Dipterocarpaceae, for example also test how these thrive after under-planting in artificial gaps.

To study how and when mycorrhiza colonize planted seedlings and if there are differences between sites in their colonization rates due to previous disturbances such as fire and soil compaction caused by logging or if the NPK fertilizer given to all plants has a positive or negative effect on inoculation of mycorrhiza in seedlings subjected to under-planting.

To test direct seeding but with other tree species and with other timing, instead of after mast-fruit spells seeding could be tested before or within heavy seed rain. The hypothesis that soil scarification and litter removal litter will improve germination – or, if remaining litter instead prevent predation -reveal further evaluation.

References

Acres, B.D., Bower, R.P., Burrough, P.A., Folland, C.J., Kalsi, M.S., Thomas, P., Wright, P.S. (1975). The soils of Sabah. Volume 1. Classification and description (with an introduction to Volumes 1-5). *Land Resource Study* 20, Land Resources Division, Surrey, England.

Ådjers, G., Hadengganan, S., Kuusipalo, J., Nuryanto, K., Vesa, V. (1995). Enrichment planting of dipterocarps in logged-over secondary forests: effect of width, direction, and maintenance method of planting line on selected Shorea species. *Forest Ecology and Management* 73: 259-270.

Aide, T.M., Zimmerman, J.K., Pascarella, J.B., Rivera, L., Marcano-Vega, H. (2000). Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restoration Ecology* 8: 328-338.

Anderson, M.L. (1951). Spaced group-planting and irregularity of stand-structure. *The Empire Forestry Review* 30: 328-332.

Anderson, M.L. (1953). Spaced group-planting. *Unasylva* 7: 55-63.

Anon. (2005). WinScanopy 2005a. For hemispherical image analyses. Regent Instruments Inc., Canada.

Anon. (1999). *SAS/STAT User's guide*, version 8, Cary, NC. SAS Institute Inc.

Anon. (2011). *The state of forest resources – a regional analyses.* FAO, Rome.

Appanah, S., Weinland, G.(1993). Planting quality timber trees in Penisular Malaysia – a review. *Malayan Forest Records* No. 38. Forest Research Institute Malaysia, Kuala Lumpur, Malaysia

Arroyo-Mora, J.P., Sánchez-Azofeifa, G.A., Rivard, B., Calvo, J.C., Janzen, D.H. (2005). Dynamics in landscape structure and composition for the Chorotega region, Costa Rica from 1960 to 2000. *Agriculture, Ecosystems and Environment* 106: 27-39.

Ashton, P.M.S., de Zoysa, N.D. (1989). Performance of Shorea-Trapezifolia (Thwaites Ashton) seedlings growing in different light regimes. *Journal of Tropical Forest Science* 1: 356-364.

Ashton, M.S. (1995). Seedling growth of co-occurring Shorea species in the simulated light environments of a rain forest. *Forest Ecology and Management* 72: 1-12.

Ashton, M.S. (1998). Seedling ecology of mixed-dipterocarp forest. In *A review of Dipterocarps. Taxonomy, ecology and silviculture*, pp 89-98.

Ashton, M.S., Gunatilleke, C.V.S., Singkakumara, B.M.P., Gunatilleke, I.A.U.N. (2001). Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. *Forest Ecology and Management* 154: 409-430.

Bagchi, R., Press, M.C., Scholes, J.D. (2010). Evolutionary history and distance dependence control survival of dipterocarp seedlings. *Ecology Letters* 13: 51-59.

Bagchi, R., Press, M.C., Scholes, J.D. (2010). Evolutionary history and distance dependence control survival of dipterocarp seedlings. *Ecology Letters* 13: 51-59.

Bazzaz, F.A. (1975). Plant species diversity in old-field successional ecosystems in Southern Illinois. *Ecology* 56: 485-488.

