Artificial canopy gaps and the establishment of planted dipterocarp seedlings in *Macaranga spp*.-dominated secondary tropical rain forests of Sabah, Borneo

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Abstract

The continued losses of primary tropical rain forests have increased the pressure on secondary tropical rain forests and led to additional logging and changes to other land uses. A requirement for a secondary tropical forest to recover the main traits of old-growth forests is the regeneration of non-pioneer (climax) species. To accelerate the recovery of non-pioneer species where natural regeneration is insufficient, enrichment planting can be used in artificially created gaps or lines. The studies underlying this thesis evaluated several approaches to canopy gap creation in *Macaranga spp*.-dominated secondary tropical rain forests in Sabah, Borneo, and their effects on light conditions close to the forest floor and both survival and relative growth rates among under-planted seedlings of four dipterocarp (*Dipterocarpaceae*) species (*Dipterocarpus applanatus*, *D. caudiferus*, *Shorea argentifolia* and *S. pauciflora*; all non-pioneers). On average the total basal area of trees with diameters at breast height (DBH) >0.1 m in the *Macaranga*-dominated experimental sites was 35 m^2 ha^{-1} and the mean number of stems of this size was 480 per ha.

Three canopy treatments (selective girdling or selective felling of canopy trees and control (untreated)) were combined with two sub-canopy treatments (slashing smaller woody pioneer stems or untreated control) in a randomized split-plot block design. Hemispherical photographs (showing canopy openness) and recordings of above-canopy and forest floor photosynthetic photon flux densities (PPFD) were simultaneously taken in four of the seven blocks before the treatments and 0, 6, 18 and 30 months later. Seedling survival was registered every third month and seedling height every six months in all blocks, and a sample of seedlings was selected for destructive measurements (fresh and dry weight determination) both at the start of the experiments and at the final revision after 30 months. Analyses of variance (ANOVA) using general linear models (GLM) were used to evaluate treatment effects.

The basal area ratio of canopy trees selected for girdling or felling averaged 31.2 % of the initial basal area. The results showed that the artificial gap creation, by means of canopy and sub-canopy treatments, had positive effects on both light conditions above the forest floor and the establishment of under-planted dipterocarp seedlings. The light intensities under the closed canopies and in the gaps after the treatments averaged ca. 2 % and 10-30% of above-canopy levels, respectively. Canopy openness on the forest floor means were ca. 10 % before and 10-15 % after the treatments. Sub-canopy slashing of pioneer saplings and smaller trees significantly increased light intensities, measured as both canopy openness and relative PPFD ($PPFD_R$-values were 3 – 6 percent units higher than in the control) as well as seedling survival rates (for three out of the four species) and their relative height and biomass increments. These positive sub-canopy treatment effects persisted throughout the study period. Canopy treatments (felling or girdling of selected canopy trees) also had significantly positive effects on light conditions and seedling relative growth, but did not significantly affect seedling survival. 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 seedling relative height growth were detected. Felling canopy trees and sub-canopy slashing resulted in the highest relative biomass increments during the study period. The survival rates averaged 73-86 %, after 30 months, for the four dipterocarp species. There were also significant between-species differences in seedling survival and growth rates.

Key words: canopy openness, canopy treatments, *Dipterocarpaceae*, enrichment planting, logging and fire, relative PPFD, seedling growth, seedling survival.

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II. Romell, E., Hallsby, G., Karlsson, A. and Garcia, C. 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. Manuscript

Introduction

Secondary tropical forests in South-East Asia

Secondary forests are defined as forests that have grown naturally after an important disturbance (e.g. logging, fire, storm or insect attack) displaying major differences in structure and/or canopy species composition compared to nearby primary forests on similar sites (Woods 1989, Brown and Lugo 1990, Nykvist 1996). In recent decades, changes in forest land use patterns following logging have caused large-scale forest losses in Southeast Asia. Climatic factors have also played a role in these changes, notably dry spells associated with El Niño southern oscillations (Walsh 1996) that have repeatedly occurred in Borneo, and elsewhere, during the last century (Walsh and Newbery 1999). Prolonged El Niño-induced dry spells followed by fire in tropical Bornean lowland rainforests occurred in 1982-83 (Woods 1989, Nykvist 1996) and 1997-98 (Dennis 1999). Drought either alone or in combination with fire may cause substantial mortality among seedlings, saplings and adult trees (Slik et al. 2002).

The continued loss of old-growth (primary) tropical rain forest cover (Anon. 2001) has increased the pressure on secondary rain forests and led to additional logging and finally changes to other land uses. A requirement for a secondary forest to recover the main traits of old-growth forests is the successful regeneration of non-pioneer (climax) species.

The time required for a secondary forest to recover the characteristic structure, function and diversity of a primary (old-growth) forest may depend on the timing and intensity of previous disturbance factors, i.e. logging and/or fire (Woods 1989, Ashton et al. 2001, Slik et al. 2003). Secondary forests pass through several succession phases, and the tree species composition of the canopy layer changes over time (Ashton et al. 2001). Other factors may also influence the duration and quality of forest recovery, including the local climate, soil conditions and land use in surrounding areas (which affects factors such as the distance to possible seed sources). The regeneration patterns and species diversity among seedlings and saplings may be greatly changed in comparison to the old-growth forest (Slik and Eichhorn, 2003). Typically, natural regeneration in logged and/or fire-ravaged rainforests in Borneo is dominated by pioneer tree species of the *Macaranga* genus (*Euphorbiacecae*) (Slik et al. 2002, Slik and Eichhorn 2003, Slik 2005).

In Bornean lowland primary forests a majority of the prominent non-pioneer tree species belong to the *Dipterocarpaceae* family (Slik et al. 2003). These dipterocarp species are highly valued in management plans where the objectives may be commercial forestry, restoration projects or forest conservation. These long-lived canopy dominants that characterise the old-growth lowland rain forests of Borneo have a number of traits that hinder their regeneration relative to the pioneer species that colonize logged and burnt sites. Logging depletes the potential seed supply from adult dipterocarps and emerging advance growth seedlings and saplings are killed by fire (Woods 1989, Slik and Eichhorn 2003). In combination with dry spells, prospects for natural recovery of severely disturbed dipterocarp forests do not look very promising. Delissio and Primack (2003) found seedlings and saplings of non-pioneer (climax) species to be particularly sensitive to drought. The reproduction of dipterocarps and other non-pioneers are in addition irregular, the reproduction of many species being aggregated in mast fruiting years (Cockburn 1975, Delissio et al. 2003, Wong et al. 2005). Examples of the success-ful natural regrowth of dipterocarps and other non-pioneer species in secondary (logged) forests have been reported (cf. Bischoff et al. 2005), but basic knowledge regarding regeneration patterns of non-pioneer tree species in secondary forests that have established after logging and forest fires is still limited.

