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Secondary succession and dipterocarp recruitment in Bornean rain forest after logging

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Abstract

To understand succession in dipterocarp rain forest after logging, the structure, species composition and dynamics of primary (PF) and secondary (SF) forest at Danum were compared. In 10 replicate 0.16-ha plots per forest type trees $\geq$10 cm gbh (3.2 cm dbh) were measured in 1995 and 2001. The SF had been logged in 1988, which allowed successional change to be recorded at 8 and 13 years. In 2001, saplings (1.0–3.1 cm dbh) were measured in nested quadrats. The forest types were similar in mean radiation at 2 m height, and in density, basal area and species number of all trees. Among small ($10 \leq 31.4$) and large ($\geq$31.4 cm gbh) trees, in both 1995 and 2001, there were 10- and 3-fold more dipterocarps in SF than PF respectively; and averaging over the two dates, there were correspondingly ca. 10- and 18-fold more pioneers. Mortality was ca. 60% higher in SF than PF, largely due to a seven-fold difference for pioneers: for dipterocarps there was little difference. Recruitment was similar in PF and SF. Stem growth rates were 37% higher in SF than PF for all trees, although dipterocarps showed the opposite trend. Among saplings, dipterocarps dominated SF with a 10-fold higher density than in PF. For dipterocarps, the light (LH) and medium-heavy (MHH) canopy hardwoods, and the shade-tolerant, smaller-stature other (OTH) species (e.g. *Hopea* and *Vatica*) were in the ratios ca. 40:15:45 in SF and 85:<1:15 in PF. LHs had higher mortality than OTHs in SF. In PF ca. 80% of the saplings were LH: in SF ca. 70% were OTH. The predominance of OTHs in SF is explained by the logging of primary rain forest which was in a likely late stage of recovery from natural disturbance, plus the continuing shaded conditions in the understorey promoted by dense pioneer vegetation. At 13 years after logging succession appeared to be inhibited: LHs were being suppressed but MHHs and OTHs persisted. Succession in lowland dipterocarp rain forests may therefore depend on the successional state of the primary forest when it is logged. A review of logged versus unlogged studies in Borneo highlights the need for more detailed ecological comparisons.

Keywords: Danum; Dipterocarps; *Hopea*; Logging; Mortality; Pioneers; Succession; Sabah; Shade tolerance; Stem growth

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1. Introduction

Selective logging is the most widely employed method of commercial timber production in S.-E. Asia, and its impact on forest structure, composition and regeneration dynamics is considerable. Logging often destroys more than 50% of trees in a forest, with the damage being spread fairly evenly across all tree taxa and size classes (Nicholson, 1958, 1979; Johns, 1988). In some areas, conditions for regeneration remain unsuitable for at least 15 years (Pinard et al., 1996).

In 1999–2003, Malaysia had an annual round-wood production of ca. 20 million m^3 and was then the world's third largest tropical timber producer (ITTO, 2003). The production of round-wood from the east Borneo state of Sabah was alone 8.4 million m^3 in 1990 (Marsh and Greer, 1992; Kleine and Heuveldop, 1993). One of the major timber producing areas within Sabah is the 972,800-ha Yayasan Sabah Concession Area (YSCA), which covers 21% of the state's forested land. Since 1970 logging has progressed steadily westwards from Taliwas, 8 km inland of the east coast: 20% of YSCA has been scheduled to stay primary forest (Marsh and Greer, 1992).

To provide better systems of sustainable management, different harvesting intensities and techniques have been analysed (Pinard and Putz, 1996; Sist et al., 1998, 2003b,c). Bertault and Sist (1997) and Sist et al. (2003a) have recommended that extraction should not exceed 8 trees ha^{-1} $\geq$60 cm stem diameter and 80 m^3 ha^{-1} to benefit from environmentally sound practices. Since the 1970s selective logging management (i.e. desired species above a minimum diameter cut) without treatment has been applied widely in Sabah and other parts of S.-E. Asia (Nicholson, 1979; Thang and Yong, 1988; Kleine and Heuveldop, 1993; Pinard and Cropper, 2000; Okuda et al., 2003; Sist et al., 2003a). As current plans for timber producing dipterocarp forests foresee a 60-year cutting cycle (Sabah Forestry Department, 1989; in Pinard and Cropper, 2000) it is important to continually update information on the course of succession in these untreated secondary forests. Data are also needed to refine models of tropical secondary forest regrowth (e.g. Köhler and Huth, 1998; Huth and Ditzer, 2001).

Although many permanent sampling plots were established in Sabah since 1966, growth and yield data are surprisingly scarce for logged forests (Ong and Kleine, 1995). Lack of data on regrowth in Kalimantan was also noted by Cannon et al. (1994). For instance, how long increased stem growth rates (immediately after logging) continue to be high is uncertain. The time needed for a forest to restock also depends critically on this variable and the rotation period to a second harvest is determined by it (Nguyen-The et al., 1998). In the present paper, 'secondary forests' mean forests, which are recovering from logging, and not those recovering from large natural disturbances.

Several studies have been carried out on the dynamics of secondary forests, but most of them were either in very young (1–6-year-old) forests (Chiew and Garcia, 1988; Thang and Yong, 1988; Pinard and Cropper, 2000; Sist and Nguyen-The, 2002; Sist et al., 2003b), in much older forests where management involved poison-girdling of non-commercial species, liberation thinning and other treatments (Meijer, 1970; Kohler et al., 2001; Sist and Nguyen-The, 2002; Okuda et al., 2003; Sist et al., 2003b), or where there had been shifting cultivation with burning long ago (Brearley et al., 2004). The structure and dynamics of these old and/or treated secondary forests are not, however, directly comparable to recent ones where only selective logging was applied.

Many pioneer species require 5–6 years to reach $\geq$10 cm dbh, diameter at breast height (Woods, 1989; Primack and Lee, 1991), and their persistence in the stand can be up to 30 years (Whitmore, 1984; Swaine and Whitmore, 1988; Pinard and Cropper, 2000). Studies of mortality and growth of trees $\geq$10 cm dbh in forests logged <6 years ago might however conclude that they were already similar in their dynamics to primary forest without taking into account the pioneer recruitment to come and its effect on the dynamics of the other tree species over the ensuing ca. 25 years. Compared to primary forest, young secondary forests ($\leq$6 years) can have high mean growth rates as a result of the increased photosynthetically active radiation (PAR) into the understorey after logging. Older forests (>6 years) can achieve similarly high rates, but for the different reason that pioneers then make up a high contribution of the monitored populations of trees $\geq$10 cm dbh. Repeated measurements would probably best be made in secondary forest stands 10–15 years after logging to record this transition (Liew, 1978). This approach is followed in the present paper.

Canopy gaps created by tree felling can be occupied by mixtures of large numbers of pioneer, late-secondary and primary understorey and overstorey tree species (Kuusipalo et al., 1996). Whilst larger saplings are more prone to logging damage than smaller ones (Fox, 1973), gap extent (Woods, 1989; Tuomela et al., 1996; Okimori and Matius, 2000), seedling–sapling bank composition (Woods, 1989; Brown and Whitmore, 1992; Brown et al., 1999) and seedling size (Whitmore and Brown, 1996) appear to be the main factors which affect tree competition and survival, and consequently to determine recruitment in any one gap. Integrated over several hectares, these processes determine succession and species composition of the recovering forest for the next ca. 30–150 years (Richards, 1996).

The seedlings, saplings and small trees that survive logging have an important role in succession. Their growth is usually stimulated in the short-term, i.e. first 3 years (Nicholson, 1979; Silva et al., 1995; Sterck et al., 2001). Seedlings of the commercial timber species (mostly the canopy-forming dipterocarps) also suffer competition from the fast-growing pioneers in these early years (e.g. Tuomela et al., 1996). Little information exists, though, on how and to what extent the original seedling–sapling bank develops under the canopy of pioneers in secondary forests (Kuusipalo et al., 1996). Curran et al. (1999) and Tuomela et al. (1996) reported reduced regeneration potential in logged forests in Kalimantan because most of the seed-bearing trees ($\geq$50 cm dbh, Nguyen-The and Sist, 1998) of commercial timber species had been harvested. Cannon et al. (1994) found a reduced density of small dipterocarp trees due to logging-induced mortality, suggesting that regeneration in their logged sites in W. Kalimantan was concentrated in a few generally non-dipterocarp species, whilst other studies (Silva et al., 1995; Pelissier et al., 1998; Carvalho et al., 2004) found reductions in shade-tolerant species and stimulation of light-demanding timber species. Pelissier et al. (1998) found the composition of logged forest in southern India to become similar to that of unlogged forest within 20 years: there selective felling appeared to be beneficial to the growth of the commercial timber species. Verburg and van Eijk-Bos (2003), furthermore, found no well-defined communities towards to which recovering logged forests tended to shift.

