



Structure and floristics of an old secondary rain forest in Central Kalimantan, Indonesia, and a comparison with adjacent primary forest

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Received 14 March 2003; received in revised form 24 December 2003; accepted 20 February 2004

Abstract

The study of tropical secondary forests, and of the time taken for them to revert to ‘primary’ forest, is of increasing importance given the current global destruction of tropical rain forests. We describe a 55-year-old secondary rain forest at Barito Ulu, Central Kalimantan, Indonesia, and compare it with the adjacent, undisturbed, primary forest. Three 0.25 ha plots were set up in each forest type and all stems over 10 cm dbh were measured and identified, soil samples were taken and analysed, and the composition of the seed bank was examined. Although the basal area, tree height and biomass of the old secondary forest approached that of the primary forest (82% for basal area, 88% for tree height and 74% for biomass), there were still major differences in the floristics and species diversity. The old secondary forest was dominated by *Cratogeomys arborescens* (Hypericaceae) and *Pternandra caerulea* (Melastomataceae), whereas the primary forest was dominated by dipterocarps. The Shannon–Wiener diversity index was 3.40 for the old secondary forest plots and 4.17 for the primary forest plots; the Jaccard’s coefficient of similarity was 24%. Mortality, recruitment, turnover and tree growth rates were greater in the old secondary forest. The seed bank of the old secondary forest contained more than double the number of seeds of the primary forest seed bank and many more seeds were of shrub species; there were the same number of species in the two forests seed banks. There were no major differences between the two forest types in terms of soil chemistry. Despite the close proximity to potential seed sources, succession in the Barito Ulu area has proceeded more slowly than in some other tropical areas. This may be due to the low concentrations of soil nutrients and/or the poor dispersal of dipterocarp seeds. Fifty-five years of succession is concluded to be insufficient time for the return of most primary forest species. However, the forest structure of the old secondary forest shows a closer resemblance to the primary forest than does the floristic composition.

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Keywords: Borneo; Old secondary forest; Seed bank; Shifting cultivation; Soils; Tropical secondary succession

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1. Introduction

One of the most pressing environmental concerns is the destruction of tropical rain forests for silviculture and to make way for human habitation, agriculture and industry. Increasing attention is now being placed on tropical secondary forests (Brown and Lugo, 1990; Finegan, 1992, 1996; Corlett, 1995; Guariguata and Ostertag, 2001) since, the sustainable use of the resources they provide is essential for the continued protection of undisturbed primary forest areas. Secondary forests may act as buffer zones and serve as a habitat for forest plants and animals displaced from primary forest which has been destroyed. They may also act as reservoirs for recolonisation and as corridors between remaining primary forest fragments. Much of the deforestation has been caused by the conversion of forests to agricultural areas; indeed, two-thirds of the world's secondary forest in 1980 was shifting cultivation fallow (Lanly, 1982). In Kalimantan (Indonesian Borneo), especially in upriver areas, shifting cultivation is still an important form of agriculture (de Jong, 1997; Nagy and Proctor, 1999) and a total of 4.4×10^6 ha (ca. 8% of the land area) is estimated to be under this form of land use, sustaining 17% of the population (de Jong, 1997).

Considerable work has been done on the dynamics of secondary succession immediately following clearance and burning and the early stages of tropical succession are well documented (Uhl et al., 1981, 1988; Swaine and Hall, 1983; Toky and Ramakrishnan, 1983a,b; Uhl and Jordan, 1984; Uhl, 1987; Nagy and Proctor, 1999; Ohtsuka, 1999). From a biodiversity conservation perspective, it is important to know how secondary forests compare with primary forests in terms of species richness and species similarity. Again, work has been done on the early stages of succession (see above references) but less work has been done on older secondary forests. As succession proceeds, it would be expected that secondary forests will continue to increase in their similarity to primary forests until, after a certain amount of time, they are indistinguishable. The time taken for succession from forest clearance to forest resembling primary rain forest has been variously estimated at 50 years (Kochummen, 1966), 50–80 years (Brown and Lugo, 1990), 73 years (Hughes et al., 1999), 150–200 years (Richards, 1952; Knight, 1975), 150–500 years

(Riswan et al., 1985), 250–500 years (Kartawinata, 1994) and 'centuries' (Whitmore, 1991). The main problem with most of these estimates is that they are based on extrapolations of data for biomass increase and species accretion up to around 50 years of age. Beyond 50 years, these processes are unlikely to continue in a linear fashion. Furthermore, forests are likely to recover the structural characteristics of 'primary' forest a number of years before they recover the floristic characteristics. The actual time taken to revert to 'primary' forest will depend on many factors, including initial environmental conditions, intensity and scale of the disturbance, length of time of abandonment, amount of forest remaining in the surrounding landscape and the distance from the seed sources of primary forest species.

In this paper, we describe the structure and floristics of an area of old (55 years in 1998) secondary rain forest at the Barito Ulu study site in central Kalimantan, Indonesia. This is then compared with an adjacent, equally sampled, area of primary lowland evergreen rain forest. The main objective of the study is to compare the two forest types and determine whether a secondary forest can obtain the structure and floristics of a primary forest after 55 years of succession.

