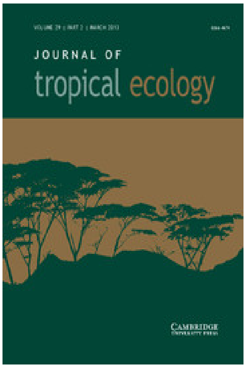

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Effects of tree species heterogeneity on leaf fall in primary and logged dipterocarp forest in the Ulu Segama Forest Reserve, Sabah, Malaysia

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ABSTRACT. Effects of tree species heterogeneity on leaf fall were studied in a primary (4 ha) and in a selectively logged forest plot (2.5 ha) in the Ulu Segama Forest Reserve, Sabah, Malaysia, from April 1988 to December 1989. Leaf fall was collected at 30 sampling points in each plot, and identified to species.

Dipterocarpaceae, Euphorbiaceae, Lauraceae, Fagaceae and Meliaceae are important tree families in both plots with regard to their contribution to total basal area, tree density and annual leaf fall. The total number of tree species was higher in the primary forest plot (267) than in the logged forest plot (218), although the number of climber species was higher in the logged forest (44) than in the primary forest plot (33). The overlap in species composition between the two forest plots was relatively small (49%) compared with that in family composition (88%).

In the primary forest plot, the Dipterocarpaceae contributed 29% of the total basal area and 34% of the annual leaf fall. In the logged forest plot these contributions were much lower, 11% and 15%. The contribution to annual leaf fall made by climbers and pioneer trees was higher in the logged forest plot (34%) than in the primary forest plot (8%).

In the primary forest plot, leaf fall was dominated by large emergent and main canopy trees, mainly dipterocarps, and occurred as regular large peaks. In the logged forest leaf fall was dominated by climbers and many, relatively small trees of pioneer species, such as *Macaranga hypoleuca*, and was more evenly distributed in time.

KEY WORDS: climbers, decomposition, dipterocarps, heterogeneity, leaf fall, *Macaranga* spp, patchiness, rainforest, Sabah, selective logging.

INTRODUCTION

The contribution of different tree species to leaf fall and leaf litter decomposition is an important consideration within the nutrient cycle of many rainforests (Golley 1983, Swift & Anderson 1989). Even in seasonal tropical forests, where the dry season is long enough to result in a generally large peak in leaf fall, tree species differ in the patterns of their leaf fall with time (Frankie *et al.* 1974, Kunkel-Westphal & Kunkel 1979, Lieberman 1982). In aseasonal tropical forests these differences are more pronounced (Addicott 1978, Koriba 1958, Medway 1972), and are expected to cause a heterogeneous mosaic of leaf fall and litter mass on the forest floor (Heatwole 1961, Medway 1972). This mosaic structure of the litter layer might reflect differences between individual trees, tree species or tree families and, on a larger scale, between developmental phases of the forest canopy.

Tree species possibly affect heterogeneity of the forest floor by (i) leaf biomass or the quantity of leaf fall, (ii) leaf phenology, such as leaf life spans (Chabot & Hicks 1982), timing of leaf-flushing and leaf-shedding (Holttum 1940, Ng 1984), (iii) chemical characteristics of leaves, such as nutrient concentrations and allelopathic secondary metabolites (Hornung 1985, Waterman & McKey 1989), and (iv) physical characteristics of leaves, such as hairiness and leaf toughness (Coley 1983). These four variables may affect the direct leaching of nutrients from the canopy and freshly fallen leaves, and contribute to the attractiveness of accumulated leaf litter to decomposer invertebrates and micro-organisms. Tree species heterogeneity, therefore, is likely to affect the spatial patchiness of litter layer mass, litter turnover, nutrient availability and humus formation. This patchiness is presumed to be an important determinant of seedling establishment (Sydes & Grime 1981) and contributes to niche diversification (Remmert 1991, Tilman 1988), in particular in many tropical rainforests (Molofsky & Augspurger 1992, Swift & Anderson 1989). In the latter, the vegetation greatly relies upon the decomposition of litter to support its nutrient demand, when nutrient supply by the soil parent materials is low (Bruijnzeel 1990).