One reason for the qualitatively variable patterns of recovery and succession after logging found among Bornean and other lowland dipterocarp rain forests of the region could be the different successional stages of the ‘primary’ forests at the time they were logged. It is unlikely that every forest was in a long-term mature (maximum-biomass, steady-turnover, stable) state. Evidence from several studies on primary forest structure and dynamics, suggests that effectively all forests are in some state of recovery from a concatenation of recent and earlier natural disturbances of varying intensities and extents (Whitmore and Burslem, 1998; Newbery et al., 1999). This means that some ‘primary’ forests are probably of ‘late secondary status’. The relatively closed canopy of such forests, lacking large tree fall gaps, will influence which are the most abundant species within the sapling–small tree size classes (Newbery et al., 1999). The idea that logging of a recovering forest ecosystem affects succession differently from logging a mature one is explored in this paper. Rarely, if ever, though is this point considered in the literature on secondary forests, although it is clearly of potential significance for understanding forest succession and management after logging. In a general context the question is whether logging inhibits natural secondary successional processes (Drury and Nesbit, 1973; Connell and Slatyer, 1977; Huston and Smith, 1987).

In the present study, the structure and dynamics of secondary forest, 8 and 13 years after logging, was compared with neighbouring primary forest at Danum, Sabah, to understand the present and likely future course of succession. Particular attention was given to pioneer and dipterocarp tree species as groups.

2. Methods

2.1. Sites and plots

The research took place in lowland rain forest close to the Ulu Segama river in Sabah, East Malaysia, ca. 65 km inland of the eastern coast of Borneo. The forest in this region has been classified as dipterocarp forest, of type *Parashorea malaanonan* (Fox, 1972). Monthly mean temperatures between 1986 and 1998 deviated from an annual mean of 26.7 °C by ca. 1.9 °C, and the range in daily mean temperature was 8.4 °C (Walsh, 1996; Walsh and Newbery, 1999). Mean annual rainfall for 1986–2002 was 2783 mm (Newbery and Lingenfelder, 2004), and for the 1995–2002 study period it was 2878 mm. The region is affected by occasional droughts of moderate intensity (Walsh, 1996); since records began at Danum in 1985 there were two significant events in 1992 and 1998 (Newbery and Lingenfelder, 2004) and before that one inferred from Beaman et al. (1985).

Primary forest (PF) plots (4°58′16″N, 117°48′29″E, ca. 255 m a.s.l.) were located inside the 438-km^2 Danum Valley Conservation Area (DVCA), ca. 1.1 km NW of the Danum Valley Field Centre (DVFC). Secondary forest (SF) plots (4°58′35″N; 117°49′51″E; ca. 295 m a.s.l.) were located 4 km east of DVFC in 'Coupe-88', a 2.5-km^2 area (Marsh, 1995) which was logged in 1988 within the YSCA (Marsh and Greer, 1992). In both forests, the topography gently undulates in elevation by ca. 100 m, with slightly steeper slopes in SF than PF. The soils are ultisols of the Bang association; they lie over the Kuamut formation, which is largely sandstone but also containing mudstone, tuff and chert (Wright, 1975; Chappell et al., 1999).

In SF, many of the trees with stem diameters $\geq$60 cm were harvested in 1988: 83.0 m^3 ha^{-1} of an estimated pre-felling cruise volume of 98.5 m^3 ha^{-1} was extracted (Innoprise Corporation 1992, unpublished data). These data come from six 'set-ups', ranging in area from 22 to 41 ha, in which the SF plots lay. Volumes of the genera extracted were: *Shorea*, 40.1; *Parashorea*, 14.8; *Dipterocarpus*, 14.1; *Dryobalanops*, 10.6; *Hopea*, 0.3; others, 3.1 m^3 ha^{-1}.

2.2. Estimation of stem volumes before logging

2.2.1. Primary forest

The stem volume of trees $\geq$60 cm dbh was estimated for PF in 1986, the first and closest date to 1988 when two main 4-ha primary plots were set up at Danum (Newbery et al., 1992). The numbers of stems $\geq$60 cm dbh in these main plots 1 and 2 were 65 and 91, respectively, of which dipterocarps numbered correspondingly 50 and 70. Species were placed in 9 of 15 groups recognized by Ong and Kleine (1995). For each group their regression equations were used to convert dbh to height, and then these to find the volume of each tree. The equations were derived for trees $\geq$40 cm diameter (dbh or above buttress); for volume they assumed an upper bole diameter of 30 cm (Forestal International Limited, 1973).

2.2.2. Secondary forest

Of the large trees remaining in 1995, the dbhs of those expected to have been $\geq$60 cm dbh in 1988 were found by back-calculating with individual 1995–2001 relative growth rates (rgrs) ($n = 15$ in 1.6 ha, of which nine were dipterocarps). Their estimated total volume in 1988, using the equations of Ong and Kleine (1995), was 87.45 m^3 ha^{-1}. Since 1988 some trees $\geq$60 cm dbh are likely to have died. From the 4-ha primary plots, annual mortality (m_a) in this size class was 0.845% (1986–1996) and when applied to SF this suggests a loss of 1.6 trees in 1.6 ha, or 1.0 ha^{-1} between 1988 and 1995. As dbhs of the dead trees are unknown, an average value of 83.2 cm for the 15 survivors was taken to give a volume of 9.82 m^3 ha^{-1}, this further being the average of estimates from the most likely groups of Ong and Kleine (1995) ranging from 7.50 to 12.14 m^3 ha^{-1}.

2.3. Tree measurements

Between June and November 1995, ten 40-m × 40-m plots were set up in SF at five paired ridge and lower-slope locations. The plots, with a total area of 1.6 ha, were distributed over a ca. 20-ha area of forest. Ten plots of the same dimensions and layout design were set up in PF between September and November 1995, as satellites to the two 4-ha main plots of Newbery et al. (1992, 1996). They were distributed over an area of ca. 12 ha of forest. In the first enumeration, every living tree with a girth at breast height (gbh; height of 1.3 m from the ground on the uphill side) or girth above the buttresses, $\geq$10 cm was mapped, tag-numbered, and gbh measured with a tape (to the nearest mm) at a painted point of measurement (POM). Occasionally, some girths had to be taken (using a ladder) at alternative heights to avoid stem irregularies; some trees of 10.0–15.7 cm gbh (i.e. 3.2–5.0 cm dbh) were measured using callipers.

All dead, surviving and recruiting (to $\geq$10 cm gbh) trees were recorded or remeasured in SF plots from February to April 2001 (in random plot order), and in PF plots, from October 2001 to February 2002 (in order of plot pairs). Each tree was categorized by its status (in seven classes, e.g. alive, undamaged, alive but broken, alive uprooted, etc.), and the condition of each stem at the POM was recorded in one of 16 classes (e.g. stem normal, deformed and irregular, cracked, fluted, liana-embedded, with stripped bark, termite-encrusted; see Newbery et al., 1999). Where buttresses reached heights > ca. 5 m, a Bitterlich-relascope was used to measure stem diameter in 2001. Recruits were mapped, tagged and identified.

Botanical vouchers are housed in the herbaria at Sandakan, Sabah and Leiden, Netherlands. Authorities and nomenclature for species mentioned in this paper follow Lee (2003) and the International Plant Names Index, Kew (http://www.ipni.org).

2.4. Sapling measurements

Five 5-m × 5-m randomly located subplots (NSPs) were set up in each of the 10 plots of the two forest types between 9 April and 14 May 2001. Locations avoided trees >1.5 m gbh, tree stumps >2 m girth, temporary streambeds and subplots from an earlier manipulation experiment in PF of Gibbons (1998). To achieve independence, the NSPs were not allowed to be adjacent to one another, although a diagonally opposite (meeting corners) placement was acceptable. In each NSP, all tree saplings (individuals with stem diameters ≥1.0 cm and ≤3.1 cm) were measured at 1.3 m height by taking two calliper readings at 90° to one another. All saplings were tagged, mapped, marked and identified.