2. Study site

The project Barito Ulu research area is situated in Central Kalimantan, Indonesia, at 114°0'E, 0°06'S. The research area covers 430 ha and is diverse, containing a mosaic of forest types. These include several types of tropical lowland evergreen rain forest and heath forest (kerangas) as well as several areas of shifting cultivation fallow of various ages. The old secondary forest studied in this paper covers an area of about 3 ha and dates from the occupation by Japanese military forces (1942–1945) when villagers were forced to farm areas which would normally be impractically far from the river; after the military forces left, the area was not reformed. The plots are ca. 130 m a.s.l. and the geology is based on a Tertiary sedimentary formation which has given rise to sandy ultisols which are acidic and low in nutrients (Mirmanto et al., 1999). The topography is rugged with ridges up to 100 m high and slopes often in excess of 30°. Annual rainfall is about 3750 mm per annum; the wettest

months are January–March and the driest are June–September.

3. Methods

3.1. Plots

In August 1993, six 50 m × 50 m (0.25 ha) forest plots were set up in representative areas of vegetation: three in old secondary forest (OSF; numbered 13–15) and three in an adjacent area of primary lowland evergreen rain forest (PF; numbered 16–18). All the OSF plots were within 250 m of all the PF plots. Each plot was divided into 25 sub-plots of 10 m × 10 m. The diameter at breast height (dbh; 1.3 m) and location of all trees and lianas greater than 10 cm dbh within the plots was recorded; if buttresses were present, the dbh was measured 30 cm above the top of the buttress. All trees were identified as individual morphospecies, with 68% to species level, 19% to genus level only, 2% to family level only and 3% only as a morphospecies. Trees were identified by the last author, members of the Herbarium Bogoriense and dipterocarps by P.S. Ashton and the late T.C. Whitmore. Eight percent remained unidentified and most of these were still awaiting identification when they were killed by a strong wind which struck the site in November 1997 (Proctor et al., 2001). Voucher specimens collected from the trees are in the Project Barito Ulu Rekut Base Camp herbarium.

The dbh of all trees and lianas (including new recruits into the smallest size class, 10–20 cm dbh) was re-recorded in August 1998. The diameter increment of all the trees in the forest plots was calculated. Their growth rate was examined by regressing the diameter increment on to dbh in 1993, thus allowing a comparison of size-specific growth rates across all size classes.

The mortality rate for each plot was calculated according to Swaine and Lieberman (1987) and the recruitment rate was calculated according to Phillips et al. (1994). Turnover was calculated as the mean of the mortality and recruitment rates (Phillips et al., 1994). These measures are annual rates based on logarithmic models.

The height of 41% of the trees was measured using a graduated pole for small trees and a clinometer

(Suunto PM-5/360) and measuring tape for larger trees. A regression equation was created for each forest type to regress height onto dbh for the remaining trees (OSF: height = 7.88 + 0.654 × dbh, r^2 = 82.5%, P < 0.001; PF: height = 13.31 + 0.545 × dbh, r^2 = 74.1%, P < 0.001). The volume of each tree was estimated as height × basal area × 0.5 and a correction factor of 0.6 was applied to estimate above-ground biomass (see Proctor et al., 1983).

For each plot, the Shannon–Wiener diversity index (H') was calculated using the equation:

$$H' = -\sum_{i=1}^s p_i \ln p_i$$

where s is the number of species and p_i the abundance of the i th species expressed as a proportion of the total number of stems.

For all three plots in each forest type combined, Jaccard's coefficient of similarity (C_J) was calculated using the equation:

$$C_J = \frac{a}{a + b + c}$$

where a is the number of species in both forest types, b the number of species in the OSF but not the PF and c the number of species in the PF but not the OSF.

3.2. Soils

Five soil samples (0–10 cm depth) were taken from each of the six plots in a stratified random manner after removing the surface litter layer. The samples were air-dried, sieved to 2 mm and returned to the UK for analysis. The moisture content of the air-dried soil was determined by heating 5 g subsamples to 105 °C for 24 h. The same subsamples were used to measure loss-on-ignition at 350 °C for 16 h in a muffle furnace. pH was measured by adding 10 g of soil to 25 ml of 0.01 M potassium chloride solution. It was stirred and left to equilibrate for 1 h before the pH was measured with a pH meter (Corning EEL Model 7). Total nitrogen and phosphorus were determined by digesting 0.2 g samples in 4.4 ml of a sulphuric acid/hydrogen peroxide mixture with a selenium catalyst. The digested solutions were analysed on a FIAstar 5010 flow-injection analyser using the molybdenum blue method for phosphorus and the indophenol blue method for nitrogen. Exchangeable cations were leached from

5 g samples by the addition of 100 ml of 1 M ammonium acetate. The solutions were adjusted to pH 3.5 with hydrochloric acid and potassium and sodium were measured by flame emission with an air-acetylene flame and calcium and magnesium were measured by atomic absorption spectrophotometry with a nitrous oxide-acetylene flame (Varian AA-575). To determine total acidity, 5 g subsamples were leached by the addition of 100 ml of 1 M potassium chloride. A 10 ml extract was titrated against 2.5 mM sodium hydroxide in the presence of two drops of phenolphthalein indicator. After the addition of 10 ml of sodium fluoride, the solution was back-titrated with 0.01 M hydrochloric acid to determine aluminium. Hydrogen was calculated by subtraction. The sum of the exchangeable cations plus total acidity was used to determine the cation exchange capacity (CEC). The percentage-base saturation was calculated as the proportion of exchangeable cations (excluding aluminium and hydrogen) to the CEC.

3.3. Seed bank

Five soil samples of 25 cm × 25 cm × 5 cm deep were collected in a stratified random manner from each plot. The samples were spread out in wooden boxes to a uniform depth of 3 cm and covered with a neutral density shade cloth. The soils were watered as required and the topsoil in each box was occasionally disturbed to promote germination. The germinating seeds were recorded over a 5 months period and seedlings were removed following identification.