Enrichment planting

Enrichment planting is a method that can be used in attempts to supplement natural regeneration where it is judged to be insufficient (Chai 1975, Appanah and Weinland 1993). The method involves planting nursery-raised seedlings in cleared lines or in gaps that have either been created artificially or naturally occur (Wyatt-Smith 1963).

Line-planting is now an established method (cf. Lamb 1969, Montagini 1997, Bebber et al. 2002, Peña-Claros 2002). However, gap-planting techniques in which clusters of seedlings are under-planted in artificially created gaps (cf. Otsamo 2000) or pre-existing gaps (cf. d'Oliviera 2000) are still at an experimental stage. The gap-cluster planting approach is similar to "group-planting" as described by Anderson (1951 and 1953) and Donis (1956) or "nest-planting" (cf Andersson 1951, Ramos and del Amo 1992), in which seedlings of different species are planted together in a cluster. In contrast to planting in regularly spaced lines, gap cluster planting has some resemblance to natural gap dynamics (c.f. Denslow 1987, Kuuluvainen et al. 2002), which could be considered advantageous in restoration programs. Dupuy and Chazdon (2006) recommended that 50-100 m^2 gaps should be used to resemble natural gap sizes in humid tropical rain forests. Ådjers et al. (1995) proposed, for technical reasons, gap planting in "multi-storey forests" in areas with undulating topography, and line planting in even-aged successions on former shifting cultivation sites.

Practical examples of enrichment plantations in tropical rain forests have been reported. However, drawing general conclusions regarding the effects of various treatments and the optimal conditions for enrichment planting is not straightforward due to the variability and dynamic nature of enrichment planting sites, and the lack of knowledge of post planting site requirements of the nursery-reared seedlings of many species. The accumulated knowledge about enrichment planting in secondary tropical forests and the performance of planted species is limited (Ramos and del Amo 1992, Ådjers et al. 1995, Kammesheidt 2002). Considered to be important factors for the survival (cf. Peña-Claros 2002) and early growth (cf. Denslow 1987, Tuomela 1996) of under-planted non-pioneer seedlings in tropical secondary forests are canopy openness (cf. Jennings et al. 1999) and the quality of light (Chazdon and Pearcy 1991, Rijkers et al. 2000, Leakey et al. 2003a) close to the forest floor. In addition, Ramos and del Amo (1992) claim that the intensity of gap creation has to be matched with species-specific light requirements to achieve sufficient survival and growth rates.

Artificial gap creation

Creating gaps artificially by reducing above-ground vegetation (Wyatt-Smith 1963, Ådjers et al. 1995) has been suggested to favour the introduction of non-pioneer species in secondary forests (Appanah and Weinland 1993). Gaps increase the photosynthetic photon flux density (PPFD) transmission to the forest floor (Whitmore et al. 1993), although this does not necessarily mean a lasting relaxation in the competition experienced by tree species emerging below a pioneer-dominated canopy. Since canopy cover and forest floor light reception in secondary tropical forests are complex, dynamic variables (Jennings et al. 1999, Montgomery and Chazdon 2001), the choice of gap creation strategy merits special attention. Canopy composition and openness, the sub-canopy development and the resident forest floor vegetation interactively affect the amount and quality of light transmitted to the forest floor (Montgomery and Chazdon 2001).

If the under-growth is vigorous, artificial gaps may release thickets of pioneer vegetation and obstruct the establishment of slow-growing tree seedlings. Under such conditions it may be favourable to create openings gradually or to focus on avoiding a flush of pioneer vegetation in the understorey. Since many non-pioneer species (i.e. dipterocarps) are adapted to long periods of suppression in their seedling stage (Delissio et al. 2002) these species may benefit from a controlled, gradual increase in light conditions. Sub-canopy and forest floor individuals may also acquire large energy inputs from short, intense sun flecks (Chazdon and Pearcy 1991, Rijkers et al. 2000, Leakey et al. 2003b) and thus survive outside obvious canopy gaps. When planting non-pioneer tree seedlings, gap creation can be an important pre-planting treatment to improve their photosynthetic capacity and favour their establishment and early growth.

Objectives

The objectives of the studies underlying this thesis were to develop and evaluate alternative methods for the artificial regeneration of non-pioneer tree species (dipterocarps) in secondary forests dominated by *Macaranga spp.*

The study described in Paper I explored the efficacy (i.e. net effect and persistence) of canopy and sub-canopy treatments for controlling canopy openness and light conditions in *Macaranga*-dominated secondary forests. The study compared the effects on canopy openness and light conditions close to the forest floor of felling or girdling selected canopy trees to create artificial gaps and leaving the forest untreated. In addition, the study examined the effects of a more concentrated clearing of the sub-canopy pioneer vegetation on canopy openness and light conditions close to the forest floor.

Paper II deals with different approaches to artificial gap creation in secondary tropical rain forests and compares gap effects on the survival, height and biomass increment of under-planted dipterocarp seedlings. The specific objectives were to determine seedling establishment responses to pre-planting gap creation involving the same canopy treatments (selective felling and girdling of canopy trees) and sub-canopy treatment (slashing of woody stems) in *Macaranga*-dominated tropical secondary forests described in Paper I.

Material and methods

Study site and forest land use history

The study sites were located in the Kalabakan Forest Reserve (lat 4°36'N, long 117°14'E), 25 km west of Luasong Forestry Centre in Tawau district, Sabah, Malaysia (Figure 1). The natural vegetation type is lowland tropical rain forest (Whitmore 1998), classified as mixed dipterocarp forest (Fox 1972) and the landscape (300-700 m a.s.l.) has formed from eroded sedimentary bedrock with hills and valleys (Acres 1975). The soils in Borneo are a mixture of acrisols, alisols and plinthosols (Anon. 2006). The climate is tropical humid with a diurnal temperature ranging between 22.0-32.7°C and the mean precipitation throughout the study period was 2890 mm per year (Paper II, Figure 1).