Berry, N.J., Phillips, O.L., Ong, R.C., Hamer, K.C. (2008). Impacts of selective logging on tree diversity across a rainforest landscape: the importance of spatial scale. *Landscape Ecology* 23: 915-929.

Bischoff, W., Newbery, D.M., Lingenfelder, M., Schnaeckel, R., Petol, G.H., Madani, L., Ridsdale, C.E. (2005). Secondary succession and dipterocarp recruitment in Bornean rain forest after logging. *Forest Ecology and Management* 218: 174-192.

Brearley, F.Q., Prajadinata, S. Kidd, P.S., Proctor, J., Suriantata (2004). Structure and floristics of an old secondary rain forest in Central Kalimantan, Indonesia, and a comparison with adjacent primary forest. *Forest Ecology and Management* 195: 385-397.

Brown, S., Lugo, A.E. (1990). Tropical secondary forests. *Journal of Tropical Ecology* 6: 1-32.

Buschbacher, R., Uhl, C., Serrao, E.A.S. (1988). Abandoned pastures in Eastern Amazonia (II). Nutrient stocks in the soil and vegetation. *Journal of Ecology* 76: 682-699.

Buschbacher, R.J. (1990). Natural forest management in the humid tropics: ecological, social and economic considerations. *Ambio* 19: 253-258.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A.m White, P. (1990). Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Canadian Journal of Forest Research* 20: 620-630.

Cedergren, J. (1996). A silvicultural evaluation of stand characteristics, pre-felling climber cutting and directional felling in a primary dipterocarp forest in Sabah, Malaysia. *Acta Universitatis Agriculturae Sueciae* No. 9, Umeå.

Chazdon, R.L., Fetcher, N. (1984). Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* 72: 553-564.

Chazdon, R.L., Pearcy, R.W. (1991). The importance of sunflecks for forest understorey plants. *BioScience* 41: 760-766.

Chin, L.T. (1973). Occurrence of seeds in virgin forest top soil with particular references to secondary species in Sabah. *Malaysian Forester* 36: 185-195.

Cochrane, M.A., Barber, C. (2009). Climate change, human land use and future fires in the Amazon. *Global Change Biology* 15: 601-612.

Cockburn, P.F. (1975). Phenology of Dipterocarps in Sabah. *Malaysian Forester* 38: 160-170.

Condit, R., Hubbell, S.P., Foster, R.B. (1996). Changes in tree species abundance in a Neotropical forest: impact of climate change. *Journal of Tropical Ecology* 12: 231-256.

Connel, J.H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in tropical rain forest trees. In *Dynamics of populations* pp 298-312 (ed. P.J. den Boer and G.R. Gradwell). PUDOC, Wageningen.

Curran,L.M., Caniago, I., Paoli, G.D., Astianti, D., Kusneti, M., Leighton, M., Nirarita, C.E., Haeruman, H. (1999). Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* 286: 2184-2188.

Curran, L., Leighton, M. (2000). Vertebrate responses to spatiotemporal variation in seed predation of mast fruiting Dipterocarpaceae. *Ecological Monographs* 70: 101-128.

Curran, L., Webb, C.O. (2000). Experimental tests of the spatiotemporal scale of seed predation in mast fruiting Dipterocarpaceae. *Ecological Monographs* 70: 129-148.

Davies, S.J. (1998). Photosynthesis of nine pioneer Macaranga species from Borneo in relation to life history. *Ecology* 79: 2292-2308.

Davies, S.J. (2001). Tree mortality and growth in 11 sympatric *Macaranga* species in Borneo. *Ecology* 82: 920-932.

Delissio, L.J., Primack, R.B., Hall, P., Lee, H.S. (2002). A decade of canopy-tree seedling survival and growth in two Bornean rain forests: persistence and recovery from suppression. *Journal of Tropical Ecology* 18: 645-648.

Denslow, J.S. (1987). Tropical rain forest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18: 431-451.