3.4. Statistical analyses

Comparisons were made between the two forest types using *t*-tests with each plot considered an independent replicate. For tree heights, a Mann–Whitney test was carried out, pooling the heights from all the plots in each forest type. Forest size class structure was compared using a χ^2 -test, again pooling the data for each forest type. An analysis of co-variance was used to compare the differences between tree growth rates in the two forest types using the dbh in 1993 as a covariate. All statistics were carried out using Minitab 12.2.

4. Results

4.1. Plots

We report the structural and floristic characteristics for the 1998 data only.

4.1.1. Structure

The mean basal area of the OSF was 82% of the PF although this was not significantly different (Table 1). Median tree height (both measured and from regression against dbh) in the OSF was 88%, and significantly, shorter than in the PF (Table 1). The mean above-ground biomass of the OSF was 74% of the PF, which was not significantly different (Table 1) although our biomass estimates do not take into account the differences in wood density

Table 1

Structural characteristics, dynamics and floristic diversity of three plots (each 0.25 ha) in old secondary forest (OSF) and three plots in primary forest (PF) at Barito Ulu, Central Kalimantan, Indonesia

	OSF	PF	
Stem density	134 ± 11	149 ± 8	$t_4 = 1.09, p = 0.34$
Basal area (m ²)	6.43 ± 1.07	7.83 ± 0.47	$t_4 = 1.19, p = 0.30$
Tree height (m)	19.0 (15.8 and 25.3)	22.1 (19.7 and 28.1)	$U_{401,446} = 60147, p < 0.001$
Above-ground biomass (t)	66.0 ± 13.6	89.6 ± 6.6	$t_4 = 1.56, p = 0.19$
Mortality (%)	2.37 ± 0.46	0.88 ± 0.70	$t_4 = 1.79, p = 0.15$
Recruitment (%)	0.74 ± 0.05	0.67 ± 0.03	$t_4 = 1.14, p = 0.32$
Turnover (%)	1.55 ± 0.25	0.78 ± 0.36	$t_4 = 1.76, p = 0.15$
Number of species	55 ± 7.6	85 ± 1.9	$t_4 = 3.77, p = 0.020$
Species:stem ratio	0.41 ± 0.03	0.57 ± 0.02	$t_4 = 5.23, p = 0.006$
Number of families	26 ± 1.5	30 ± 0.9	$t_4 = 2.46, p = 0.07$
Shannon–Wiener diversity index	3.40 ± 0.21	4.17 ± 0.06	$t_4 = 3.57, p = 0.023$

All values are mean ± S.E. with the exception of tree height which is median (lower quartile and upper quartile).

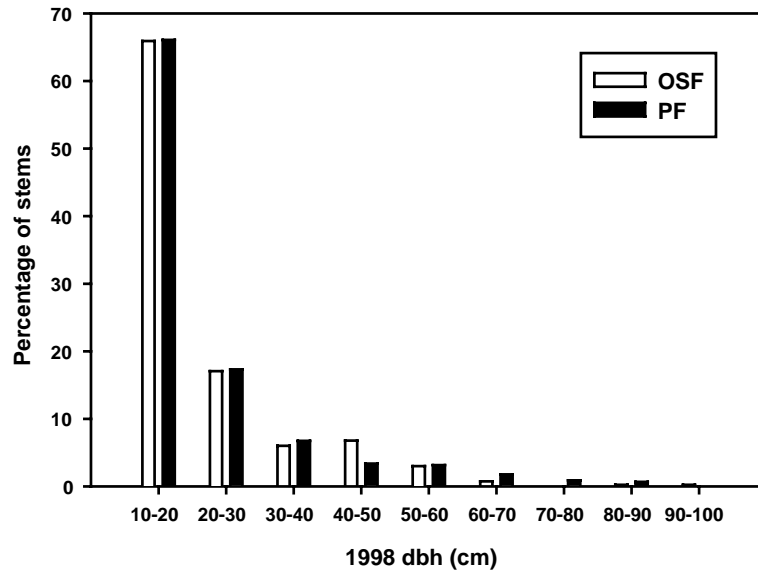


Fig. 1. Percentage of stems in different size classes in a 55-year-old secondary forest (OSF; open bars (□)) and primary forest (PF; filled bars (■)) at Barito Ulu, Central Kalimantan, Indonesia.

which may be around 10% less in the old secondary forest (Saldarriaga, 1987). Total stem density was also greater in the PF than in the OSF although, again, this was not significantly different (Table 1).

If two large remnant dipterocarps in plot 15, which were not cut during clearance for agriculture, are removed from the analyses, then we find that the results are slightly different with a significant difference between the above-ground biomass of the two forest types ($t_4 = 3.07$, $P = 0.037$) but not the basal area ($t_4 = 1.96$, $P = 0.12$). These two large trees contributed 28% of the above-ground biomass and 15% of the basal area of plot 15.

There were no significant differences between the two forest types in terms of size class structure ($\chi^2_7 = 10.53$, $P = 0.16$; Fig. 1). However, regarding the larger size classes, only 1.25% of the trees in the OSF were greater than 60 cm dbh, whereas in the PF the corresponding value was 3.37%.

4.1.2. Dynamics

The mean mortality rate was over 2.5 times greater in the OSF than in the PF, but was not significant due to high variation in the PF (Table 1). The mean recruitment rate was only slightly higher in the OSF

(Table 1). Therefore, overall, turnover in the OSF was about double that of the PF (Table 1). The regression line of diameter increment against 1993 dbh was significantly steeper for the trees in the OSF ($F_{1,772} = 30.89$, $P < 0.001$; Fig. 2) indicating a greater growth rate for a given diameter in this forest type.