2.5. Light measurements

A hemispherical photograph was taken at 2 m height above ground in the centre of each NSP using a camera with a fish-eye lens (Model LC-ER1; Nikon, Tokyo, Japan). Pictures were taken between 17 May and 8 June 2001, in the early morning (06:00–06:40 h). Gap Light Analyzer software (Version 2.0: Frazer et al., 1999) was used to calculate the light environment. The solar model settings were as follows: solar constant = 1370 W m^{-2}, (direct) beam fraction = 0.39 (Whitmore et al., 1993), spectral fraction = 0.51 (Stigter and Musabilha, 1982), cloudiness index = 0.45 (calculated from the sunshine data at Danum between 1996 and 2001). The transmission coefficient under standard overcast sky was set at 0.4 (Whitmore et al., 1993). The magnetic declination at Danum during the sampling period was 0°32′E. Subjective processing of the photographs was avoided by holding the threshold pixel intensity at 245 (see Mitchell and Whitmore, 1993; Whitmore et al., 1993; Frazer et al., 1999).

Two NSPs were selected at random in each plot and photosynthetic active radiation (PAR) was measured at the same height and location as the hemiphotographs (PF, 8 April–13 June 2001; SF, 15 March–23 May 2001). Four quantum sensors (Model SKP215, Skye Instruments Ltd., Powys, UK) were supported at the ends of a cross-frame (50-cm arms), and daily $\mathrm{PAR_{in}}$ (mol m^{-2} day^{-1}) integrated using the trapezoidal method in MATLAB (Vers. 5.3). Between 30 April and 13 June 2001, radiation outside of the forest was measured ($\mathrm{PAR_{out}}$), and for this period relative radiation ($\mathrm{PAR_{rel}} = \mathrm{PAR_{in}}/\mathrm{PAR_{out}}$) found.

2.6. Tree dynamics calculations

The census interval in SF was 5.51 years: exact dates for each tree's measurement were not recorded in 1995 so the difference in mean dates in 2001 and 1995 was taken. Mean census interval in PF was 6.15 years (range: 6.04–6.29 years), and here dates were known for each tree. Annualized mortality (m_a) and recruitment (r_a) rates were calculated following Alder (1995) and Sheil et al. (1995):

$$m_a\,(\%\,\mathrm{year}^{-1}) = \left(1 - \left(1 - \frac{n_d}{n_{95}}\right)^{1/t}\right) \times 100$$

$$r_a\,(\%\,\mathrm{year}^{-1}) = \left(\left(1 + \frac{n_r}{n_{95}}\right)^{1/t} - 1\right) \times 100$$

where n_{95} is the population size in 1995, n_d the number of dead trees, n_r the number of recruits and t is the census interval (in years). The difference in interval length for PF and SF was too small to warrant a correction to m_a (Sheil and May, 1996; Newbery and Lingenfelder, 2004). Absolute (agr) and relative growth rates (rgr) of survivors were calculated in terms of girth increment as:

$$\mathrm{agr}\,(\mathrm{mm\,year^{-1}}) = \frac{\mathrm{gbh}_{01} - \mathrm{gbh}_{95}}{t} \times 10$$

$$\mathrm{rgr}\,(\mathrm{mm\,m^{-1}\,year^{-1}}) = \frac{\ln(\mathrm{gbh}_{01}) - \ln(\mathrm{gbh}_{95})}{t} \times 1000$$

All trees with deformed or damaged stems were excluded from the growth rate calculations, as were trees that had lost one or more stems with gbh ≥10 cm on multiple-stemmed trees and trees ($n = 29$ in PF, $n = 10$ in SF) with highly negative (assumed-erroneous) agrs (threshold ≤ -4 mm year^{-1}; see Newbery et al., 1999). In tests of comparison between forest types, when both variables had normally distributed residuals the *t*-test was used, otherwise the Mann–Whitney *U*-test. Statistical tests were performed in GenStat 6.1/7.1 (Payne, 2000).

2.7. Definitions of size classes, familial groups and functional subgroups

All trees (≥10 cm gbh or ≥3.2 cm dbh), were divided into two size classes: small trees (10–<31.4 cm gbh), and large trees (≥31.4 cm gbh or ≥10 cm dbh). Within the large-tree class, individuals ≥157.1 cm gbh (≥50 cm dbh) were referred to as being very large. Within size classes, family groups were defined as having (i) all, (ii) dipterocarp and (iii) non-dipterocarp, trees. Within the non-dipterocarp group, functional subgroups, (iv) pioneers (see Appendix A) and (v) non-pioneers, were made. (Dipterocarpaceae have no pioneers.)

3. Results

3.1. Light environment

Total radiation above the canopy (for PF and SF) was 38.03 mol m^{-2} day^{-1} (direct and indirect components: 14.83 and 23.20 mol m^{-2} day^{-1}, respectively). At stations outside of the forest, PAR-values calculated from hemispherical photographs (34.03 and 36.79 mol m^{-2} day^{-1} in SF and PF, respectively) were similar to those values directly measured with PAR sensors (35.42 and 36.90 mol m^{-2} day^{-1}; differences of 4.0 and 0.3%). Canopy openness at the PAR-sensor stations outside the forest was 73.0% for the DVFC Met-Hill station and 61.6% for the station outside of SF. Site factors obtained from the photographs at the height of 2 m above ground (Table 1) were very similar in the two forest types ($P > 0.6$; differences of 1–3%). Values of PAR measured with sensors also differed slightly and non-significantly ($P = 0.23$): the S.E. of the values in SF was almost twice that in PF. Relative PAR was only correlated with total site factor ($r_s = 0.58$, d.f. = 18, $P = 0.008$).

Table 1
Mean canopy openness and site factors (±S.E.) obtained from hemispherical photographs, and photosynthetically active radiation (PAR), measured with sensors in 10 primary (PF; DVCA) and 10 secondary forest (SF; Coupe 88) plots, Danum, Sabah

Variable	PF	SF	*t*	*P*
Canopy openness (%)	4.54 ± 0.20	4.45 ± 0.19	0.37	0.72
Site factors (%)				
Direct	8.65 ± 0.65	8.38 ± 0.55	0.34	0.74
Indirect	7.19 ± 0.38	6.97 ± 0.33	0.50	0.62
Total	7.76 ± 0.48	7.52 ± 0.41	0.42	0.68
PAR (mol m^{-2} day^{-1})	0.51 ± 0.11	0.79 ± 0.20	1.25	0.23

3.2. Estimation of stem volumes before logging

3.2.1. Primary forest

Calculations resulted in total volumes of 199.4 and 224.1 m^3 ha^{-1}, of which correspondingly dipterocarps were 179.0 and 189.2 m^3 ha^{-1}, and other species 20.4 and 34.9 m^3 ha^{-1}, in main plots 1 and 2 respectively. Mean total volume in the main plots was thus 211.8 m^3 ha^{-1}, of which dipterocarps formed 184.1 m^3 ha^{-1}. Further, the basal area of trees ≥60 cm dbh in 1995–1996 in PF plots was 1.07-fold that in the main plots (11.94 m^2 ha^{-1} versus 11.13 m^2 ha^{-1}). Multiplying the estimated main-plot volumes in 1986 by this ratio, PF-values became 226.6 and 197.0 m^3 ha^{-1} for all trees and dipterocarps, respectively.

3.2.2. Secondary forest

The volume estimates for living trees in 1988 taken together (i.e. 97.27 m^3 ha^{-1}) were added to the volume extracted (83.0 m^3 ha^{-1}) to give an overall estimate of 180.3 m^3 ha^{-1} in SF in 1988 before the logging operations. In 1995, 72% of the volume of the trees ≥60 cm dbh were dipterocarps; and 96.3% of the extracted volume was of this family. Assuming that this former percentage could apply in 1988, the volume of dipterocarps was 150.0 m^3 ha^{-1}.

Using the same approach of back-calculation from 1995 to 1988 in PF led to a volume estimate of

221.9 m^3 ha^{-1}—a value very close to the interpolated estimate above and endorsing its application in SF.

3.3. Species composition and diversity

In 1995, 3663 (97.4%) trees $\geq$10 cm gbh in PF and 3849 (97.6%) trees in SF, were identified to the species level. In 2001, the corresponding values were 3576 (98.6%) and 3613 trees (98.7%). Of all trees in SF and PF, 2.4 and 2.2%, respectively, were identified to genus only in 1995, while in 2001 the correspondingly contributions were 1.3 and 1.2%. In PF, only 0.4% in 1995 and 0.2% in 2001, of all trees were of unknown families; in SF none remained at the family-only level. The accuracy and completeness of tree identifications was therefore unusually high for this type of study.