Doust, S. J., Erskine, P. D., Lamb, D. (2008). Restoring rainforest species by direct seeding: Tree seedling establishment and growth performance on degraded land in the wet tropics of Australia. *Forest Ecology and Management* 256: 1178-1188.

Enfield, D.B. (1992). Historical and prehistorical overview of El Niño/Southern Oscillation. In *Henry F. Diaz and Vera Markgraf (Eds.):* El *Niño. Historical and paleoclimatic aspects of the Southern Oscillation.* Cambridge University Press.

Engel, V. L., Parotta, J. A. (2001). An evaluation of direct seeding for reforestation of degraded lands in São Paolo state, Brazil. *Forest Ecology and Management* 152: 169-181.

Finegan, B. (1992). The management potential of neotropical secondary lowland rain forest. *Forest Ecology and Management* 47: 295-321.

Finegan, B. (1996) Pattern and process in neotropical secondary rain forests: the first 100 years of succession. *Trends in Ecology and Evolution* 11: 119-124.

Finegan, B, Delgado, D.A. (2000). Structural and floristic heterogeneity in a 30-year-old Costa Rican rain forest restored on pasture through natural secondary succession. *Restoration Ecology* 8: 380–393.

Florentine, S.K., Westbrooke, M.E. (2004). Restoration on abandoned tropical pasturelands- do we know enough? *Journal for Nature Conservation* 12: 85-94.

Forshed, O. (2006). *Stand structure and development after selective logging with systematically aligned skid trails, directional felling and climber cutting in a dipterocarp rainforest in Sabah, Malaysia.* Doctoral thesis No. 2006: 30. Faculty of Forest Sciences, Swedish University of Agricultural Sciences, Umeå, Sweden.

Fox, J.E.D. (1972). *The natural vegetation of Sabah and natural regeneration of dipterocarps.* PhD thesis, Department of Forestry and Wood Sciences, University College of North Wales, Bangor, UK.

Garcia, C. (1999). Innoprise-IKEA Forest Rehabilitation Project (INIKEA). *Unpublished working report.* Luasong Forestry Centre, Sabah, Malaysia.

Goldammer, J.G. (2007). History of equatorial vegetation fires and fire research in Southeast Asia before the 1997-98 episode: A reconstruction of creeping environmental changes. *Mitigation and Adaptation Strategies for Global Change* 12: 13-32.

Goldammer, J.G. (1996). Fire in dipterocarp forests. In *Schulte and Schöne (Eds.) 1996. Dipterocarp forest ecosystems: towards sustainable management.*

Goldammer, J.G., Seibert, B. (1990). The impact of droughts and forest fires on tropical lowland rain forest of East Kalimantan. In Goldammer, J.G., (Ed.) Fire in the tropical biota: Ecosystem processes and global challenges. *Ecological Studies* 84: 32-44. Springer-Verlag, Berlin and New York.

Grainger, A. (1992). *Controlling tropical deforestation.* Earthscan, London.

Grainger, A. (2008). Difficulties in trading the long-term global trend in tropical forest area. *PNAS* 105: 818-823.

Guariguata, M.R., Ostertag, R. (2002). Sucesión secundaria. In *Ecología y conservación de Bosques Neotropicales.* Guariguata, M.R., Kattan, G.H., (Eds.). Libro Universitario Original, Cartago, Costa Rica.

Gunatilleke, C.V.S., Gunatilleke, I.A.U.S., Esufali, S., Harms, K.E., Ashton, P.M.S., Burslem, D.F.R.P., Ashton, P.S. (2006). Species-habitat associations in a Sri Lankan dipterocarp forest. *Journal of Tropical Ecology* 22: 371-384.

Harger, J.R.E. (1995)a. ENSO variations and drought occurrence in Indonesia and the Phillipines. *Atmospheric Environment* 29: 1943-1955.

Harger, J.R.E. (1995)b. Air-temperature variations and ENSO effects in Indonesia, The Philippines and El Salvador. ENSO patterns and changes from 1866-1993. *Atmospheric Environment* 29: 1919-1942.