4.1.3. Floristics and diversity

The commonest families in the old secondary forest, in terms of numbers of stems, were Melastomataceae (14.71%) (all of which were *Pternandra caerulea* Jack), Hypericaceae (10.72%) (all of which were *Cratoxylon arborescens* (Vahl) Blume) and Dilleniaceae (10.72%). In terms of basal area, the highest values were for Hypericaceae (31.53%), Dipterocarpaceae (12.88%) and Euphorbiaceae (7.85%) (Table 2).

This contrasts markedly with the primary forest where the commonest families, in terms of numbers of stems, were Dipterocarpaceae (20.18%), Euphorbiaceae (7.17%) and Anacardiaceae (6.73%). In terms of basal area, the highest value was again for Dipterocarpaceae (38.36%) followed by Fabaceae (9.29%) and Anacardiaceae (7.32%). It is also notable that the primary forest lacked any individuals of *C.*

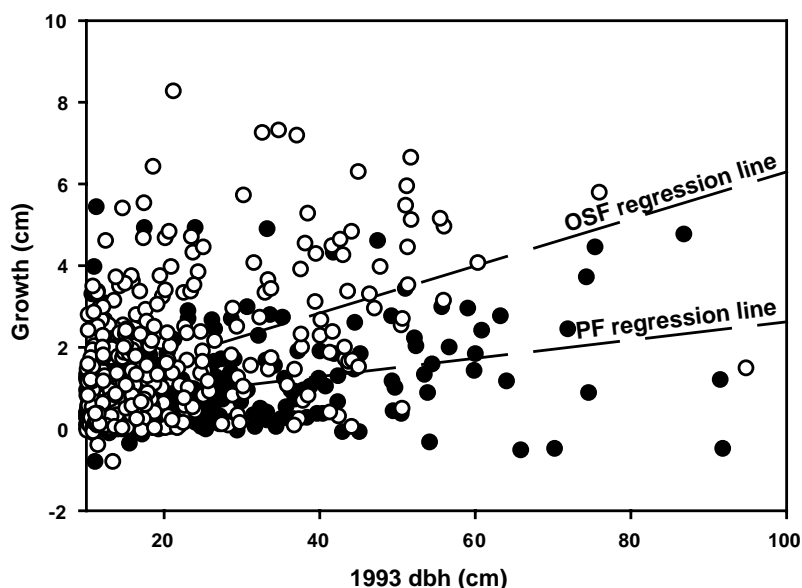


Fig. 2. Regression of diameter increment against initial diameter at breast height for trees in a 55-year-old secondary forest (OSF; open circles (○)) and primary forest (PF; filled circles (●)) at Barito Ulu, Central Kalimantan, Indonesia.

arborescens or *P. caerulea*, the two species with the greatest number of individuals in the OSF (Table 2).

The number of species and families per plot was greater in the PF than the OSF although only significantly so for the number of species (Table 1). There were 111 species in all three OSF plots combined and 174 species in all three PF plots. There were 36 families in all three OSF plots and 42 families in all three PF plots (Tables 1 and 2). The Shannon–Wiener diversity index was significantly greater in the PF plots than in the OSF plots (Table 1) as was the species:stem ratio (Table 1). When the data for all three plots in each forest type was combined, Jaccard’s coefficient of similarity between the two forest types was 24%.

4.2. Soils

The soils were acidic and low in nutrients (Table 3). There were no significant differences between the soils under the two forest types ($P > 0.05$ in all cases; Table 3) with the exception of exchangeable calcium which was at a higher concentration in the OSF soils ($t_4 = 4.37$, $P = 0.012$; Table 3).

4.3. Seed bank

The total number of germinating seeds was greater in the OSF (573 m^{-2}) when compared with the PF (175 m^{-2} ; Table 4) although there were about the same number of species found in the two forest types (OSF: 24; PF: 25; Table 4). About half the germinating seeds, in both forest types, were from tree species and there were about equal proportions of seeds of tree and liana species in the two forest types (Table 4). There were many more seeds of shrub species, both in absolute numbers and proportions, in the OSF when compared with the PF (Table 4).

5. Discussion

When compared with the primary forest, the Barito Ulu old secondary forest still retained many of the structural characteristics typical of secondary forests such as lower canopy height, basal area and above-ground biomass (Brown and Lugo, 1990). Although the forests size class structures were not different, values for many of the other structural characteristics of the old secondary forest were around 80% of the

Table 2

Family contributions to percentage stem density and basal area in three plots (each 0.25 ha) in old secondary forest (OSF; 13–15) and three plots in primary forest (PF; 16–18) at Barito Ulu, Central Kalimantan, Indonesia