To reveal the contribution of tree species heterogeneity to spatial patchiness, we describe in the present study the botanical composition of vegetation and leaf fall in a Bornean dipterocarp forest in relation to spatial and temporal variation in leaf fall as measured in Burghouts *et al.* (1992). Temporal variation in leaf fall was small compared with spatial variation at 30 sampling points in a primary (4 ha) and in a selectively logged dipterocarp forest plot (2.5 ha) in the Danum Valley in Sabah, East Malaysia. In the primary forest plot, spatial variation in litter layer mass was related to the abundance of different taxonomic groups of forest floor invertebrates, and was more pronounced than in the logged forest plot (Burghouts *et al.* 1992).

In the present study the following aspects were investigated:

(i) Large dipterocarp trees dominate the biomass of lowland dipterocarp forest (Newbery *et al.* 1992, Whitmore 1984), but do they dominate annual leaf fall and determine the pattern of total leaf fall?

(ii) To what extent does high tree species diversity in evergreen rainforest result in heterogeneous leaf fall? Is it possible to distinguish cycles of leaf fall caused by the synchronization among individual trees or tree species (Medway 1972, Ng 1984, Swift & Anderson 1989)?

(iii) Removal of emergent dipterocarp trees through selective logging decreases the contribution of dipterocarps to total biomass. To what extent will the contribution to leaf fall by climber and pioneer species increase?

In our study a comparison was made between a primary forest plot and a plot located in 12-year-old selectively logged forest. A variety of development phases of the forest growth cycle were included.

STUDY PLOTS AND THEIR ENVIRONMENT

The study was carried out during March 1988–January 1990 in the Danum Valley Field Centre (DVFC) in Sabah, Malaysia, in the north-eastern part of Borneo (4° 58′ N, 117° 48′ E; Marsh & Greer 1992). In the eastern half of Sabah, the remaining primary lowland forests and some regenerating logged forests are extremely rich in large trees from the family Dipterocarpaceae (Whitmore 1984). Sabah has about 180 species (Ashton 1982, Y. F. Lee, personal communication) in this commercial tree family which can be grouped according their timber properties (Burgess 1966). Combined with the strong export demand for hardwood, this encourages extraction levels that are among the highest in the tropics (Marsh & Greer 1992, Sundberg 1983). In Sabah logging is carried out according to the Malayan Uniform System. Commercial trees are removed in a single operation and the cutting cycle is about equal to the rotation age of the trees (Kartawinata *et al.* 1989, Whitmore 1984). In some logging coupes, extraction levels of up to 166 m^3 ha^{-1}, with an average of 118 m^3 ha^{-1} are associated with heavy damage of the dipterocarp forest (Fox 1972, Marsh & Greer 1992, Nicholson 1979).

Two research plots were selected in the vicinity of the DVFC. In an undisturbed lowland dipterocarp forest, use was made of a 4 ha (100 m × 400 m) set up by D. M. Newbery and co-workers in the Danum Valley Conservation Area (plot 1, cf. Newbery *et al.* 1992). In addition, in November 1988 we selected a 2.5 ha (100 m × 250 m) plot in the 1978 logging coupe North Area 'B' in the Pacific Hardwood Industrial Reserve Area (Marsh & Greer 1992), some 15 km east of the DVFC and easily accessible from the main logging road. The forest area in which the plot was sited was selectively logged in 1978 using crawler tractors. Recordings of timber yields were available from Silam Forest Products (1978).