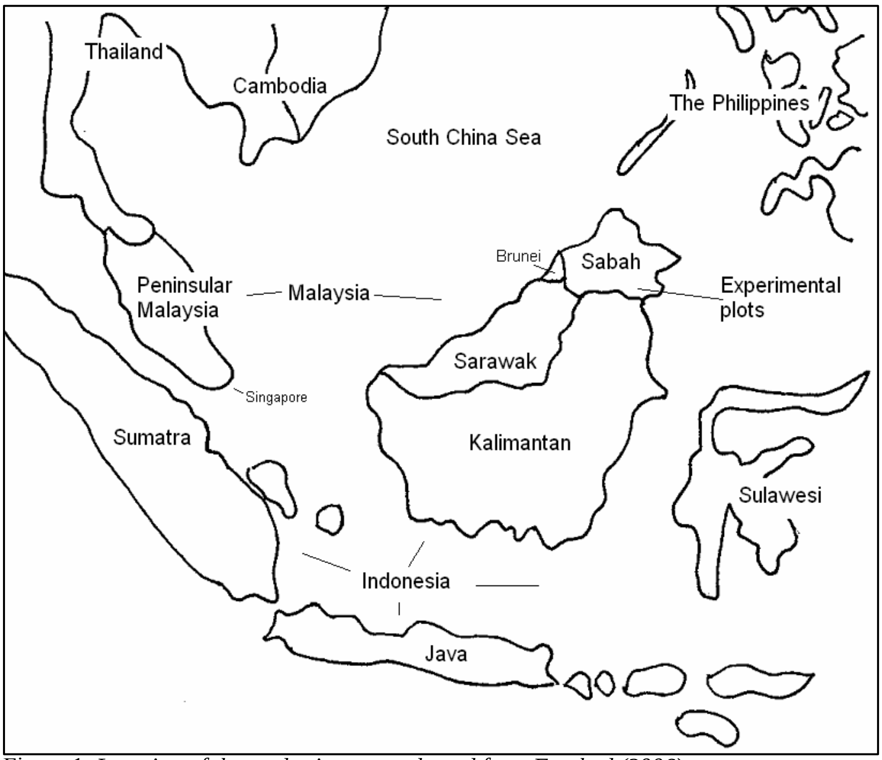


Figure 1. *Location of the study site, map adapted from Forshed (2006).*

The forest was undisturbed by man until selective logging of commercial tree species, mainly dipterocarps, took place in the years 1975-1985 (Garcia pers comm.). A nine-month long El Niño Southern Oscillation induced dry spell affected this forest in 1982-83 (Walsh 1996) followed by fire in 1983 (Woods 1989, Nykvist 1996). The fire hit the area from the southeast and the area was partly burnt (Garcia pers. comm.).

Two decades after this fire, trees defined as pioneers, mainly *Macaranga spp*. (*Euphorbiaceae*), dominated the main canopy (Figure 2) and accounted for approximately 80-90 % of the standing basal area (Paper I, Table 1). The most abundant species were identified as *Macaranga triloba* (Reinw.) Müll. Arg., *M. hypoleuca* Müll. Arg., *M. tanarius* Müll. Arg., *M. beccariana* Merr., *M. pearsonii* Merr., *M. gigantea* (Rehb.f. & Zoll.) Müll. Arg. and *M. winkleri* Pax. & K. Hoffm.

(Alloysius pers. comm.). Tree species defined as non-pioneers mainly of the *Dipterocarpaceae* family and *Eusideroxylon zwageri* Teijsm. & Binnend (belian), accounted for 3 % of the standing basal area of trees > 10 cm in diameter at breast height (DBH). In the study area adult non-pioneers were found on hill tops, along rivers and scattered in the forest. The vegetation below the pioneer-dominated main canopy comprised advanced regeneration of seedlings, saplings and pole-sized trees of pioneer and non-pioneer species (Romell and Hofgaard, unpublished data). Ginger (*Zingiberaceae* family) together with ferns partly occupied the forest floor and understorey and locally the non-woody vegetation was dense close to the forest floor.

Figure 2. *Photograph of the experimental site (blocks 1-4) showing Macaranga spp.-dominated canopy (middle), residual emergent dipterocarps (top) and an abandoned logging road (central bottom).*

Experimental design

Canopy treatments (selective girdling, selective felling and untreated controls) were combined with sub-canopy treatments (slashing woody stems or untreated controls) in a randomized split-plot block design (Stehman and Meredith 1995). Each of the seven blocks included all canopy and sub-canopy treatment combinations. The blocks were divided into main plots, and the main plots were split into subplots. The three canopy treatments were randomly assigned to 1600 m^2 main plots. Main plots were divided into 16 square subplots (10*10 m) arranged as a connected unit (Figure 3). The two sub-canopy treatments were randomly applied to the subplots within each main plot, resulting in eight replicates (8 subplots) of each sub-canopy treatment per main plot (Figure 3). To limit potential edge effects, each main plot was surrounded by a buffer zone of equally-sized subplots subjected to the same canopy treatment. Each main plot including buffer zone required an unbroken canopy of pioneer trees, occasionally necessitating slight modification of the subplot configuration (Figure 3).