Plot	13		14		15		OSF		16		17		18		PF	
	Stems	Basal area	Stems	Basal area	Stems	Basal area	Stems	Basal area	Stems	Basal area	Stems	Basal area	Stems	Basal area	Stems	Basal area
Actinidiaceae	–	–	–	–	1.33	0.44	0.50	0.19	–	–	–	–	–	–	–	–
Anacardiaceae	–	–	0.89	0.37	1.33	3.60	0.75	1.59	2.58	1.82	7.59	11.10	8.86	10.00	6.73	7.32
Annonaceae	1.44	1.17	2.68	2.16	2.00	1.09	2.00	1.36	3.87	1.21	1.27	0.30	2.53	1.22	2.69	0.94
Apocynaceae	–	–	–	–	–	–	–	–	–	–	–	–	0.63	0.99	0.22	0.33
Araliaceae	–	–	–	–	–	–	–	–	–	–	–	–	0.63	0.11	0.22	0.04
Bombacaceae	–	–	–	–	–	–	–	–	1.29	0.60	1.27	0.37	–	–	0.90	0.33
Burseraceae	–	–	–	–	2.00	0.57	0.75	0.24	5.81	1.83	1.27	0.38	2.53	0.99	3.36	1.11
Celastraceae	–	–	0.89	0.32	1.33	0.43	0.75	0.25	1.94	1.10	0.63	0.17	1.90	1.89	1.57	1.08
Chrysobalanaceae	–	–	–	–	–	–	–	–	0.65	1.16	–	–	1.27	2.75	0.67	1.34
Clusiaceae	1.44	0.59	0.89	0.20	1.33	0.35	1.25	0.40	0.65	0.38	2.53	0.64	2.53	1.46	2.02	0.81
Ctenolophonaceae	–	–	–	–	–	–	–	–	–	–	0.63	0.15	–	–	0.22	0.05
Dilleniaceae	8.63	2.30	12.50	6.23	11.33	5.82	10.72	4.68	–	–	0.63	0.25	–	–	0.22	0.08
Dipterocarpaceae	7.91	8.87	0.89	1.54	10.67	22.44	6.98	12.88	19.35	49.66	15.82	33.97	22.15	29.81	20.18	38.36
Ebenaceae	0.72	0.16	0.89	0.22	2.00	1.23	1.25	0.62	4.52	1.35	2.53	0.90	1.27	1.64	2.91	1.31
Elaeocarpaceae	1.44	0.47	–	–	0.67	0.20	0.75	0.25	0.65	0.24	–	–	–	–	0.22	0.09
Euphorbiaceae	6.47	4.90	4.46	10.76	6.67	8.75	5.99	7.85	8.39	3.28	5.06	2.11	6.96	3.24	7.17	2.91
Fabaceae	2.16	0.92	0.89	0.44	–	–	1.00	0.42	4.52	6.88	2.53	5.58	3.80	15.30	3.81	9.29
Fagaceae	1.44	0.95	1.79	0.49	1.33	0.47	1.50	0.64	3.23	6.47	0.63	0.35	0.63	1.46	1.57	2.97
Flacourtiaceae	–	–	–	–	–	–	–	–	1.29	0.52	–	–	0.63	0.39	0.67	0.32
Hypericaceae	16.55	47.43	5.36	18.39	9.33	25.34	10.72	31.53	–	–	–	–	–	–	–	–
Lauraceae	1.44	1.45	1.79	1.28	6.00	4.11	3.24	2.53	3.23	3.60	1.27	1.53	3.16	0.93	2.69	2.10
Lecythidaceae	–	–	–	–	–	–	–	–	–	–	1.90	0.90	–	–	0.67	0.27
Loganiaceae	–	–	–	–	–	–	–	–	0.65	0.10	–	–	–	–	0.22	0.03
Magnoliaceae	2.16	7.74	0.89	4.44	–	–	1.00	3.74	0.65	0.10	–	–	–	–	0.22	0.04
Melastomataceae	15.11	4.41	29.46	12.09	3.33	0.94	14.71	4.72	1.29	0.25	–	–	0.63	0.20	0.67	0.16
Meliaceae	0.72	0.26	–	–	–	–	0.25	0.09	1.94	1.19	4.43	1.61	1.90	1.14	2.91	1.30
Moraceae	5.04	2.81	8.04	4.75	4.67	1.76	5.74	2.81	1.94	0.85	2.53	5.79	0.63	0.26	1.79	2.13
Myristicaceae	0.72	0.14	1.79	3.65	2.67	2.45	1.75	1.91	6.45	2.28	3.16	4.01	2.53	1.41	4.26	2.51
Myrtaceae	2.88	4.17	5.36	14.28	4.67	6.22	4.24	7.34	2.58	1.36	0.63	0.36	1.27	5.12	1.57	2.31
Ochnaceae	0.72	0.16	–	–	–	–	0.25	0.06	–	–	0.63	0.33	–	–	0.22	0.10
Olacaceae	–	–	–	–	–	–	–	–	–	–	0.63	0.20	0.63	0.17	0.45	0.12
Oleaceae	–	–	–	–	–	–	–	–	1.29	0.49	0.63	0.25	1.90	1.11	1.35	0.63
Podocarpaceae	–	–	–	–	–	–	–	–	–	–	–	–	1.27	0.27	0.45	0.09
Polygalaceae	0.72	0.42	–	–	0.67	0.18	0.50	0.22	–	–	1.90	1.84	2.53	2.52	1.57	1.38
Rhizophoraceae	–	–	0.89	0.22	–	–	0.25	0.05	–	–	–	–	–	–	–	–
Rubiaceae	6.47	1.86	10.71	11.24	5.33	2.76	7.23	4.39	1.94	0.66	1.27	0.67	1.27	0.35	1.57	0.56
Rutaceae	1.44	1.68	0.89	1.90	1.33	0.55	1.25	1.26	0.65	0.14	–	–	–	–	0.22	0.05
Sapindaceae	2.88	1.62	–	–	0.67	1.69	1.25	1.28	1.29	0.53	1.90	2.18	1.27	0.23	1.57	0.92
Sapotaceae	0.72	0.15	–	–	–	–	0.25	0.05	0.65	0.09	1.90	2.18	5.06	4.47	2.69	2.17
Sterculiaceae	–	–	–	–	0.67	0.36	0.25	0.15	1.94	4.72	1.90	2.39	0.63	0.31	1.57	2.56
Symplocaceae	1.44	0.55	–	–	–	–	0.50	0.20	–	–	–	–	0.63	0.75	0.22	0.25
Tetrameristaceae	0.72	0.17	0.89	0.39	–	–	0.50	0.15	–	–	1.27	6.08	–	–	0.45	1.82
Theaceae	2.16	1.96	–	–	0.67	0.70	1.00	0.98	–	–	–	–	–	–	–	–
Thymeleaceae	–	–	–	–	0.67	0.50	0.25	0.21	–	–	2.53	1.09	6.96	2.02	3.36	1.00
Tiliaceae	–	–	0.89	0.23	–	–	0.25	0.05	–	–	–	–	0.63	0.43	0.22	0.14
Ulmaceae	0.72	0.21	–	–	0.67	0.21	0.50	0.16	–	–	–	–	–	–	–	–
Verbenaceae	0.72	0.23	0.89	0.25	1.33	0.26	1.00	0.24	1.94	0.95	1.27	1.61	0.63	0.80	1.35	1.10
Unknown	5.04	2.25	5.36	4.17	15.33	6.57	8.98	4.50	12.90	6.20	12.03	10.70	10.13	6.25	12.33	7.56