Euphorbiaceae had the highest numbers of trees $\geq$10 cm gbh in both forest types (means of 1995 and 2001: PF, 1264; SF, 1288). Among the next four most numerous families there was a striking difference between forests for Dipterocarpaceae (PF, 164; SF, 1127): the ratio of diptercarps to euphorbs was nearly 1:8 in PF but close to 1:1 in SF, with these families being codominant in SF. Numbers of Annonaceae in PF (308) were >3 times, and those in Lauraceae (238) and Meliaceae (242) ca. twice, those in SF (94, 118, 113, respectively). The most noticeable changes between 1995 and 2001 were the decreases in Euphorbiaceae in SF (−15%) and Lauraceae in PF (−14%).

In 1995 and 2001, numbers of tree species were 296 and 307 in PF, and 300 and 302 in SF, respectively (50–53 families per forest type). Numbers of species per plot, Shannon's diversity index, Pielou's measure of evenness, species–individual ratios (SIR) for all trees were all not significantly different between forest types ($P \geq 0.66$) and changed very little between 1995 and 2001: their respective mean values were 99, 3.75, 0.82, 0.275. For trees $\geq$10 cm gbh, evenness and SIR were signficantly higher in PF than SF, however ($P < 0.015$). Species frequencies in the two forest types were also not significantly differently distributed across $\log_2$-abundance classes for all and large trees in 1995 and 2001 ($P > 0.20$). Log-series α-diversity values per plot did not differ significantly between forest types either (overall mean = 45.6; $P > 0.6$).

The three most abundant species in PF were *Mallotus wrayi* King ex Hook. *f*. (Euphorbiaceae), *Dimorphocalyx muricatus* (Hook. *f*.) Airy Shaw (Euph.) and *Fordia splendidissima* (Mij.) Buijsen (Leguminosae); in SF *Koilodepas longifolium* Airy Shaw (Euph.), *Hopea nervosa* King (Dipterocarpaceae) and *Macaranga gigantea* Muell. Arg. (Euph.) in 1995 or *Dipterocarpus caudiferus* Merr. (Dipt.) in 2001. Other species which more strongly differentiated the forest types ($n \geq 60$) were, in PF: *Ardisia sanguinolenta* Blume (Myrsinaceae), *Madhuca korthalsii* (Pierre) Lam. (Sapotaceae), *Polyalthia cauliflora* Hook. *f*. & Thoms, *P. xanthopetala* Merr. (Annonaceae) and *Urophyllum corymbosum* Korth (Rubiaceae); in SF: *Macaranga hypoleuca* (Rchb. *f*. & Zoll.) Muell. Arg. (Euph.), *Shorea faguetiana* Heim, *S. macroptera* Dyer (Dipt.) and *Vatica dulitensis* Sym. (Dipt.).

A principal components analysis ordination (normalized PCA with chord distance) clearly separated the plots into the two forest types, but showed no gradient between lower-slope and ridge plots. Extensive testing for differences in the structural and dynamic variables which follow for this topographic factor showed no consistent and significant differences: the 10 plots per forest type were therefore treated as single samples.

3.4. Forest structure

Total numbers of all and small trees per plot did not differ significantly between forest types in either 1995 or 2001 ($P > 0.40$; Table 2). Large trees, however, had significantly ($P < 0.05$) higher densities in SF than PF in both years, although very large trees had similar densities in both forest types. Among the small and large trees, the Dipterocarpaceae had, respectively, more than 10- and 3-fold more trees in SF than PF in both 1995 and 2001 ($P < 0.001$; Table 2): among all trees the ratio was 7-fold ($P < 0.001$). Small pioneers were also more than 15- and 5-fold more dense in SF than PF in 1995 and 2001, respectively ($P < 0.001$): in both years for large trees the ratio was ca. 18-fold, and for all trees ca. 10-fold ($P < 0.001$; Table 2). Non-dipterocarp/non-pioneers had the highest numbers of trees in both forest types and in all size classes: their mean contributions in 1995 and 2001 were 62% in SF and 95% in PF. Numbers of all and small trees in both forest types and all groups decreased, except for pioneers in PF which remained constant. The decrease in small trees was significantly higher in SF than PF (SF, −185 ha^{-1}; PF: −87 ha^{-1}; $t = 2.33$,

Table 2
Mean densities of trees in 10 primary forest (PF, DVCA) and 10 secondary forest (SF, Coupe 88) plots, Danum, Sabah, in 1995 and 2001 (n_{95}, n_{01})

Group	n_{95} (ha^{-1})				n_{01} (ha^{-1})			
	PF	SF	t or U	P	PF	SF	t or U	P
Trees ≥10 cm gbh (all)								
All species	2350	2465	0.75	0.464	2266	2288	0.15	0.881
Dipterocarpaceae	106	714	*0*	*<0.001*	98	694	*0*	*<0.001*
Non-Dipterocarpaceae	2244	1751	3.68	0.002	2169	1594	4.21	<0.001
Pioneers	14	257	*0*	*<0.001*	14	144	*2.5*	*<0.001*
Non-pioneers	2230	1494	5.29	<0.001	2154	1451	5.50	<0.001
Trees 10–<31.4 cm gbh (small)								
All species	1869	1896	0.20	0.842	1782	1711	0.61	0.551
Dipterocarpaceae	49	528	9.47	<0.001	37	500	9.23	<0.001
Non-Dipterocarpaceae	1821	1368	5.33	<0.001	1745	1211	5.72	<0.001
Pioneers	9	150	*0*	*<0.001*	9	52	*13.5*	*0.004*
Non-pioneers	1812	1218	*7.5*	*<0.001*	1736	1159	*4*	*<0.001*
Trees ≥31.4 cm gbh (≥10 cm dbh) (large)								
All species	481	569	2.66	0.021	484	575	2.40	0.033
Dipterocarpaceae	57	187	6.70	<0.001	61	194	6.90	<0.001
Non-Dipterocarpaceae	424	382	0.98	0.347	424	384	0.85	0.413
Pioneers	6	107	*0.5*	*<0.001*	5	92	*0.5*	*<0.001*
Non-pioneers	418	276	3.95	0.002	419	292	3.35	0.005
Trees ≥157.1 cm gbh (≥50 cm dbh) (very large)								
All species	29	23	*37*	*0.353*	26	26	*49*	*0.971*

Differences between forest types were tested with either t- or Mann–Whitney U-statistics. Values of U and its P are shown in italics.

d.f.$_{adj.}$ = 12.5, P = 0.045) and was strongly affected by the loss of the pioneers in SF (−98; 65% decrease). Numbers of large dipterocarp trees and non-dipterocarp/non-pioneers increased in both forest types.

Mean basal area (BA) of all trees per plot did not differ significantly ($P > 0.20$) between PF (1995, 35.0; 2001, 32.3 m^2 ha^{-1}) and SF (1995, 30.7; 2001, 33.0 m^2 ha^{-1}), decreasing by 8% in PF and increasing by 7% in SF. In 1995 and 2001, Dipterocarpaceae in PF comprised 44.1 and 41.4% of the total BA, respectively; a similar contribution of 45.2 and 44.3% was seen in SF despite the very different numbers of trees in the two forest types. In SF, pioneers comprised 9.8 and 10.6% of the total BA in 1995 and 2001, respectively, whilst in PF it was <1% in both years. With a mean of 45.1% in 1995 and 2001, the non-dipterocarp/non-pioneers had almost the same contribution as the dipterocarps to BA in SF. In PF, the corresponding mean contribution of non-dipterocarp/non-pioneers was 56.5%, ca. 14% more than that of dipterocarps.

The effect of logging was still evident in the BA data. The species with the highest BA in PF were *Shorea johorensis* Foxw., *S. argentifolia* Sym. and *S. parvifolia* Dyer (all Dipterocarpaceae). In SF, the pioneer *M. gigantea* had the highest BA in 1995 and 2001, followed by *S. faguetiana* and *H. nervosa* (also Dipt.).