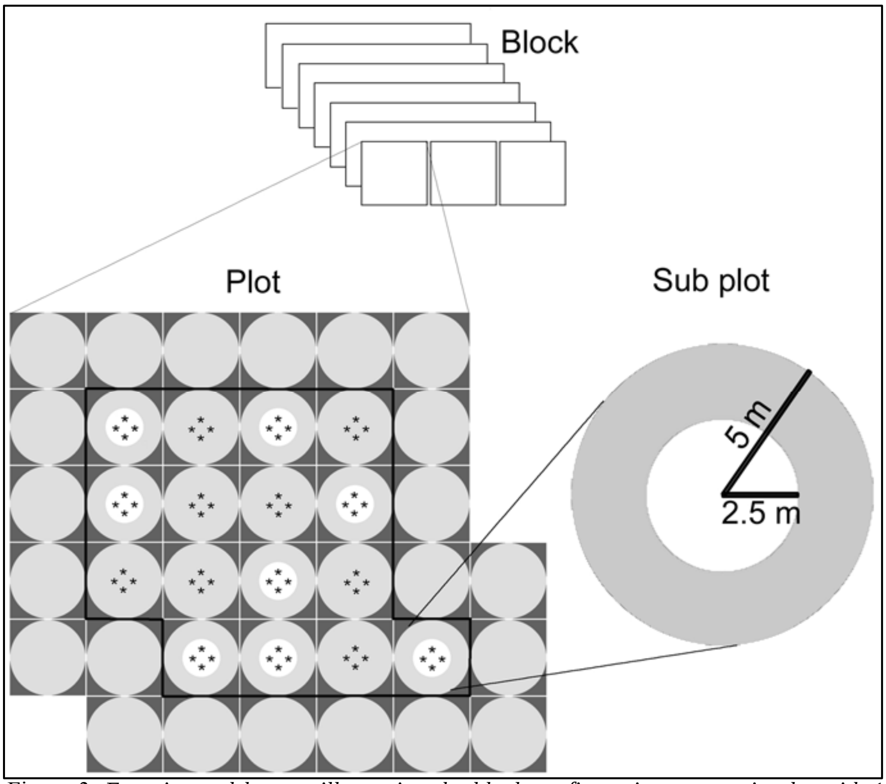


Figure 3. *Experimental lay-out illustrating the block configuration, one main plot with 16 subplots (white circle is sub-canopy slashing, grey is control). The four planting spots are marked with dots in each subplot.*

Canopy treatments were performed in each of the 16 subplots in a main plot using a circular area (r=5 m) in each subplot (1257 out of 1600 m^2 (total main plot area) were treated). *Macaranga spp.* and other pioneer trees with stems exceeding 10 cm DBH were selected for treatment according to a function using stem DBH and distance from the plot centre as coordinates (Paper I, Figure 2). The function was intended to provide standardised, unambiguous selection criteria that were simple to apply to all plots regardless of the assigned canopy treatment. The main aim was to concentrate the selection of treated stems towards the centre of the subplot unless the trees had a large DBH, in which case trees within 3-5 m from the gap centre could be subject to treatment. All non-pioneers were excluded from treatment.

Trees selected for felling were cut with a chain-saw at the stem base. The logs were moved from the central “gap area” where necessary to prevent them from obstructing planting and measurements. Girdling involved stripping off the outer and inner bark of the trunk 50-100 cm above ground using a parang (a long, sharp jungle-knife). Canopy trees selected for felling and girdling accounted, on average, for 30 % (10.4 of 35 m^2 ha^{-1}) and 33 % (11.6 m^2 ha^{-1}) of the initial basal area, respectively.

The sub-canopy treatment (slashing or control) was applied in a 19.6 m^2 subplot inner circle (Figure 3). All seedlings, saplings and small trees identified as pioneers with a diameter less than 10 cm (DBH) were cut at the stem base using a parang. Both canopy and sub-canopy treatments were carried out at the start of the experiment in the last days of June 2002. Under-planting of four dipterocarp tree species in each subplot was then carried out.

Pre-planting preparation of the planting sites involved removal of non-woody forest floor vegetation, mainly ginger, ferns and climbers. The vegetation was cut just above the soil surface using a parang. This preparation was done in a circular area (r=2m) in the central part of each subplot 1-2 days before planting and repeated six months later. Species positions 1-4 (Figure 3) were marked with sticks to randomise the distribution of the four species within each subplot. Locations were distributed in a cross, placing the seedlings 1.25-1.50 m from the gap centre, 1.77-2.12 m apart and at least 0.5 m from the edge of the prepared planting site.

The initial seedling size and weight differed among species. The mean heights of both *Dipterocarpus applanatus* and *D. caudiferus* seedlings were both 0.18 m while those of *Shorea argentifolia* and *S. pauciflora* were 0.32 and 0.29 m, respectively. The estimated mean dry weight of the *D. applanatus* seedlings was 4.06 g while that of each of the three other species was 1.46-2.33 g (Paper II, Table 2). Planting was performed in the beginning of July 2002. One week after planting, ten seedlings were used for filling-in to replace seedlings damaged by wild-boars. A barbed wire fence was then set up around each main plot in order to avoid further destruction by mammals.

Measurements

Seedling survival was registered every third month and height every six month in all blocks (Paper II). Hemispherical photographs and recordings of above-canopy (Figure 4) and forest floor photosynthetic photon flux density (PPFD) were simultaneously taken in four of the seven blocks (Paper I) immediately before treatments and 0, 6, 18 and 30 months later. In the final assessments (December 2004) height, height up to the lowest living branch, diameter at stump level and diameter at breast height (plants ≥1.30 m) were recorded for all surviving seedlings. At the final revision, 30 months after the treatments, 312 seedlings divided into three height classes (small, medium and large) were selected for destructive sampling and fresh weight determination in the field (Paper II).

Figure 4. *Above-canopy platform for the reference recordings of photosynthetic photon flux density (PPFD).*

To assess the above-ground fresh weight of seedlings that were not destructively sampled, secondary fresh weight functions were constructed by regression analysis using data from the seedlings chosen for fresh weight determination. Two separate functions, one for the wood component and the other for the foliage component, were created for each species. Dry matter contents, for each species and component, were then calculated after dry weight determinations of samples of the destructively measured seedlings, and used to convert the fresh weights to dry weights (Paper II).

Calculations and statistical evaluation

Treatment effects on light conditions were expressed in terms of $PPFD_R$ (i.e. the ratio between measured PPFD levels above the forest floor and above the canopy) and as canopy openness (i.e. the calculated percentage of sky in hemispherical photographs) (Paper I). To account for between-species differences in initial seedling sizes when comparing canopy treatment effects on seedling development (Paper II), relative growth rates (relative height growth and relative biomass increment; RGR_H and RGR_B, respectively) of all seedlings that survived the whole study period were used. In addition, the treatment effects on seedling survival were compared (Paper II).

The main method used to analyse treatment effects in both studies were analyses of variance using a general linear model (GLM).