The logged forest plot was necessarily smaller than the primary forest plot to avoid inclusion of steep slopes and soil types that differed too much from those in the primary forest plot. Hence, the two plots showed similar means and ranges in slopes (*c.* 25°, 10–40°) and a similar type with similar chemical characteristics (Burghouts & Bruijnzeel, in prep.). The elevation of the primary forest plot was 210–240 m asl (above sea level), of the logged forest plot between 100 and 130 m asl.

Both plots were underlain by an ultisol soil type (Marsh & Greer 1992, Newbery *et al.* 1992) of sandy-loam texture and with a typical particle size distribution at 30 m depth of *c.* 38% clay, 36% silt, 26% sand. In some areas, the logged forest plot had sandier soils, with again at 30 cm depth, 30% clay, 37% silt, 33% sand, possibly reflecting a less complete weathering of the substrate (Van der Plas & Bruijnzeel 1993).

The general climate of the Danum Valley is described by Marsh & Greer (1992), whereas characteristics of the forest micro-climate have been given by Brown (1990) and Brown & Whitmore (1992). Rainfall data over a period of five years (1986–1990) suggested a slightly bimodal distribution with a mean of *c.* 2800 mm. This pattern is influenced by the edge effects of two monsoons: the wetter north-east monsoon from November to March and the drier but more consistent south-western monsoon in June and July. Although the onset of both monsoons is quite variable, there is a general trend for drier spells during the transition months of April and September (Marsh & Greer 1992). Showers usually fall as short, intensive events in the afternoon or evening. Temperatures vary little throughout the year, with a mean of 26.7°C, but there is considerable diurnal variation (typically between 22.5°C in the early morning and 30.9°C shortly after noon). In the nearby forest, mean maximum and mean minimum temperatures were 21.2 and 28.4°C, respectively (Brown 1990). At the DVFC, from 1800 h to 0800 h the average relative humidity in an open area in the shade is close to 100%. During the day-time it fluctuates between 60 and 100% with an annual mean of 95% at 0800 h and 72% at 1400 h (Burghouts *et al.* 1992, Marsh & Greer 1992).

Differences in climatic factors between the primary and the logged forest plot were expected to be relatively small due to closure of gaps in the canopy by vigorously growing pioneer trees and climbers.

METHODS

Sampling areas and sampling points

Within each of the two plots 30 pairs of coordinates were randomly selected, and defined as 'sampling points' at which litterfall was collected. The tree species composition of litterfall was studied in relation to the trees surrounding the litter trap and potentially contributing to leaf fall in that trap. To this end, we defined 'sampling areas' by a circle of 10 m radius (314 m^2) around each sampling point. Consequentially, sampling areas were overlapping when two randomly selected sampling points were less than 20 m apart.

Leaf fall

Total litterfall was collected at each of 30 sampling points in the primary forest plot from April 1988 to January 1990, and in the logged forest plot from December 1988 to January 1990. Comparisons between forest plots were based on leaf data from the period December 1988–January 1990. The litter traps consisted of 0.1 mm nylon mesh, with an area of 0.7 m^2, suspended on 4 PVC poles, 0.5 m above ground level. Litterfall was collected weekly, dried to constant weight for 7 days in a solar drying house (65°C) and separated into different fractions on a monthly basis, as described in Burghouts *et al.* (1992) and Burghouts & Bruijnzeel (in prep.).

Tree species and family composition. For each of the 30 sampling points in both forest plots, the leaf fraction of litterfall was weighed and identified as far as possible to species, on a monthly basis. (For unknown families and species a code number was used throughout the collection period, to enable further identification.) Because weighing leaves of each species was too laborious, only contributions of species exceeding 10 g were recorded. The difference between the total weight of leaves of these species and that of all species identified, was equally divided between the remaining species (that contributed less than 10 g). Finally, annual and monthly leaf fall were estimated, for each species, for each sampling point and plot, and summarized for each family.