Table 3

Soil characteristics (0–10 cm depth) from three plots in old secondary forest (OSF; 13–15) and three plots in primary forest (PF; 16–18) at Barito Ulu, Central Kalimantan, Indonesia

	OSF	PF
pH _{KCl}	3.1 ± 0.03	3.2 ± 0.02
Loss on ignition (%)	9.3 ± 0.53	8.2 ± 0.47
Total N (mg g ⁻¹)	0.80 ± 0.09	0.95 ± 0.12
Total P (mg g ⁻¹)	0.04 ± 0.003	0.04 ± 0.002
K ⁺ (m-equiv. 100 g ⁻¹)	0.14 ± 0.02	0.17 ± 0.01
Na ⁺ (m-equiv. 100 g ⁻¹)	0.01 ± 0.003	0.01 ± 0.001
Ca ²⁺ (m-equiv. 100 g ⁻¹)	0.22 ± 0.02	0.10 ± 0.02
Mg ²⁺ (m-equiv. 100 g ⁻¹)	0.25 ± 0.03	0.24 ± 0.02
Al ³⁺ (m-equiv. 100 g ⁻¹)	8.90 ± 0.36	9.07 ± 0.35
H ⁺ (m-equiv. 100 g ⁻¹)	0.22 ± 0.07	0.08 ± 0.04
CEC (m-equiv. 100 g ⁻¹)	9.74 ± 0.75	9.67 ± 0.16
Base saturation (%)	6.37 ± 0.37	5.42 ± 0.39

All results are presented on an oven-dry (105 °C) basis.

primary forest values. Despite the lack of statistically significant differences in a number of cases, we consider the results to be important bearing in mind: (i) the limited number of plots (three) in each forest type, (ii) the disproportionate effect of two remnant trees in one of the old secondary forest plots and (iii) the tree mortality following the 1997 storm (Proctor et al., 2001) which obscured patterns of natural senescence. More time is needed to accumulate an above-ground biomass similar to the primary forest as the trees in the old secondary forest are still shorter and their wood is likely to be less dense (Saldarriaga, 1987). The species richness (as assessed by number of species and Shannon–Wiener diversity index) of the old secondary forest was considerably lower than that of the primary forest and the compositional similarity (Jaccard's coefficient) between the two forest types was only 24%. Ferreira and Prance (1999) obtained similar findings to ours: after 40 years of succession, the forest biomass and basal area was slightly lower than in the primary forest but there were still major differences in terms of floristics. They found a similarity between the two forest types of only 12%.

Our results for above-ground biomass in the old secondary forest are equivalent to 264 tonnes ha⁻¹ which can be compared with a number of other studies. Hughes et al. (1999) found 287 tonnes ha⁻¹ for a 40-year-old secondary forest which was 71% of the primary forest value, Ferreira and Prance (1999) found 471 tonnes ha⁻¹ for a 40-year-old forest (95%

Table 4

Number of germinating seed and species, in four life forms, present in the soil seed bank in old secondary forest and primary forest at Barito Ulu, Central Kalimantan, Indonesia

	Old secondary		Primary	
	No.	%	No.	%
Trees				
<i>Ardisia</i> sp.	–	–	3	1.7
<i>Callicarpa cana</i> L.	58	10.1	25	14.3
<i>Cratogeomys</i> sp.	13	2.3	3	1.7
<i>Euodia latifolia</i> DC.	15	2.6	–	–
<i>Ficus geocarpa</i> King (Becc.)	21	3.7	8	4.6
<i>Geunsia pentandra</i> Merr.	2	0.3	18	10.3
<i>Glochidion</i> sp.	30	5.2	6	3.4
<i>Macaranga gigantea</i> Muell. Arg.	10	1.7	5	2.9
<i>Macaranga hosei</i> King <i>ex</i> Hook.f.	22	3.8	6	3.4
Moraceae sp.	2	0.3	2	1.1
<i>Pternandra caerulea</i> Jack	15	2.6	8	4.6
<i>Saurauia nudiflora</i> DC.	–	–	1	0.6
<i>Trema orientalis</i> (L.) Blume	93	16.2	9	5.1
	281	49.0	94	53.7
Shrubs				
<i>Costus speciosus</i> (Koenig) Smith	4	0.7	3	1.7
<i>Labisia</i> sp.	22	3.8	8	4.6
<i>Leea indica</i> (Burm. f.) Merr.	3	0.5	–	–
<i>Melastoma malabathricum</i> L.	194	33.9	4	2.3
	223	38.9	15	8.6
Grasses				
Cyperaceae sp.	31	5.4	21	12.0
<i>Scleria lithosperma</i> (L.) Sw.	–	–	9	5.1
<i>Sorghum propinquum</i> (Kuhth) Hitc.	7	1.2	7	4.0
	38	6.6	37	21.1
Lianas				
<i>Rubus moluccanus</i> L.	–	–	1	0.6
<i>Uncaria</i> sp.	16	2.8	9	5.1
	16	2.8	10	5.7
Unidentified				
1	3	0.5	4	2.3
2	3	0.5	3	1.7
3	–	–	3	1.7
4	–	–	3	1.7
5	4	0.7	6	3.4
6	3	0.5	–	–
7	1	0.2	–	–
8	1	0.2	–	–
	15	2.6	19	10.9
Total seeds	573		175	
Total species	24		25	