The model for evaluating the effects of canopy and sub-canopy treatments on $PPFD_R$ and canopy openness in blocks 1-4 (Paper I) was:

$$Y_{ijk}=\mu+B_i+C_j+Sc_k+(BC)_{ij}+(BSc)_{ik}+(CSc)_{jk}+E_{ijk} \qquad (1)$$

where Y_{ijk} is the response variable, μ is the grand mean, and the model is mixed. The canopy treatment effect C_j, the sub-canopy treatment effect Sc_k, and their interaction $(CSc)_{jk}$ were regarded as fixed effects. The block effect B_i and the interactions $(BC)_{ij}$ and $(BSc)_{ik}$ were regarded as random effects, and E_{ijk} is the random remaining error (Paper I).

The model for evaluating seedling survival and seedling growth (Paper II) included three treatment variables (canopy, sub-canopy and species) and was applied to data from blocks 1-7:

$$Y_{ijkm}=\mu+C_i+Sc_j+(CSc)_{ij}+S_k+(CS)_{ik}+(ScS)_{jk}+(CScS)_{ijk}+B_m+(CB)_{im}$$
$$+(ScB)_{jm}+(SB)_{km} + (CScB)_{ijm}+(ScSB)_{jkm}+(CSB)_{ikm}+E_{ijkm} \qquad (2)$$

This is a mixed model where Y_{ijkm} is the response variable and μ is the grand mean. The responses to Canopy treatments (C_i), Sub-canopy treatments (Sc_j,) and Species (S_k) and their interactions $(CSc)_{ij}$, $(CS)_{ik}$, $(ScS)_{jk}$, $(CScS)_{ijk}$ were regarded as fixed effects. The block effect B_m and the interactions with treatments $(CB)_{im}$, $(ScB)_{jm}$, $(CScB)_{ijm}$ and species $(SB)_{km}$, $(CSB)_{ikm}$, $(ScSB)_{jkm}$ were regarded as random effects, and E_{ijkm} is the random remaining error (Paper II).

To determine differences between treatments, Tukey's Studentized range test was used (cf. Zar 1999) with α (the significance level) set to 0.05. The residuals were studied by plotting (Sabin and Stafford 1990) and the Anderson-Darling test for normality in the SAS Procedure Univariate (SAS Institute Inc., Anon. 1999). The assumptions of normality and constant variance for the residuals were fulfilled in almost all analyses. However, when $PPFD_R$-data were analysed these assumptions were violated and data were logit transformed (c.f. Sabin and Stafford, 1990), to obtain a normal distribution, before analyses of variance.

Results

Canopy treatment effects

Before treatments, in June 2002, no statistically significant differences in the forest floor conditions ($PPFD_R$ and canopy openness) were found between or within blocks. Recorded $PPFD_R$ and canopy openness values in the untreated forest ranged between 1.8-2.3 % and 8.8-10.7 %, respectively.

The basal area ratio of canopy trees selected for girdling or felling averaged 31.2 % (median, 28.1; S.D., 7.45) of the initial basal area (35 m^2 ha^{-1}) in the seven blocks. In the individual main plots the basal area ratio selected for treatment varied from 23 to 51 %. In blocks 1-4, 13 % of the residual trees were estimated to have been unintentionally damaged in the felling plots six months after the treatments.

There were no statistically significant interactions between canopy and sub-canopy treatments on canopy openness or $PPFD_R$. The canopy treatments (felling, girdling and control) displayed statistically significant responses to canopy openness and $PPFD_R$. Directly and six months after treatments the canopy openness averaged 11.8 and 11.8 % respectively after girdling, 14.6 and 14.2 % after felling and 11.7 % and 11.7 % in the control. The $PPFD_R$ averaged 4.1 % and 3.3 % at 0 and 6 months after girdling respectively, 13.7 % and 30.2 % after felling and the control averaged 2.41 % immediately and 4.4 % six months after the treatments (Paper I, Figure 3). After 18 months the $PPFD_R$ in the girdling plots had increased by ca. 10 % compared to 12 months earlier, while the $PPFD_R$ in the felling plots had decreased; the effects of these two treatments were not significantly different, but the $PPFD_R$ was still significantly higher in the felling plots than in the control plots in which no canopy treatment was performed (Paper I, figure 3). Canopy openness, on the other hand, did not increase during the period 6 to 18 months. After 30 months no statistically significant canopy treatment effects were detected in either canopy openness or $PPFD_R$, and there were also no significant differences in relative height growth in months 24-30 between the felling, girdling and no canopy treatments in this respect.

There were no statistically significant interactions between canopy and sub-canopy treatments on seedling survival, RGR_H or RGR_B. Canopy treatments did not have any statistically significant effects on seedling survival. However, relative height increment (RGR_H) displayed statistically significant responses to the canopy treatments (felling, girdling and control) in the first six months following the treatments. The RGR_H values for the period 0-6 months were 1.32, 0.77 and 0.34 m m^{-1} $year^{-1}$ in the felling, girdling and control plots and these three treatment were significantly different (Figure 3, Paper II). In the following period (6-12 months), RGR_H declined in the felling and girdling plots to 0.83 and 0.50 m m^{-1} $year^{-1}$, respectively, while it increased in the control plots to 0.46 m m^{-1} $year^{-1}$. The RGR_H in the felling plots was significantly different from that in the girdling and control plots. In months 12-18 the RGR_H in girdling plots increased again (to 0.60 m m^{-1} $year^{-1}$) and was significantly different from the RGR_H in the control plots (0.42 m m^{-1} $year^{-1}$), but not the felling plots (0.70 m m^{-1} $year^{-1}$) (Paper II, figure 3).

Canopy treatments had statistically significant effects on relative biomass growth during the 30 month post treatment period. Among the treatments, 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 treatment effects were statistically distinguished ($p<0.05$) (Paper II).

Sub-canopy treatment effects

Sub-canopy treatments and species significantly interacted according to the analyses of survival at 12 and 18-30 months after the treatments. The survival rates of the seedlings of three out of the four tested species were higher after sub-canopy slashing, but those of the other one (*S. pauciflora*) were higher without the sub-canopy treatment (Paper II, figure 3).