Hjerpe, J., Hedenås, H., Elmqvist, T. (2001). Tropical rain forest recovery from cyclone damage and fire in Samoa. *Biotropica* 33: 249-259.

Holmgren, M., Scheffer, M., Ezcurra, E., Gutierraz, J.R., Mohren, G.M.J. (2001). El Niño effects on the dynamics of terrestrial ecosystems. *Trends in Ecology and Evolution* 16: 89-94.

Ilstedt, U. (2002). Soil Degradation and Rehabilitation in Humid Tropical Forests (Sabah, Malaysia. Doctoral thesis. Swedish University of Agricultural Sciences, Umeå.

Jacobs, M. (1981). The tropical rain forest. A first encounter. Springer-Verlag. Berlin.

Janzen, D.H. (1970). Herbivores and the number of trees in tropical forests. *American Naturalist* 104: 501-528.

Jennings, S.B., Brown, N.D., Sheil, D. (1999). Assessing forest canopies and understorey illumination, canopy closure, canopy cover and other measures. *Forestry* 72: 59-73.

Josefsson, T. (2009). Pristine forest landscapes as ecological references. Doctoral thesis. *Acta Universitatis Agriculturae Sueciae* 2009:77, Umeå.

Kammesheidt, L. (2002). Perspectives on secondary forest management in tropical humid lowland America. *Ambio* 31: 243-250.

Kartawinata, K., Adisoemarto, S., Riswan, S., Vayda, A.P. (1981). The impact of man on a tropical forest in Indonesia. *Ambio* 10: 115-125.

Kellman, M., Tackaberry, R. (1997). Tropical environments: the functioning and management of tropical ecosystems. Routledge, London and New York.

Kennedy, D.N., Swaine, M.D. (1992). Germination and growth of colonizing species in artificial gaps of different sizes in dipterocarp rain forest. *Philosophical Transactions of the Royal Society of London* B 335: 357-366.

Lamb, A.F.A. (1969). Artificial regeneration within the humid tropical rain forest. *The Commonwealth Forestry Review* 48: 41-43.

Lamb, D. (1998). Large-scale restoration of degraded tropical forest lands: the potential role of timber plantations. *Restoration Ecology* 6: 271-279.

Lamb, D., Erskine, P., Parrotta, J.A. (2005). Restoration of degraded tropical forest landscapes. *Science* 310: 1628-1632.

Langner, A., Siegert, F. (2009). Spatiotemporal fire occurence in Borneo over a period of 10 years. *Global Change Biology* 15: 48-62.

Leakey, A.D.B., Scholes. J.D., Press, M.C. (2005). Physiological and ecological significance of sunflecks for dipterocarp seedlings. *Journal of Experimental Botany* 56: 469-482.

Leopold, A.C., Salazar, J. (2008). Understory species richness during restoration of wet tropical forest in Costa Rica. *Ecological Restoration* 26: 22-26.

Luc, V. (2010). *Effects of ten year old enrichment plantings in a secondary dipterocarp rainforest. A case study of stem and species distribution in Sabah, Malaysia.* Graduate thesis 2010:20, Swedish University of Agricultural Sciences.

McCune, M. & Mefford, M.J. (1999) *Multivariate analysis of ecological data, version 4.20.* MjM Software design, Gleneden Beach, Oregon.

McCune, M. & Grace, J.B. (2002) *Analysis of ecological communities.* MjM Software design.

MacKinnon, K., Hatta, G., Halim, H., Mangalik, A. (1996). *The Ecology of Kalimantan, Indonesian Borneo.* The Ecology of Indonesia Series, Volume III. Periplus Editions Ltd.

Malmer, A., van Noorsdwijk, M., Bruijnzeel, L.A. (2005). Effects of shifting cultivation and forest fire. In *Forests, Water and People in The Humid Tropics*, ed. M. Bonell and L.A. Bruijnzeel, Cambridge University Press.