3.5. Mortality and recruitment

Mean annual mortality (m_a) for all trees at the plot level was significantly higher (61.6%) in SF than PF, mostly due to the 7-fold difference in m_a of pioneers ($P < 0.001$; Table 3). Among the small trees, the higher m_a in SF than PF was not only a result of the much higher mortality of pioneers but came also from the 25% higher mortality of non-dipterocarp/non-pioneers. For the large-tree class, no differences were significant for non-dipterocarp/non-pioneers but the m_a of dipterocarps in SF was significantly ca. 2.4-fold that in PF. Mortality (m_a) of small trees was not affected by n_{95} (F = 3.01, d.f. = 1,16, P = 0.102), although forest type

Table 3
Mean annual mortalities (m_a) and relative stem growth rates (rgr) between 1995 and 2001 in 10 primary forest (PF, DVCA) and 10 secondary forest (SF, Coupe 88) plots, Danum, Sabah

Group	m_a (% year^{-1})				rgr (mm m^{-1} year^{-1})			
	PF	SF	U	P	PF	SF	t	P
Trees $\geq$10 cm gbh (all)								
All species	2.00	3.22	8	<0.001	13.87	19.03	2.58	0.024
Dipterocarpaceae	2.73	3.41	37	0.353	33.30	21.75	2.04	0.064
Non-dipterocarpaceae	1.95	3.45	6	<0.001	13.21	17.82	2.31	0.040
Pioneers	1.48[a]	10.96	7	<0.001	19.94[c]	52.59	–	–
Non-pioneers	1.95	2.20	32	0.190	13.17	14.50	0.64	0.534
Trees 10–<31.4 cm gbh (small)								
All species	1.93	3.37	6	<0.001	14.15	17.74	1.43	0.180
Dipterocarpaceae	5.00	3.33	37	0.353	39.10	22.89	1.91	0.081
Non-dipterocarpaceae	1.85	3.57	5	<0.001	13.64	17.42	1.72	0.111
Pioneers	1.20[b]	13.65	–	–	15.56[c]	48.45	–	–
Non-pioneers	1.85	2.32	19	0.019	13.63	14.42	0.33	0.748
Trees $\geq$31.4 cm gbh ($\geq$10 cm dbh) (large)								
All species	2.33	2.82	38	0.393	12.58	23.13	6.64	< 0.001
Dipterocarpaceae	1.04	2.47	23	0.043	27.44	21.06	1.29	0.223
Non-dipterocarpaceae	2.48	3.20	42	0.579	11.18	24.13	7.28	< 0.001
Pioneers	4.00[b]	8.18	–	–	27.44[c]	53.25	–	–
Non-pioneers	2.47	1.77	36	0.315	10.96	14.43	1.98	0.070
Trees $\geq$157.1 cm gbh ($\geq$50 cm dbh) (very large)								
All species	2.60	0.51	28	0.105	13.99[d]	10.78[d]	1.11	0.285

Differences between forest types were tested for m_a and rgr with the Mann–Whitney U- and t-statistics respectively.

[a] PF mean based on $n = 9$ plots.

[b] Due to low n_d in PF, rates found by pooling plots.

[c] Due to low n of valid trees in PF, rates found by pooling plots.

[d] In both PF and SF, $n = 9$ plots only had sufficient data.

($F = 12.94$, d.f. = 1,16, $P = 0.002$) was, but the interaction not ($F = 0.54$, d.f. = 1,16, $P = 0.472$), significant.

There were no significant differences in r_a between forest types (PF, 1.39% year^{-1}; SF, 1.75% year^{-1}; $U = 44$, $P = 0.684$). The r_a of pioneers in SF was very low (pooled 0.32% year^{-1}) with not a single recruit of *Macaranga* spp. found: in PF it was higher at 2.01% year^{-1}—tests were not possible because of too few data. Pioneers in SF, however, had the highest r_a into the large-tree size class overall (3.62% year^{-1}), and 23 of the 29 recruits were *Macaranga* spp. Although m_a and r_a were positively correlated across plots in SF ($r_s = 0.82$, d.f. = 8, $P = 0.004$) they were not in PF ($r_s = 0.04$, d.f. = 8, $P = 0.91$). Recruitment (r_a) was strongly negatively dependent upon n_{95} ($F = 13.96$, d.f. = 1,16, $P = 0.002$), forest type ($F = 4.92$, d.f. = 1,16, $P = 0.041$) and the interaction ($F = 6.07$, d.f. = 1,16, $P = 0.025$).

3.6. Growth

The final numbers of valid trees $\geq$10 cm gbh used for PF and SF were 3010 and 3086, respectively. Relative growth rates of all trees were significantly 37% higher ($P < 0.05$) in SF than PF, though for the dipterocarps the opposite was marginally significantly the case ($P = 0.064$). Most of the difference in overall rgr was due to the pioneers (Table 3). Among the small trees the only trend (significant at $P < 0.10$) was the faster growth of dipterocarps in PF than SF. Large-tree rgrs support the difference between forests for all trees (84% increase of SF over PF), this largely due to an over 2-fold difference for non-dipterocarps. However, in this size class there was no significant difference in rgr of dipterocarps. Small-tree rgrs showed negative dependence on n_{95} ($F = 6.17$, d.f. = 1,16, $P = 0.024$), forest type ($F = 5.88$, d.f. = 1,16, $P = 0.028$) and the interaction ($F = 9.47$, d.f. = 1,16, $P = 0.007$). (Absolute stem growth rates closely followed trends in rgr and are not reported.)

3.7. Saplings

Of the 488 saplings found in 50 NSPs in PF, 461 were determined to species and 27 to genus-only level (39 families). In SF there were 588 saplings, of which 582 were determined to species, and six to genus-only, level (38 families). The most abundant families were again Euphorbiaceae (143 saplings in 50 NSPs), Meliaceae (44) and Annonaceae (38) in PF; Dipterocarpaceae (211), Euphorbiaceae (148) and Myrsinaceae (39) in SF. Mean numbers of species per NSP (PF, 7.14; SF, 7.96), SIR (0.755; 0.733) or Shannon's diversity index (1.72; 1.85) showed no significant differences between forest types ($P > 0.3$). The frequency distributions of species in $\log_2$-abundance classes also did not differ ($P = 0.77$).

Saplings of Dipterocarpaceae were dominant in SF (211 individuals of 21 species; 36% of all saplings), whereas this family was ranked seventh in PF (21 saplings of nine species; 4% of all saplings)—a 10-fold difference. There were 109 species in PF and 126 in SF. The most abundant species in PF were *M. wrayi* (51), *D. muricatus* (43) and *F. splendidissima* (32), whereas in SF they were *H. nervosa* (126), *K. longifolium* (49) and *A. sanguinolenta* (38). The numbers of pioneers, with six (1.23%) in PF and nine (1.53%) trees in SF, were low and similar for the two forest types. Numbers of saplings per NSP were highly variable (PF: mean = 9.76 ± 0.58, range = 1–18; SF: mean = 11.76 ± 0.73, range = 2–26; $t = 1.56$, $\text{d.f.}_{\text{adj.}} = 17.1$, $P = 0.14$). Numbers of dipterocarp saplings and trees were not significantly correlated across plots in either forest type (PF: $r_s = -0.24$, d.f. = 8, $P = 0.39$; SF: $r_s = 0.064$, d.f. = 8, $P = 0.87$).

3.8. Dipterocarp groups

Dipterocarpaceae were subdivided into (i) light hardwoods (LH), (ii) medium and heavy hardwoods (MHH) and (iii) Dipterocarpaceae without commercial potential (OTH), groups according to Newman et al. (1996, 1998). In the present study, all *Vatica* spp. (*V. dulitensis*, *V. oblongifolia* Hook. *f.*, *V. albiramis* van Slooten, *V. micrantha* van Slooten and *V. sarawakensis* Heim) and *Hopea* spp. (*H. nervosa* and *H. ferruginea* Parijs) fell into the OTH group. Apart from their non-commercial value, OTH species are known for their high shade-tolerance and their slow growth rates (Meijer and Wood, 1964; Newman et al., 1996, 1998; Kohler et al., 2000; Phillips et al., 2002).

For trees ≥10 cm gbh in 1995, 42.1% in SF were LH, 14.8% MHH and 43.1% OTH, and correspondingly 38.7, 14.6 and 46.7% in 2001. In PF in 1995, 86.5% of all dipterocarps were LH, 0.6% MHH and 12.9% OTH, correspondingly 82.3, 1.2 and 16.5% in 2001. Percentage change over the census interval for LH in PF, and also in SF, was −11.6% for all trees; but small trees had a loss of −38.3% in PF—almost the double that in SF with −19.9%. Large trees showed increases of 5.0% in SF and 6.9% in PF. Whereas LH showed losses of small trees over the interval, there were increases in OTH for all trees of 4.5% in SF and 18.2% in PF. Among saplings the fraction of LH dipterocarps was 81%, a value similar to that found for trees in PF but not in SF where the fraction of OTH was 69.2%.