The sub-canopy slashing treatment had statistically significant effects on canopy openness at all post-treatment measurement times (0-30 months). The treatment effects on $PPFD_R$ were statistically significant at six and 18 months after the treatments. After sub-canopy slashing, average $PPFD_R$ values were 3.3-5.8 % higher than in the control (untreated) plots, and corresponding canopy openness values were 2.0-2.4 % higher (Paper I, Figure 3). Canopy openness and $PPFD_R$-values also increased after the treatments in the control plots, an effect that was observed from directly after treatment until the final assessments 30 months later.

The sub-canopy treatment also had a significant effect on RGR_H except in the period 6-12 months (Paper II, Figure 3). Sub-canopy slashing resulted in higher RGR_H-values compared to the control in each of the five six-month 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 these 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 analysed, RGR_B was found to be significantly higher after slashing (1.31 g g^{-1} $year^{-1}$) than after the control (0.72 g g^{-1} $year^{-1}$).

Species

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 (Paper II, Figure 3). The initial RGR_H was also highest in *S. pauciflora* (0-6 months, 0.98 m m^{-1} $year^{-1}$) while *S. argentifolia* grew most strongly over the 30-month period (Paper II, Figure 3). The RGR_B after 30 months was 1.00-1.10 g g^{-1} $year^{-1}$ for *D. applanatus, S. argentifolia* and *S. pauciflora*, and significantly lower for *D. caudiferus* (0.86 g g^{-1} $year^{-1}$).

Discussion

In recent decades repeated logging, fire and dry spells (Woods 1989, Slik et al. 2002, Slik and Eichhorn 2003) have caused an expansion of *Macaranga* spp.-dominated secondary forest in Eastern Borneo. *Macaranga* stands in the study area were typically dense (Paper I, Table 3) and single-storied, forming fairly high set canopies that restricted forest floor light supplies to levels previously found in primary forests in Sabah (Whitmore 1998). As demonstrated by Slik et al. (2002), the *Macaranga* dominance in the current stage of stand development may be closely related to the previous fire history in the area. Fire scars (Appendix 4, Photo C) on remaining old-growth stems and charcoal were encountered within the research area supporting local testimonies of fire incidents dating back to about 20 years before the experiment was initiated. Slik and Eichhorn (2003) compared unburnt mixed dipterocarp forest in Kalimantan (Indonesian Borneo) with forest burnt once and twice and found that the number of trees of non-pioneer (climax) species in the size classes 0-5 and 5-10 cm in DBH was ca. 80 % lower in burnt than in unburnt forest sites. Under-planting of non-pioneer species may help to accelerate the forest recovery, but seedling establishment and survival rates must be sufficient if such a measure is to be successful.

Light supply in the artificial gaps of Macaranga spp.-dominated secondary forests

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. When making plans for enrichment planting in *Macaranga*-dominated secondary forests the key issue to consider is the best method for ensuring prolonged alleviation of the competition for light at the seedling level. Measurements of light availability (Paper I) indicated that gap-centred felling or girdling of trees accounting for up to 50 % of the canopy basal area could double or treble the $PPFD_R$ values compared to the no canopy treatment during the initial 30 months after treatment. The visual impact of canopy treatments was dramatic, but maximum PPFD 1.5 m above the forest floor corresponded to only 30 % of above-canopy values (Paper I, Figure 3). In fact, over the entire study period the estimated average PPFD for felling and girdling plots would be closer to 15 % of above-canopy values. Below the *Macaranga* canopy, 1.5 m above the forest floor, about 85-90 % of a hemispherical view did not contain open sky. During the study period felling caused maximum increases in mean canopy openness values of 4-5 % compared to the untreated control (Paper I, Figure 3), but there were no significant differences in this respect between the girdling and control treatments.

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

Results from Paper I 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 when logging and wild fires occurred in the Kalabakan Forest Reserve was in the range 20-30 years (Garcia pers. comm.). In Sri Lankan secondary rain forests Ashton et al. (2001) claim that the natural dominance of pioneer *Macaranga* spp. persists for about 30 years. Davies et al. (2001) also report 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 five-metre radii in the sub-canopy by slashing all forest floor vegetation provided a more consistent improvement in light availability 1.5 m above the forest floor than the canopy treatments (Paper I, Figure 3). A 3-6 % increase in $PPFD_R$ 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 favour the introduction of non-pioneer species in mature *Macaranga*-dominated secondary forests similar to the forest at the site investigated in the studies this thesis is based upon.

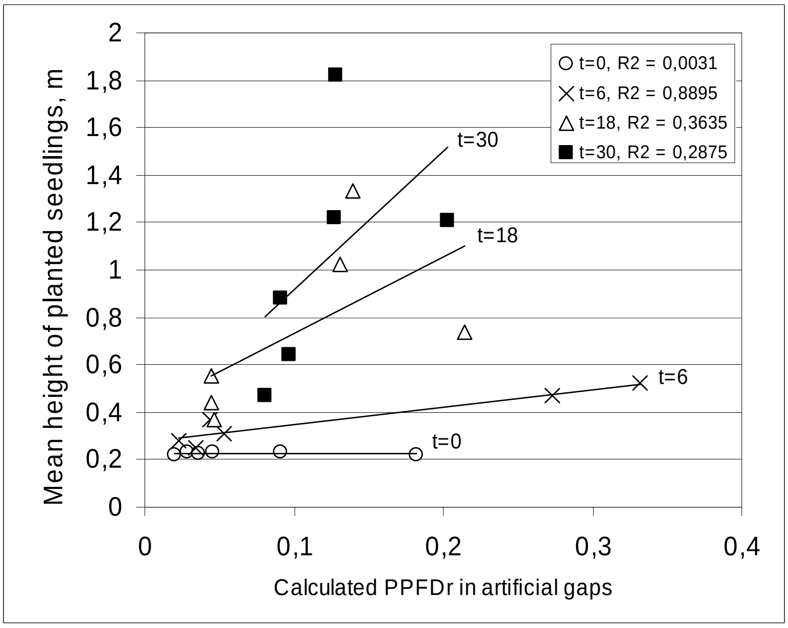
Treatment effects and establishment of under-planted seedlings