Malmer, A. (1996). Observations on slope processes in a tropical rain forest environment before and after forest plantation establishment. In *Anderson and Brooks (Eds) Advances in hillslope processes*, vol 2, John Wiley and Sons Ltd.

Manokaran, N., Swaine, M.D. (1994). Population dynamics of trees in dipterocarp forests of Peninsular Malaysia. *Malayan Forest Records* No. 40. Forest Research Institute Malaysia, Kepong, Kuala Lumpur, Malaysia.

Marsh, C.W. (1995). *Danum Valley Conservation Area. Management plan.* Yayasan Sabah, Innoprise Corporation Sdn. Bhd., Kota Kinabalu.

Meijard, E., Sheil, D., Nasi, R., Augeri, D., Rosenbaum, B., Iskandar, D., Setyawati, T., Lammertink, M., Rachmatika, I., Wong, A., Soehartono, T., Stanley, S., O´Brien, T. (2005). *Life after logging: Reconciling wildlife conservation and production forestry in Indonesian Borneo.* Center for International Forestry Research (CIFOR), Bogor, Indonesia.

Montagini, F., Eibl, B., Grance, L., Maiocco, D., Nozzi, D. (1997). Enrichment planting in overexploited forests of the Paranese region of Misiones, Argentina. *Forest Ecology and Management* 99: 237-246.

Montgomery, R.A., Chazdon, R.L. (2001). Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology* 82: 2707-2718.

Meijer, W., Wood, G.H.S. (1964). Dipterocarps of Sabah (North Borneo). *Sabah Forest Record* No. 5, Forest Department, Sandakan.

Newbery, D.McC., Campbell, E.J.F., Lee, Y.F., Ridsdale, C.E., Still, M.J. (1992). Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative abundance and family composition. *Philosophical Transactions of Royal Society London Series-B* 335: 341-356.

Newman, M.F., Burgess, P.F., Whitmore, T.C. (1996). *Manuals of Dipterocarps for Foresters. Borneo Island Light Hardwoods.* Royal Botanic Garden, Edinburgh and Centyer For International Forestry Research, Bogor, Indonesia.

Newman, M.F., Burgess, P.F., Whitmore, T.C. (1998). *Manuals of Dipterocarps for Foresters. Borneo Island Medium and Heavy Hardwoods.* Royal Botanic Garden, Edinburgh and Centyer For International Forestry Research, Bogor, Indonesia.

Norisada, M., Kojima, K. (2005). Photosynthetic characteristics of dipterocarp species planted on degraded sandy soils in southern Thailand. *Photosynthetica* 43: 491-499.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. (2002). Low host specificity of herbivorous insects in a tropical forest. *Nature* 416: 841-844.

Nykvist, N. (1996). Regrowth of secondary vegetation after the Borneo fire of 1982-83. *Journal of Tropical Ecology* 12: 307-312.

Otsamo, R. (2000a) Early development of three planted indigenous tree species and natural understorey vegetation in artificial gaps in an Acacia mangium stand on an Imperata cylindrical grassland site in South Kalimantan, Indonesia. *New Forests* 19: 51-68.

Otsamo, R., (2000b). Secondary forest regeneration under fast-growing forest plantations on degraded Imperata cylindrica grasslands. *New Forests* 19: 69-93.

Paoli, G.D., Curran, L.M., Slik, J.W.F. (2008). Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo. *Oecologica* 155: 287-299.

Peña-Claros, M., Boot, R.G.A., Dorado-Lora, J., Zonta, A. (2002). Enrichment planting of Betholletia excelsa in secondary forest in the Bolivian Amazon: effect of cutting line width on survival, growth and crown traits. *Forest Ecology and Management* 161: 159-168.

Pinard, M. (1996). Site conditions limit pioneer tree recruitment after logging of dipterocarp forests in Sabah, Malaysia. *Biotropica* 28: 2-12.