Annual mortality rates for either all (PF, 3.2%; SF, 3.6%) or small (PF, 7.0; SF, 4.7%) LH dipterocarps did not differ between forest types ($P > 0.25$). Relative growth rates of small LH trees (89 and 360 valid trees in PF and SF respectively) differed significantly between forest types, but were not affected by gbh in 1995 when included as a covariate (ANOVA: forest type, $F = 5.69$, d.f. = 1,18, $P = 0.028$; ANCOVA: forest type, $F = 4.98$, d.f. = 1,17, $P = 0.039$; gbh_{95}, $F = 0.09$, d.f. = 1,237, $P > 0.7$). Mean rgrs were 45.5 mm m^{-1} year^{-1} for PF and 24.1 mm m^{-1} year^{-1} −1 for SF. For large LH trees no differences between forest types were found, although gbh in 1995 did have a significant effect (ANCOVA: forest type, $F = 0.01$, d.f. = 1,17, $P > 0.9$; gbh_{95}, $F = 19.2$, d.f. = 1,70, $P < 0.001$).

4. Discussion

4.1. Logging intensity and residual trees

Mean tree volume extracted in SF set-ups (83 $\text{m}^3\ \text{ha}^{-1}$) in 1988 was equal to that extracted by conventional logging techniques (CNV) at Malinau, Indonesia (Sist et al., 2003c), but was lower than that reported by Pinard and Putz (1996) in the Yayasan

Sabah Concession Area (YSCA) at 154 ± 20 m^3 ha^{-1}, and by Bertault and Sist (1997) in E. Kalimantan at 107.2 ± 59.6 m^3 ha^{-1}. Even so, the volume in SF was higher than the average 70 m^3 ha^{-1} cut over the whole YSCA during the 1980s (Marsh and Greer, 1992) and similar to the 80 m^3 ha^{-1} extracted at Tawau (also YSCA) in 1986 (Chiew and Garcia, 1988). Whilst the most productive dipterocarp forests of Borneo have commonly been harvested at intensities of >100 m^3 ha^{-1} (Sist et al., 2003c), the 83 m^3 ha^{-1} estimate lies at the lower end of the range of CNV values, but also towards the middle of the range of volumes extracted by reduced impact logging (RIL: Pinard and Putz, 1996; Bertault and Sist, 1997; Sist et al., 2003c: 60–104 m^3 ha^{-1}). The 10–11 trees ha^{-1} $\geq$60 cm dbh, estimated to have remained after logging, indicate an operation closer to RIL than CNV.

The degree of logging can also be seen from the contribution of pioneer species (Primack and Lee, 1991; Pinard et al., 1996; Davies et al., 1998; Sterck et al., 2003). Densities of *Macaranga* $\geq$10 cm dbh in SF (92 ha^{-1} at 8 years; 76 ha^{-1} at 13 years) were less than the 110 found by Kuusipalo et al. (1996) 12 years after logging in S. Kalimantan, but higher than the 20 ha^{-1} found by Primack and Lee (1991) 11 years after logging in Sarawak. By contrast to CNV logged sites, Cannon et al. (1998) found the contribution of pioneers 8 years after selective logging in W. Kalimantan to be insignificantly low.

Taken together, the results for SF in Coupe 88 at Danum suggest that the selective logging applied there extracted volumes, and initiated the corresponding successional processes, at a scale lying towards the lower end of the range practised in Borneo. The SF was logged at moderate intensity.

4.2. Light environments

Total radiation above the canopy was very close (with maximum error 1.2%) to that calculated by Whitmore et al. (1993) for Danum (14.95 direct, 22.92 indirect and 37.87 total, mol m^{-2} day^{-1}). Canopy openness at Danum was also similar to that of closed forest at Pasir Mayang (Walter and Torquebiau, 1997), and between that of closed forest and forest with very small gaps at Danum (Brown and Whitmore, 1992; Whitmore et al., 1993) and at Lambir Hills, Sarawak (Davies et al., 1998). Total site factors lay between those for closed forest (5.2%) and forest with very small gaps (13.3%) found by Whitmore et al. (1993). Although some measurements of PAR in this study were made in or near small gaps in the otherwise closed forest, the values are low compared to the 1.0–1.1 mol m^{-2} day^{-1} of Brown and Whitmore (1992).

The PAR in PF and SF was similarly low, but the reasons may have been different in each forest. In PF it was most probably due to the special forest structure of few gaps, dense understorey and few large trees (i.e. the late long-term recovery stage), and in SF it was likely caused by the high abundance of pioneers in 1988-created large gaps, giving a low continuous canopy, and high densities of small dipterocarps and other understorey trees (Bischoff, 2001).

4.3. Primary forest structure

Density of trees $\geq$10 cm dbh ($\geq$31.4 cm gbh) in PF (Table 2) was at the lower end of the range with regard to density of trees in other Bornean sites (Newbery et al., 1992; Phillips and Gentry, 1994; Phillips et al., 1994; Slik et al., 2003). Bertault and Sist (1997), Sist and Nguyen-The (2002), Okuda et al. (2003) and Brearley et al. (2004) found higher tree densities (528–596 ha^{-1}) in primary forests of Malaysia and Indonesia, but Kuusipalo et al. (1996) reported a lower value of 420 ha^{-1}. Densities of ca. 480 ha^{-1}, as in PF, were reported by other authors (Chiew and Garcia, 1988; Woods, 1989; Sist and Nguyen-The, 2002). Including saplings in the calculations, PF at Danum had a mean of 6170 trees ha^{-1} $\geq$1 cm dbh, slightly less than at Pasoh with 6580 trees ha^{-1} (Okuda et al., 2003).

Basal area of trees $\geq$10 cm dbh in PF was also within the range of 24.9–33.1 m^2 ha^{-1} in pre-logging stands in YSCA (Pinard and Putz, 1996) and was similar or only slightly lower than the 26.6–31.4 m^2 ha^{-1} found by Chiew and Garcia (1988), Primack and Lee (1991), Bertault and Sist (1997), Sist and Nguyen-The (2002), Okuda et al. (2003) and Brearley et al. (2004). Thus, for this size class, Danum PF was similar to other forests in Borneo. For trees of dbh $\geq$20 cm (the threshold used by Cannon et al., 1994 and Sist et al., 2003c), PF plots at Danum had only 155 trees ha^{-1} in 1995 and 153 ha^{-1} in 2001, with corresponding BAs of 25.5 and 23.0 m^2 ha^{-1}. At Malinau, E. Kalimantan, Sist et al. (2003c) reported

249 ha^{-1} with BA of 31.2 m^2 ha^{-1} before logging, and Cannon et al. (1994) reported 221 ha^{-1} and BA of 32.3 m^2 ha^{-1} in their unlogged stands in W. Kalimantan. Therefore, for the larger tree-size classes, Danum PF was less well stocked than at other sites (see also Newbery et al., 1992).

Compared to the control plots of Sist and Nguyen-The (2002) in E. Kalimantan, PF at Danum had only 54% the density of dipterocarp trees $\geq$10 cm dbh (Table 2 cf. 109 ha^{-1}) although the contributions to total BA in both studies were very similar (14.4 for Danum cf. 14.5 m^2 ha^{-1}). In W. Kalimantan, ca. 44 dipterocarps ha^{-1} 20–< 50-cm dbh were recorded (Cannon et al., 1994), whereas in PF at Danum the density was less than half (17 ha^{-1} in 1995; 22 ha^{-1} in 2001): for the 50–143-cm dbh size class there were 19 ha^{-1} in 1995 (18 in 2001) in PF at Danum and 24 ha^{-1} in W. Kalimantan. Combining these data with those summarized in Newbery et al. (1992), Danum had relatively few (especially medium and larger) dipterocarps compared with other primary lowland dipterocarp forests in N.-E. and E. Borneo.

The 10 PF 'satellite' plots used in this study were located 50–400 m from the two 4-ha long-term dynamics, primary plots at Danum (Newbery et al., 1992, 1996, 1999). These main plots had BAs of 26.1 and 26.5 m^2 ha^{-1} in 1986 and 28.0 and 30.3 m^2 ha^{-1} in 1996. The very few and small gaps, near lack of pioneers, relatively few very large standing or fallen trees, the high abundance of lianas, relatively high density of understorey trees and a relatively low tree species diversity in comparison to other dipterocarp forests, all suggested a low level of *recent* disturbance but indicated a forest still rebuilding in a *late* stage of recovery from a probable major drought event in 1878 (Newbery et al., 1992, 1999; Walsh, 1996). Because of their proximity, it is reasonable to argue that PF and SF plots in this study were also in a similarly late stage of natural succession in 1986–1988. The PF–SF comparison needs to be interpreted in this context, and is a central point of the argument of this paper.