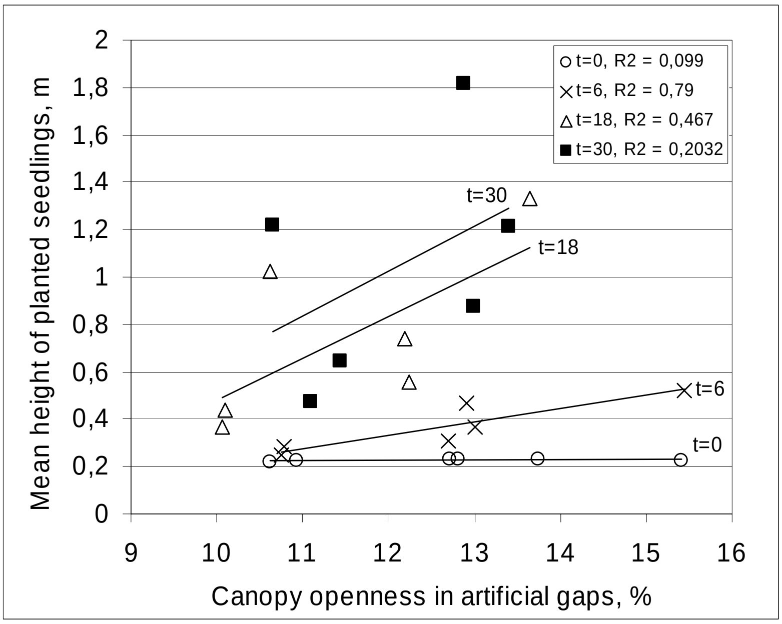
Canopy treatments did not appear to affect overall seedling survival ratios after 30 months. Sub-canopy slashing, on the other hand, generally improved seedling survival compared to the no sub-canopy treatment. Of the four studied species *S. pauciflora* seedlings tended to maintain the highest survival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

The height rankings of the species included in the studies described in Paper II 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* 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 underlying this thesis (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 be alive 15 years after the treatments.

The range of $PPFD_R$ and canopy openness observed in the artificial gaps indicated that seedlings were growing under relatively shaded conditions (Figure 5-6). 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 occasions, except at six months after planting when it was strong. The influence of other factors that were not accounted for in the current study (i.e. in addition to light availability and gap properties) on seedling performance seemed to increase towards the end of the study period (Figs. 5-6, Paper II, Figure 3).

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 dipterocarp seedlings of the four species used in the studies underlying this thesis – *Dipterocarpus applanatus, D. caudiferus, Shorea argentifolia and S. pauciflora* – all grew better with increased canopy openness and relative PPFD-levels (Figure 5-6).





Figures 5-6. *The relationship between registered light availability (expressed as $PPFD_R$ (top) and canopy openness (below)) and mean height of under-planted dipterocarp seedlings, directly after planting (t=0) and at the time of three consecutive measurements 6, 18 and 30 months later. R^2 values are coefficients of determination for simple linear regressions at each occasion.*

In contrast, some previous studies have found that partially shaded environments favour 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 current experiments, 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 is low among *Macaranga* species (Davies et al. 1998). A partial reduction of sub-canopy vegetation may supply enough light to allow 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).

Experimental design and methodological considerations

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. 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. The $PPFD_R$ peaked six months after the felling treatment and 18 months after girdling (Paper I, Figure 3). This could partly be described by a delayed effect of felling (some of the 20-30 m 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. This problem mainly existed in block 2 where the distance between the canopy reference station exceeded 600 m. In block 1, 3 and 4, the maximum distance to the reference station were approximately 400 m or less.

Conclusions

Artificial gap creation in *Macaranga*-dominated secondary tropical rain forests, by means of 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 10 cm, significantly improved light availability near the ground, measured in terms of either canopy openness or $PPFD_R$, 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. 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.

Secondary forest restoration– silvicultural applications

Artificial gap creation has been suggested to favour the introduction of non-pioneer species in secondary tropical rain forests. From the current experiments with pre-planting canopy treatments, under-planting of *Dipterocarpaceae* species and subsequent measurements over a 2.5 year study period, some general conclusions for practical applications could be made:

The sub-canopy treatment (slashing pioneer saplings and smaller trees) improved light availability near the ground and had a positive influence upon seedling survival, establishment and height increment. Since this treatment is relatively cost-efficient it can be recommended as a pre-planting treatment when enrichment planting is planned in *Macaranga*-dominated secondary forests (similar to those in the present study). In addition, a key issue to consider is the best method for ensuring prolonged alleviation of the competition, and in this context sub-canopy treatment can be repeated for maintenance of a favourable environment for the under-planted seedlings.

The canopy treatments (girdling and felling pioneer trees ≥ 10 cm in DBH) improved early seedling growth but did not significantly increase seedling survival. Since these treatments ought to be more expensive to carry out, it could be questioned whether they should be recommended as pre-planting treatments. However, the results from the present studies lead to more questions, e.g. what is the long-term significance of a good initial seedling growth on seedling survival and seedling growth? If the initial seedling growth is important in the long-term perspective it may advocate the use of canopy treatments.

The disadvantage with felling or girdling pioneer canopy trees would be that the actual impact is difficult to predict and control. The effect on gap size and additional damage to residual trees depends on the average height of the main canopy, the topography and soil conditions (slopes and wet soils are likely to increase landslides). The girdling treatment causes less damage to residual stems than felling but still it stimulates the initial height growth of under-planted seedlings. Therefore, girdling canopy trees close to the planting location can be recommended rather than felling.

From the current experiments it was clear the represented dipterocarp species, two of the *Shorea* genera and two *Dipterocarpus*, all are favoured by increased canopy openness and light intensities at the forest floor. This can be assumed to be true even for other non-pioneer species (dipterocarps as well as other indigenous tree species), however further studies of enrichment planting with different species are required. A more "intense" gap opening of the canopy and/or sub-canopy may stimulate height growth but are likely to increase the need for frequent repeated maintenance (i.e. slashing/weeding).

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 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, and as a continuation of the present studies, some high priority research issues can be suggested:

I. Studies of the dynamics and interactions of canopy and sub-canopy strata in *Macaranga*-dominated secondary forests 20-30 years after logging and fire.

II. Investigations of the occurrence of natural regeneration and species diversity of non-pioneer tree species in secondary tropical rain forests, and evaluation of whether tree species are evenly distributed or whether their distributions depend on site conditions or previous disturbance (which could provide important background data for future restoration efforts).