Pinard, M., Putz, F., Tay, J. (2000).Lessons learned from the implementation of reduced impact logging in hilly terrain in Sabah, Malaysia. *International Forestry Review* 2: 33-39.

Portsmuth, A., Niinemets, Ü. (2006). Interacting controls by light availability and nutrient supply on biomass allocation and growth of *Betula pendula* and *B. pubescens* seedlings. *Forest Ecology and Management* 227: 122-134.

Raich, J.W. (1989). Seasonal and spatial variation in the light environment in a tropical dipterocarp forest and gaps. *Biotropica* 21: 299-302.

Ramos, J.M., del Amo, S. (1992). Enrichment planting in a tropical secondary forest in Veracruz, Mexico. *Forest Ecology and Management* 54: 289-304.

Raven, P.H., Evert, R.F., Eichorn, S.E. (1992). *Biology of Plants.* 5th Ed. New York, United States of America.

Rich, P.M., Clark, D.B., Clark, D.B., Oberbauer, S.F. (1993). Long-term study of solar radiation regimes in a tropical wet forest using quantum sensors and hemispherical photography. *Agricultural and Forest Meteorology* 65: 107-127.

Richards, P.W. 1996. *The Tropical Rain Forest.* 2nd Ed. Cambridge University Press.

Rijkers, T. (2000a). *Leaf function in tropical rain forest trees: the effect on light in leaf morphology and physiology in different-sized trees.* PhD thesis, Wageningen University, Wageningen, The Netherlands.

Rijkers, T., de Vries, P.J., Pons, T.L., Bongers, F. (2000b). Photosynthetic induction in saplings of three shade-tolerant tree species: comparing understorey and gap habitats in a French Guiana rain forest. *Oecologia* 125: 331-340.

Sabin, T.E., Stafford, S.G. 1990. *Assessing the need for transformation of response variables. Special publication* 20. College of Forestry, Oregon State University.

Sayer, J., Chokkalingam, U., Poulsen, J. (2001). The restoration of forest biodiversity and ecological values. *Forest Ecology and Management* 201: 3-11.

Sayer, J., Chokkalingam, U., Poulsen, J. (2004). The restoration of forest biodiversity and ecological values. *Forest Ecology and Management* 201: 3-11.

Shiel, D., Sayer, J.A., O´Brien, T. (1999). Tree diversity and conservation in logged rain forest. *Science* 284: 1587.

Sist, P., Sheil, D., Kartawinata, K., Priyadi, H. (2003). Reduced impact logging in Indonesian Borneo: some results confirming the need for new silvicultural prescriptions. *Forest Ecology and Management* 179: 415-427.

Slik, J.W.F., Verburg, R.W. and Kessler, P.J.A. (2002). Effects of fire and selective logging on the tree species composition of lowland dipterocarp forest in east Kalimantan, Indonesia. *Biodiversity and Conservation 11: 85-98.*

Slik, J.W.F., Eichhorn, K.A.O. (2003). Fire survival of lowland tropical rain forest trees in relation to stem diameter and topographic position. *Oecologica* 137: 446-455.

Slik, J. W. F. (2005). Assessing tropical lowland forest disturbance using plant morphological and ecological attributes. *Forest Ecology and Management* 205: 241-250.

Slik, J.W.F., Bernard, C.S., van Beek, M., Breman, F.C., Eichhorn, K.A.O. (2008). Tree diversity, composition, forest structure and aboveground biomass dynamics after single and repeated fire in a Bornean rain forest. *Oecologica* 158: 579-588.

Stehman, S.V., Meredith, M.P. (1995). Practical analyses of factorial-experiments in forestry. *Canadian Journal of Forest Research* 25: 446-461.

Sun, D., Dickinson, G. (1995). Direct seeding for rehabilitation of degraded lands in north-east Queensland. *Australian Journal of Soil and Water Conservation* 8: 14-17.