4.4. Secondary forest structure

By contrast to PF, SF at Danum was characterized by its relatively high tree density and BA compared to other secondary forest sites involved in similar logged versus unlogged studies. For trees $\geq$10 cm dbh, Kuusipalo et al. (1996) found lower densities in 12-year-old untreated SF (504 ha^{-1}), although their PF values were even lower at 420 ha^{-1} (BAs not reported). Brearley et al. (2004) reported very similar values to SF at Danum with 536 trees ha^{-1} and 25.7 m^2 ha^{-1} BA for a much older (55 years) secondary forest in C. Kalimantan resulting from abandonment of farming. Further, Cannon et al. (1994) found 158 trees ha^{-1} $\geq$20 cm dbh and a BA of 16.4 m^2 ha^{-1} in their 8-year-old logged site, whereas the present study at Danum in 1995 had corresponding values of 173 ha^{-1} and 20.1 m^2 ha^{-1}.

In contrast to the situation in PF, dipterocarps in the 20 to $\leq$50-cm dbh size class in SF at Danum (68 ha^{-1}, 8 years after logging) were more than twice as dense as in the 8-year-old logged forest in W. Kalimantan with 28 ha^{-1} (Cannon et al., 1994). However, densities of dipterocarps were similar for the 50–<143 cm dbh size class (SF Danum: 14 ha^{-1}, W. Kalimantan: ca. 9 ha^{-1}). This again suggests that SF at Danum had unusually high densities of small dipterocarps. Likewise, the proportion of dipterocarp saplings found in SF at 36% compared to only 4% in PF (correspondingly, 29 and 2% for trees 10 to $\leq$31.4 cm gbh) was a completely different result from that of Woods (1989) who found ca. 15% in both 6-year-old logged and unlogged forests, and of Nguyen-The and Rizal (1998) with 10% in 15-year-old secondary and 13.2% in primary forest. The Danum results are closer to those of Kuusipalo et al. (1996) who found a tendency towards higher proportions of dipterocarp seedlings in 12-year-old logged than unlogged forests (51% versus 39%).

The occurrence of large densities of pioneer species (especially *Macaranga* spp.) following logging (or large natural disturbances) is a widely documented phenomenon (Whitmore, 1984) and requires no further comment except that Slik et al. (2002) showed in logged forests in E. Kalimantan that no or few *Macaranga* saplings occurred where canopy openness fell below 15%. In the present study, there were no signs of decreased regeneration in SF compared to PF 13 years after logging because the numbers of saplings and small trees were similar. Nguyen-The and Rizal (1998) produced the same result for saplings 2–10 cm dbh in unlogged and 15-year-old logged forests. Whilst Kuusipalo et al. (1996) reported higher densities of seedlings 12 years after logging than in unlogged forest, they also found, as at Danum after 13 years, inhibition of new seedlings and growth into the sapling-stage of pioneers.

The above comparions are instructive in placing the PF–SF comparison at Danum in relation to other studies with different BAs in the primary forest and times since logging.

4.5. Diversity

At Danum, PF and SF barely differed in species richness and diversity for trees $\geq$10 cm gbh, although it should be borne in mind that, because SF plots were spread over an area one third larger than those in PF, species richness and diversity in SF would probably have been slightly lower than PF when compared on an equal-area basis. The one other comparable study of Cannon et al. (1998) showed SIRs significantly higher in 8-year-old logged than unlogged plots, for trees $\geq$20 cm dbh. Using the same richness measure and size-class, SIRs were higher in PF (0.77, 0.75) than SF (0.66, 0.60) in 1995 and 2001 at Danum ($P \leq 0.004$), a strongly contrasting result. Diversity of trees 8–13 years after disturbance may not, however, be a reliable guide to the likely diversity of the forest when it has succeeded beyond the pioneer stage, so generalizations about the effect of logging – on anyway so few taxonomically complete studies – need to be made with caution.

4.6. Primary forest dynamics

Annualized mortality (m_a) and recruitment (r_a) rates for trees $\geq$10 cm dbh ($\geq$31.4 cm gbh) in PF at Danum (Table 3) were higher than at 9 of 11 comparable SE Asian sites (Phillips and Gentry, 1994; Phillips et al., 1994). Annualized rates of mortality were 46–79% higher than the 1.3–1.6% in the control plots of Sist and Nguyen-The (2002), and 1.26% at Sandakan (Chiew and Garcia, 1988). For dipterocarps alone, m_a in the present study (Table 3) was 13–42% lower than 1.2–1.8% m_a given in Sist and Nguyen-The (2002). Mortality was calculated in a different way by these last authors as [$m_a = 1/t \times n_d/n_{95} \times 100$], however, but when applied to the Danum data it reduced mean m_a by only ca. 0.2% (2.82–2.61 in SF and 2.33–2.18 in PF). As in the study of Nguyen-The et al. (1998), no difference in m_a between dipterocarps and non-dipterocarps in PF was found for trees $\geq$10 cm dbh. Nevertheless, m_a in the small size class was higher for dipterocarps than non-dipterocarps—as in the present study.

Absolute annual diameter increments for trees $\geq$10 cm dbh in PF at Danum of 2.38 mm year^{-1} were similar to those of Pelissier et al. (1998) and Sist and Nguyen-The (2002) who reported 2.1–2.3 mm year^{-1} in their unlogged forests, but were not as high as the 7.1 mm year^{-1} found at Sandakan by Chiew and Garcia (1988). The mean 8.0-mm year^{-1} increment for dipterocarps at Danum was comparable to 8.6 mm year^{-1} at Sandakan (Chiew and Garcia, 1988) but ca. 2.5-fold the 3.4 mm year^{-1} reported by Sist and Nguyen-The (2002).

4.7. Secondary forest dynamics

Annualized mortality rates (m_a) of trees $\geq$10 cm dbh in SF (Table 3) were 8 and 66% higher than the mean m_a 4–6 years after logging in E. Kalimantan (2.6 and 1.7%, respectively: Sist and Nguyen-The, 2002), but very similar to the 2.5% found 15 years after logging by Nguyen-The et al. (1998). Mortality of dipterocarps at Danum was similar to E. Kalimantan at 4–6 years (1.9–2.8%), but higher than after 15 years at 1.9%. Although m_a for all trees $\geq$10 cm dbh per plot was not significantly different between PF and SF at Danum, it showed a complex pattern when recalculated on the basis of functional group or size classes (Table 3). The influence of pioneers on overall m_a became obvious, and differences in m_a of dipterocarps in the smaller size classes between PF and SF were highlighted. Thus, the higher m_a in SF was not only due to the dying of pioneers but also of small dipterocarps.

Annual diameter increments in SF of 4.63 mm year^{-1} were 60% higher than those of 2.9 mm year^{-1} found by Pelissier et al. (1998) in their 10–15-year-old secondary forest, and 19–25% higher than values of 3.7–3.9 mm year^{-1} for logged forest found 4–6 and 15 years after logging by Nguyen-The et al. (1998) and Sist and Nguyen-The (2002). Chiew and Garcia (1988) and Thang and Yong (1988) reported increment rates from forests 5 years after logging which were even higher (6.9–7.1 mm year^{-1}).

Mean diameter increment of dipterocarps, however, was only 4.54 mm year^{-1} in SF at Danum, less than the 5.3 mm year^{-1} at 15 years (Nguyen-The et al., 1998), 5.4 mm year^{-1} at 4–6 years (Chiew and Garcia, 1988) and 6.4–8.5 mm year^{-1} at 5 years (Thang and Yong, 1988) after logging. The growth rates 8–13 years after logging at Danum were likely largely caused by the high contribution of the pioneers in SF. Seemingly, the differences between forest types in rgr of dipterocarps disappeared (Table 3), whilst agr showed a marginally significant trend ($P = 0.089$) towards higher values in PF (7.96 mm gbh year^{-1}) than SF. The most important finding concerning growth was the slower rate for dipterocarps in SF than PF, especially in the smaller size classes—a result contrary to general expectation.

The comparison between PF and SF at Danum has therefore two special features: PF forest was still in late recovery and SF was moderately logged. This contrasts with the several other recent studies on logging effects quoted above, in which PF was presumably at its maximum stature and BA before logging and SF was usually more heavily exploited. The status of the ‘primary’ (control) forest is usually left unmentioned in many logging comparison studies. Nevertheless, the Danum plots are probably representative of that part of the forest block covering the SE ca. 100 km^2 of DVCA and the adjacent area of logged forest of similar extent, and logging effects have to be judged in the light the inferred history of PF.