All values are per m⁻².

of primary forest) and Saldarriaga et al. (1988) found 150 tonnes ha⁻¹ for both 60- and 80-year-old forests (59% of primary forest). There are large differences between these values but much of this is probably due to intrinsic differences in forest biomass between the different areas. Biomass accumulation during tropical secondary succession is usually around 5–10 tonnes ha⁻¹ per year (Uhl et al., 1988; Brown and Lugo, 1990; Alves et al., 1997; Steininger, 2000) and is more rapid in the first 15 years of succession (Brown and Lugo, 1990). There is also evidence that biomass accumulation during secondary succession is dependent upon the prior land use history, with longer and more severe disturbances leading to a longer time to accumulate a given biomass (Alves et al., 1997; Hughes et al., 1999; Steininger, 2000). Hughes et al. (1999) predicted that prolonged periods of land use (<15 years) may more than double the length of time for secondary forests to accumulate a biomass equivalent to primary forests. Unfortunately, we do not know for exactly how long the land was farmed prior to succession in the Barito Ulu area but, judging from present day practice, it would be around 2 years.

Despite the close proximity of seed sources of primary forest species, the compositional similarity of the two forest types is still only 24%. Guariguata and Ostertag (2001), looking at a range of neotropical sites, found that succession in areas with more fertile soils showed more rapid basal area accumulation. Possibly, the slow time for recovery of the Barito Ulu forest is due to the low concentrations of soil nutrients when compared with a number of other Bornean sites (e.g. Gunung Mulu, Sarawak, Proctor

et al., 1983; Bukit Belalong, Brunei, Pendry and Proctor, 1997; Danum Valley, Sabah, Green, 1992; Kabili-Sepilok, Sabah, Brearley, 2003).

The usual course of changes in soil nutrient chemistry following burning of the overlying vegetation prior to agricultural use is an initial increase in soil nutrients and soil pH due to ash addition (Kleinman et al., 1995). As succession proceeds, there is a decline in these nutrients as they are taken up by the rapidly growing vegetation. There is then a decrease in base saturation as aluminium increases and potassium, calcium and magnesium decrease. In contrast, much of the nitrogen is volatilised during the burn. Prajadinata (1996), working in the Barito Ulu area, reported an increase in total soil nitrogen as succession proceeded. Robertson (1984) reported an increase in nitrogen mineralisation and nitrification during the first 16 years of succession in Costa Rica.

There were minor differences between the two forest types in terms of soils and we do not consider this to be of importance in determining forest structure or floristics at this stage of succession. A bioassay experiment, using soils from the two forest types (Brearley, 1999) showed no significant differences between the two forests soils in terms of rice seedling (*Oryza sativa* L. Poaceae) growth. Light is likely to be limiting the growth of dipterocarp seedlings and this may well be higher in the old secondary forest. Prajadinata's (1996) finding of higher herb densities in the old secondary forest lends support to this hypothesis.

The total density of germinating seeds and number of species found in the seed bank is in the range for other southeast Asian studies (Table 5) although higher

Table 5

Seed density and number of species found in the seed banks of a number of southeast Asian sites (PF: primary forest; OSF: old secondary forest)

Site	Forest type	Seeds (m ⁻²)	No. of species	Reference
Barito Ulu, Central Kalimantan, Indonesia	PF	175	25	This study
Barito Ulu, Central Kalimantan, Indonesia	OSF	573	24	This study
Chiang Mai, Thailand (site no. 2)	PF	128	24	Cheke et al., 1979
Gogol Valley, Papua New Guinea	PF	398	–	Saulei and Swaine, 1988
Gogol Valley, Papua New Guinea	OSF	757	–	Saulei and Swaine, 1988
Lungmanis, Sabah, Malaysia	PF	58	29	Liew, 1973
Pasoh, Malaysia	PF	131	30	Putz and Appanah, 1987
Sinharaja, Sri Lanka	PF	343 ^a	33 ^a	Singhakumara et al., 2000

^a Excluding seeds of the exotic shrub *Clidemia hirta* (L.) D. Don (Melastomataceae).

values have been recorded in Africa, Australia and the neotropics (Garwood, 1989). The old secondary forest seed bank had more than three times the number of seeds found in the seed bank of the primary forest, indicating a greater input of seeds from light-demanding (pioneer and generally small seeded) species in this area; there may also have been some input from adjacent areas of younger secondary forest. This agrees with Saulei and Swaine's (1988) findings, although it contrasts with Dalling and Denslow (1998) who did not find any differences in the seed bank composition of old secondary forests (40–100-year-old) and primary forest. The old secondary forest had a large number of seeds of shrub species indicating that this life-form was still more important in this forest type than in the primary forest. It is also notable that there were no seeds of forb or herb species in either forest type which were found in all the other studies noted in Table 5, as well as in secondary forests at least up to 20 years of age in the Barito Ulu area (Prajadinata, 1996).