Swaine, M.D., Whitmore, T.C. (1988). On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81-86.

Swanberg, L. (2005). *Biomass functions for under-planted dipterocarp seedlings in a secondary tropical rain forest dominated by Macaranga spp.* Graduate thesis 2005-6. Department of Silviculture, Swedish University of Agricultural Sciences, Umeå, Sweden.

Tangki, H., Chappel, N.A. (2008). Biomass variation across selectively logged forest within a 225-km^2 region of Borneo and its predictions by Landsat TM. *Forest Ecology and Management* 256: 1960-1970.

Tennakoon, M.M.D., Gunatilleke, I.A.U.N., Gunatilleke C.V.S., Hafeel, K.M., Seneviratne, G., Ashton, P.M.S. (2005). Ectomycorrhizal colonization and seedling growth of Shorea (Dipterocarpaceae) species in simulated shade environments of a Sri Lankan rain forest. *Forest Ecology and Management* 208: 399-405.

Turner, I.M. (2001). The ecology of trees in the tropical rain forest. *Cambridge Tropical Biology Series.* University Press, Cambridge.

Uhl, C., Vieira, I.C.G. (1989). Impacts of selective logging in the Brazilian Amazon: A case study from the Paragominas region of the State of Para. *Biotropica* 21: 98-106.

Uhl, C. (1998). Perspectives on wildfire in the humid tropics. *Conservation Biology* 12: 942-943.

Van Kuijk, M. (2008). *Forest regeneration and restoration in Vietnam.* PhD thesis, Utrecht University, The Netherlands.

van Nieuwstadt, M.G.L., Sheil, D., Kartawinata, K. (2001). The ecological consequences of logging in the burned forests of East Kalimantan, Indonesia. *Conservation Biology* 15: 1183-1186.

Verburg, R., van Eijk-Bois, C. (2003). Effects of selective logging on tree diversity, composition and plant functional type patterns in a Bornean rain forest. *Journal of Vegetation Science* 14: 99-110.

Vincent, A., Davies, S.J. (2003). Effects of nutrient addition, mulching and planting-hole size on early performance of Dryobalanops aromatic and Shorea parvifolia planted in secondary forest in Sarawak, Malaysia. *Forest Ecology and Management* 180: 261-271.

Walsh, R.P.D. (1996). Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. *Journal of Tropical Ecology* 12: 385-407.

Walsh, R.P.D. and Newbery, D.M. (1999). The ecoclimatology of Danum, Sabah, in the context of the world´s rainforest regions, with particular reference to dry periods and their impact. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 354: 1869-1883.

Whitmore, T.C. (1998). *An introduction to tropical rain forests.* Oxford University Press, UK.

Woods, P. (1989). Effects of logging, drought and fire on structure and composition of tropical forests in Sabah, Malaysia. *Biotropica* 21: 290-298.

Wyatt-Smith, J. (1995). Manual of Malayan Silviculture for inland forests. *Malayan Forest Records* 1:23. Kuala Lumpur, Malaysia.

Yasman, I., Hernawan (2002). *Manual persemaian Dipterocarpaceae.* Jakarta, Indonesia.

Zar, J.H. (1999). *Biostatistical analyses.* Upper Saddle River, N.J., Prentice Hall, U.S.

URL:

http://www.licor.com/env/Products/Sensors/190/li190_description.jsp

Personal communication:

Alloysius, D. (2004). Project manager, Inikea Forest Rehabilitation Programme. Luasong.
Garcia, C. (2003). Project manager, Inikea Forest Rehabilitation Programme. Luasong.
Holm, S. (2009). Statstician, Swedish University of Agricultural Sciences, Umeå.
Madani, L. (2003). Forest botanist, Forestry Department, Sandakan.
Yap, S.W. (2002). Researcher, Yayasan Sabah, Kota Kinabalu.

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