As a rider to the foregoing discussion it is clear that the number of quanitative and complete studies of logged versus unlogged forests for Borneo is still too few to reach useful generalizations: sites differed critically in logging intensity, time since logging and tree size class used, besides the inevitable differences in regional climate, topography and soils.

4.8. Forest succession at Danum

Forest succession is determined by population dynamics prior to, during and after logging. Despite the 25% lower estimated volume of extractable dipterocarps in SF than PF before 1988, SF had 10 times as many dipterocarps as small trees and saplings than PF, and when non-timber dipterocarps (OTH) were excluded, the number of saplings of this family was still almost four times higher in SF than PF. The much higher densities, but lower survival and growth rates, of the dipterocarps in SF than PF is a central result of this study. Although the majority of small trees were non-dipterocarp/non-pioneer understorey species (Newbery et al., 1992, 1999) which do not grow to the canopy, the structure and composition of the forest canopy in SF in the future will be determined largely by the survival and growth of small trees of the overstorey species (particularly the dipterocarps).

Tree architectural studies at Danum have suggested that soon after disturbance many small trees (3–10 cm dbh) within large parts of SF receive less PAR than PF (Sterck et al., 2003). From ca. 5–8 years the density of pioneer, understorey and small overstorey trees 10–30-cm dbh in SF is often very high, and competition for space and resources is likely also to be very high. This is borne out in the present work by the high spatial variability in PAR in SF understorey: 13 years after logging many parts of SF received less PAR than PF, although there were some places where the converse was true. Overall, the heterogeneity averaged out to similarly low values in SF and PF.

Dipterocarp species lie along a continuum of both responsiveness to light and shade-tolerance as seedlings and saplings, and the maximum heights to which they can grow as trees. Light hardwood species are shade-intolerant as seedlings/saplings but when they receive more light can grow fast to become canopy and emergent trees. The essential difference between MHH and OTH species, is that whilst the former are more shade-tolerant than LH and their relatively slower growth allows them eventually to reach the canopy and emergent layers the latter are the most shade-tolerant and do not usually reach above the lower part of the main canopy (Meijer and Wood, 1964; Ashton, 1982). Accordingly, populations of seedlings and saplings of MHH and OTH species can increase steadily under conditions of low PAR with some recruitment and low mortality rates (high persistence) – even though their tree growth rates are low (Whitmore, 1984; Still, 1996; Brown et al., 1999) – whilst LH species have highly fluctuating populations, their strong spatial and temporal variability caused by high recruitment, mortality and growth rates (Still, 1993, 1996). In the absence of increased PAR, few saplings of the more light-demanding LH species persist long enough in the understorey to grow into small trees (Whitmore and Brown, 1996) and in forests with long intervals between mast fruiting events (which bring new cohorts of seedlings), these species fall away in the seedling bank because of shade-induced differential mortality (Brown et al., 1999). In this way, the shade-tolerant MHH and OTH species can become relatively more abundant.

In 1985 and 1986, PF at Danum was characterized by a still-closed canopy with very few small near-ground canopy gaps (Newbery et al., 1992). MHH and OTH species with low mortality rates seemingly built up their sapling banks and this could explain their high densities of small trees in the then unlogged forest. Prior to logging in 1988, the light levels in the forest were presumably low and spatially quite even (as in PF) because few gaps were formed in the preceeding years. A major mast fruiting event occurred in 1983 and 1984, 4–5 years earlier (Still, 1993; N.D. Brown, personal communication), and this was associated with an ENSO event (Beaman et al., 1985; Curran et al., 1999). General observations in primary forest by Still (1993) and D.M. Newbery support no masting in the period 1985–1988, so almost certainly no important seeding happened immediately before the logging in 1988 in SF.

It is therefore highly likely that the masting ca. 1984 led to an additional large cohort of dipterocarp seedlings which gradually thinned, with OTH species surviving better than LH species in the continuing shaded conditions. By the time of logging the absolute numbers of all seedlings or saplings would probably have been high. The temporary opening of the canopy by logging in SF may have released some surviving LH saplings but, as shown in the present work, the quickly closing cover of pioneers would have given a re-inforced advantage to the OTH species, this leading to their relatively high abundances by 1995 and 2001.

Whilst PF continued to aggrade, a few large tree falls may have allowed the LH species to increase among the small-tree size class (Newbery et al., 1999), but SF was by then almost maximally closed (Sterck et al., 2003). The next masting was in 1996 (Bebber et al., 2004). This most likely would have helped the recruitment of LH in PF but have had little effect in SF because the canopy remained closed and there were few LH trees after logging to provide seed.

The SF was probably broadly similar to PF in structure and composition before 1988, but it remains a possibility that it did coincidentally have more trees of OTH species. Logging led to a decrease in LH species, whilst MHH and OTH species increased under the low PAR conditions. Whereas LH species were *relatively* more abundant among the dipterocarps as small trees and saplings in PF (ca. 80%), LH and OTH each accounted for ca. 42% of small trees in SF, and OTH species dominated the sapling bank (ca. 70%). During the census period *H. nervosa* increased its density by 8.4% in SF. In PF, this species had a very high recruitment rate between 1986 and 1996 (Newbery et al., 1999), and low seedling mortality in 1985–1988 (Still, 1993). These results suggest that logging encouraged OTH species and in the future they will increase in SF.

In 2001, the 25 trees ≥60 cm dbh in SF were those left unlogged and those <60 cm dbh in 1988 that grew into the size class (12 LH and 4 MHH). These dipterocarps will be the main sources of mast seed and the next cohorts of LH and MH seedlings at this site. Trees of OTH species rarely exceed 60 cm dbh but nevertheless will leave seed. Dipterocarp species such as *H. nervosa* that fruit infrequently tend to have longer-lived seedlings than those such as *Shorea* species that fruit more often (Fox, 1973). If a masting were to occur shortly before the bulk of the pioneers trees died out the LH species would likely regain a predominance over the OTH species among the saplings and small trees, moving towards the proportions seen in PF. However, given that the OTH species are now well advanced they may become important competitors to the LH and MHH species in the main canopy and influence the eventual composition of the mature forest. Any further timber exploitation before the full successional process has taken place, inevitably concentrating on extraction of the large LH and MHH timber trees, will re-open the canopy, and repeat the selection of OTH species under the pioneers.

5. Conclusion

Two alternative routes appear likely for SF succession at Danum: either the OTH species consolidate their position and increase in population size so that LH and MHH populations are constrained; or the LH and MHH have the opportunity – given them by the receding pioneers in ca. 10–20 years – to have a wave of recruitment into the small-tree size class and release the current small trees to form a new main canopy.

This situation appears to have its most recent origins back at the postulated natural disturbance in 1878 (Walsh, 1996). This event set in train a succession in which the anticipation of man's intervention could have played no role. Logging therefore not only disturbs a forest's structure, like any other extreme stochastic event, but it interferes with *natural* succession. No model of regrowing dipterocarp forests appears so far to take this important point into consideration.

The effect of logging on a primary forest which itself is in a state of late succession seems to be different from one in which the forest has reached its mature, maximum biomass, state. The late successional forest selects for shade-tolerant OTH species, whilst the mature-phase forest, with a more regular turnover of large trees and gaps, allows for continual recruitment of shade-intolerant LH and MHH species. Logging can therefore lead to a temporary inhibition of natural secondary successional processes and, depending on local tree composition and recent history, this introduces a measure of uncertainity as to what forest type will occur after the pioneer stage.

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Appendix A. Pioneers

Species determined as pioneers (with numbers of trees $\geq$10 in SF in 1995): *Alstonia angustiloba, Dillenia borneensis, D. excelsa, Endospermum peltatum, Glochidion elmeri, G. lancisepalum, G. rubrum* (51), *Homalanthus populneus, Macaranga conifera, M. gigantea* (239), *M. hypoleuca* (71), *M. triloba* (16), *M. winkleri*, *Macaranga* sp., *Melicope confusa, M. glabra, M. incana, M. luna-akenda*, *Melicope* sp., *Neolamarckia cadamba, Neonauclea gigantea*, *Neonauclea* sp., *Vitex pubescens*. Other well-known pioneer species from Sabah, such as *Duabanga moluccana*, *Octomeles* spp., *Trema* spp. or *Leea* spp. did not occur in the investigated plots. Taxa from the genera *Artocarpus* and *Ficus* were not included in this group as not all of their species can be clearly identified as pioneers.

(See http://www.ipni.org/ for authorities.)

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