III. Development of labour- and cost-efficient methods for silvicultural treatments designed to improve both artificial and natural regeneration of non-pioneer tree species.

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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.

Anderson, M.L., 1951. Spaced group-planting and irregularity of stand-structure. The Empire Forestry Review 30(4): 328-332.

Anderson, M.L., 1953. Spaced-group planting. Unasylva 7(2): 55-63.

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

Anon. 2001. State of the world's forests. FAO. Rome, Italy.

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

Ashton, M.S., Gunatilleke, C.V.S., Singhakumara, 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.

Bebber, D., Brown, N., Speight, M., Moura-Costa, P., Sau Wai, Y. 2002. Spatial structure and dipterocarp seedling growth in a tropical secondary forest. Forest Ecology and Management 157: 65-75.

Bischoff, W., Newbery, D.M., Lingenfelder, M., Schnaeckel, R., Petol, 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.

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

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A.,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.

Chai, D.N.P., Udarbe, M.P., 1977. The effectiveness of current silvicultural practice in Sabah. Malaysian Forester 40: 27-35.

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

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

d'Oliveira, M.V.N. 2000. Artificial regeneration in gaps and skidding trails after mechanised forest exploitation in Acre, Brazil. Forest Ecology and Management 127: 67-76.

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: 645-658.

Dennis, R. A review of fire projects in Indonesia (1982-1998). Center for International Forestry Research (CIFOR), Bogor, Indonesia.

Denslow, J.S., 1987. Tropical rain forest gaps and trees species diversity. Annual review of Ecology and Systematics 18: 431-451.

Dupuy, J.M.,,Chazdon, R.L., 2006. Effects of vegetation cover on seedling and sapling dynamics in secondary tropical wet forests in Costa Rica. Journal of Tropical Ecology 22: 65-76.

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. Acta Universitatis Agriculturae Sueciae. Doctoral Thesis. Faculty of forest sciences 2006: 30.

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

Holmgren, M., Scheffer, M., Ezcurra, E., Gutiérrez, J.R., Mohren, G.M.J. 2001. El Niño effects on the dynamics of terrestrial ecosystems. TRENDS in Ecology and Evolution 16: 89-94.
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.
Kammesheidt, L., 2002. Perspectives on secondary forest management in tropical humid lowland America. Ambio 31: 243-250.
Kuuluvainen, T., 2002. Disturbance dynamics in boreal forests: Defining the ecological basis of restoration and management of biodiversity. Silva Fennica 36 (1): 5-11.
Lamb, A.F.A.,1969. Artificial regeneration within the humid lowland tropical forest. The commonwealth forestry review 48(1): 41-53.
Leakey, A.D.B., Press, M.C., Scholes, J.D. 2003a. Patterns of dynamic irradiance affect the photosynthetic capacity and growth of dipterocarp tree seedlings. Oecologica 135: 184-193.
Leakey, A.D.B., Press, M.C., Scholes, J.D., 2003b. High-temperature inhibition of photosynthesis is greater under sunflecks than uniform irradiance in a tropical rain forest tree seedling. Plant cell and environment 26 (10): 1681-1690.
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.
Norisada, M., Kojima, K., 2005. Photosynthetic characteristics of dipterocarp species planted on degraded sandy soils in southern Thailand. Photosynthetica 43: 491-499.
Nykvist, N., 1996. Regrowth of secondary vegetation after the `Borneo fire´ of 1982-1983. Journal of Tropical Ecology 12: 307-312.
Otsamo, R., 2000. Early development of three planted indigenous tree species and natural understorey vegetation in artificial gaps in an *Acacia mangium* stand on an *Imperata cylindrica* grassland site in South Kalimantan, Indonesia. New Forests 19: 51-68.
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.
Rijkers, T., de Vries, P.J., Pons, T.L., Bongers, F., 2000. 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.
Slik, J.W., Verburg, R.W., 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., Poulsen, A.D., Ashton, P.S., Cannon, C.H., Eichhorn, K.A.O., Kartawinata, K., Lanniari, I., Nagamasu, H., Nakagawa, M., van Nieuwstadt, M.G.L., Payne, J., Purwaningsih, Saridan, A., Sidiyasa, K., Verburg, R.W., Webb, C.O., Wilkie, P., 2003. A floristic analysis of the lowland dipterocarp forests of Borneo. Journal of Biogeography 30: 1517-1531.
Slik, J.W.F., Verburg, R.W., 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.
Stehman, S.V., Meredith, M.P., 1995. Practical analyses of factorial-experiments in forestry. Canadian. Journalu. of FForest Research. 25: 446-461.
Tuomela, K., Kuusipalo, J., Vesa, L., Nuryanto, K., Sagala, A.P.S., Ådjers, G., 1996. Growth of dipterocarp seedlings in artificial gaps: an experiment in a logged-over rainforest in South Kalimantan, Indonesia. Forest Ecology and Management 81: 95-100.
Turner, I.M., 2001. The ecology of trees in the tropical rain forest. Cambridge university press, U.K.
Uhl, C. 1998. Perspectives on wildfire in the humid tropics. Conservation biology 12: 942-943.

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., 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 British Society of London Series B-Biological Sciences 354(1391): 1869-1883.

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

Whitmore, T.C., Brown, N.D., Swaine, M.D., Kennedy, D., Goodwin-Bailey, C.I., Gong, W.K.,1993. Use of hemispherical photographs in forest ecology: measurement of gap size and radiation totals in a Bornean tropical rain forest. Journal of Tropical Ecology 9: 131-151.

Wong, S.T., Servheen, C., Ambu, L., Norhayati, A. 2005. Impacts of fruit production cycles on Malayan sun bears and bearded pigs in lowland tropical forest of Sabah, Malaysian Borneo. Journal of Tropical Ecology 21: 627-639.

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., 1963. Manual of Malayan silviculture for inland forests. Volume 1 Malayan Forest Records No.23. Kuala Lumpur, Malaysia.

Yasman, I., Hernawan, 2002. Manual persemaian Dipterocarpaceae. Jakarta, Indonesia.

Zar, J.H., 1999. Biostatistical analysis. Upper Saddle River, N.J., Prentice Hall, U.S.

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