It is interesting to note how secondary succession in different tropical areas has proceeded differently (Table 6). Succession in the Barito Ulu area does not appear to be as rapid as in the Jaú National Park, Brazil (Ferreira and Prance, 1999) where there was an accumulation of 95% of the basal area and biomass of the primary forest after only 40 years of succession although there were only 60% of the species. This rapid accumulation of biomass might be due to more

fertile soils in Amazonia although there were also a number of remnant trees of *Bertholletia excelsa* Humb. and Bonpl. (Lecythidaceae) in the area of old secondary forest studied which is likely to increase the values recorded. Succession in Barito Ulu does, however, appear to be more rapid than in the Central Catchment Nature Reserve, Singapore (Turner et al., 1997). This is most likely due to both a greater distance to seed sources, as well as severely degraded soils, in Singapore (Corlett, 1991, 1995). Saldarriaga et al. (1988) study contrasts with the other studies cited in that there was a much more rapid recovery of tree diversity, but the basal area and biomass were only 59% of primary forest values after 60–80 years of succession. This was a lower value than all the other studies in Table 6 but theirs was the only study to correct for wood density when estimating biomass.

It is also possible to compare secondary succession following agricultural use with forest recovery following logging. Simulation models for the growth of dipterocarp forests suggest that a logging cycle of at least 45 years (van Gardingen et al., 2003) to 60 years (Huth and Ditzer, 2001), preferably in combination with reduced impact logging methods, is needed for sustainable yields. If the logging cycle is less than this period of time, then the forest is unlikely to show a full recovery of structure and composition to that similar to a primary (i.e. unlogged) forest. For example, Okuda et al. (2003) found that 40 years after logging using the

Table 6

Comparison of old secondary forests (≥ 40 years) with primary forests in a number of lowland tropical forests. All values presented are the percentages found in the old secondary forests when compared with the primary forests

Location	Age (years)	Minimum tree size (cm dbh)	No. of stems	Basal area	Biomass	No. of species	Diversity index	Reference
Jaú National Park, Brazil	40	10	94	95	95	60*	–	Ferreira and Prance, 1999
Luquillo, Puerto Rico	51.5	1	89	79	–	78	83	Aide et al., 1996
Barito Ulu, Central Kalimantan, Indonesia	55	10	90	82	74	65*	82	This study
Luquillo, Puerto Rico	60	1	101	92	–	115	96	Aide et al., 1996
Moruca, Guyana	60	10	96	70	–	100	109	van Andel, 2001
Rio Negro, Colombia/Venezuela	60	1	73	70*	59*	88	99	Saldarriaga et al., 1988
Rio Negro, Colombia/Venezuela	80	1	102	69*	59*	95	100	Saldarriaga et al., 1988
Central Catchment Nature Reserve, Singapore (S1)	100	9.55	127	66*	–	47*	65*	Turner et al., 1997
Central Catchment Nature Reserve, Singapore (S2)	100	9.55	117	68*	–	62*	75*	Turner et al., 1997

* Statistically significant differences between the old secondary and primary forests are indicated as $P < 0.05$.

Malayan Uniform System, the basal area of dipterocarps in the regenerating forest at Pasoh (Peninsula Malaysia) was similar to that in primary forest but the canopy was significantly lower and more even due to a lack of emergent trees. Furthermore, tree diversity (Fisher's alpha) remained, as expected, lower in the regenerating forest.

Succession in different areas of southeast Asia has also proceeded very differently. Okimori and Matius (2000) found an area of 70-year-old secondary forest in east Kalimantan which was dominated by the dipterocarps *Shorea parvifolia* Dyer and *Shorea leprosula* Miq. (which accounted for nearly half of the basal area). In marked contrast, Corlett (1991, 1995) noted an area of 70-year-old secondary forest with an absence of dipterocarps; this was explained by a large distance to the nearest seed source. These two forests compare with the Barito Ulu old secondary forest where *S. parvifolia* is rare and the forest is dominated by *C. arborecens*. Meijer (1971) also noted an area of old secondary forest on the border of Kinabalu National Park in Sabah which had *C. arborecens* present. Both *S. parvifolia* and *C. arborecens* could be considered long-lived pioneer species. When these species start to die it will be interesting to see how succession proceeds. Many dipterocarp species do not reach reproductive maturity until around 50–60 years of age (Meijer, 1965, in Riswan et al., 1985) so individuals which arrived in this area early in the succession may now be at an age at which they will start to produce fruit and the number of dipterocarp seedlings in the old secondary forest may start to show an increase. We will continue to monitor this area of forest in the foreseeable future to record these changes.

6. Conclusions

Whilst the old secondary forest at Barito Ulu is superficially similar in structure to the primary forest, there is still only around an 80% recovery of basal area and biomass after 55 years of succession. There are still major floristic differences between the two forest types with the old secondary forest being less diverse and having only a 24% similarity with the primary forest. There are differences in the soil seed bank and tree mortality and growth rates indicating different

regeneration patterns between the two forest types. Fifty-five years is clearly insufficient time for the secondary forest to revert to 'primary' forest.

Acknowledgements

We wish to thank the Indonesian Ambassador to the UK, the Indonesian Institute of Sciences and the Indonesian Ministry of Forestry for permission to work in Indonesia; Rupert Ridgeway of Project Barito Ulu for invaluable logistical support; Laszlo Nagy, Laura Macmillan, Mulyadi, Kursani Putra and Gill Telford for assistance with the project and various financial supporters.

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