Composition according to a structural classification. Species were ecologically classified into tree species (emergent (E), main canopy (M) and understorey (U)), climber species (C) and a miscellaneous group of epiphytes, figs and other material (R). Tree species were classified according to the potential position of their crown within the forest canopy (cf. Ashton 1982, Cockburn 1976, 1980, Meijer & Wood 1964, Ng 1978, Whitmore 1972, 1973): emergents (E), main canopy (M) and understorey (U). Classification of leaf fall according to these ecological groups may reflect the structural variation of the forest canopy.

Tree species composition

For each of the 30 sampling areas in the primary forest plot, data on forest composition were obtained from D. M. Newbery. In his 4 ha plot all trees (≥10 cm gbh, tree trunk girth at breast height, 1.3 m, or above any buttresses) had already been enumerated, mapped and identified (Newbery *et al.* 1992). In the sampling areas within the logged forest plot all trees (≥10 cm gbh) were tagged and identified by staff of the Sabah Forest Department. Identifications depended largely upon vegetative material, mostly using bark and leaf characteristics, and were checked with leaf litter identifications.

Distribution and abundance of tree density and (tree trunk) basal area, size frequency distribution, species and family richness, and family and species contribution to basal area were estimated for each of the 30 sampling areas in each of two forest plots in order to describe their forest composition. Basal area data for the sampling areas in the primary forest plot were available from D. M. Newbery (see also Newbery *et al.* 1992), and for the logged forest from L. Madani (Sabah Forest Department). Density and basal area abundance were calculated for both forest plots per sampling area as well as per species and per family. Basal area contributions and densities of climbers were not measured.

The overlap in tree taxa between the primary and the logged forest plots was quantified using the similarity index of Sorenson (Pielou 1977):

$$PS = \frac{200 \times c}{a + b}$$

in which c = the number of joint taxa in both forest plots, a = the number of taxa in the primary forest plot, b = the number of taxa in the logged forest plot, based on the 30 sampling areas. (In the case of equal numbers of taxa in both forest plots PS varies from 0, or no similarity in taxa, to 100, or full similarity in taxa.)

Logging intensity

The remaining stumps of the cut trees were mapped and measured for each sampling area in the logged forest plot. From this, an approximate estimate of the basal area of dipterocarp trees before logging could be obtained. Resulting values were compared to logging yields that were available from the logging company (Silam Forest Products 1978).

Statistical analysis

The significance of rank correlations between variables was tested using Spearman's Rank Correlation test (Spearman rank correlation coefficient ϱ, in the following indicated as r_s). Differences between (geometric) mean values were tested for significance using the Student's t-test. The t-tests included the Bartlett chi-square test on homogeneity of group variances and a Tukey HSD test (Wilkinson 1990). When data did not exhibit a normal distribution and if variances were not homogeneous, log or square-root transformation of the data was applied. For both tests, the statistical package SYSTAT (Wilkinson 1990) was used.

RESULTS

Density and basal area abundance

The logarithmic frequency of enumerated trees for the six diameter size classes was similar for the primary and the logged forest plots (Figure 1a). The basal area contribution of the size class 6 (dbh $\geq$60 cm) was higher in the logged forest plot (Figure 1b). As will be later shown in Figure 3b this is caused by the presence of a few large trees of *Koompassia excelsa*.

The number of dipterocarp trees <10 cm dbh was higher in the logged forest plot (139 ha^{-1}) than in the primary forest plot (84 ha^{-1}). In the latter, the total basal area of dipterocarp trees was higher (7.5 m^2 ha^{-1}) than in the logged forest plot (4.5 m^2 ha^{-1}, Figure 1c, Table 1), due to the removal of the larger size classes ($\geq$40 cm dbh) in the logged forest.

High variation in tree biomass among the 30 sampling areas in each forest plot was shown by high standard errors on average basal area (Table 1). Variations in basal area per species and per family were even higher and are not presented here. Only in those tree families with high densities of small to medium-sized trees, such as the Euphorbiaceae, variations were smaller. Densities of small Euphorbiaceae trees <10 cm dbh differed only slightly between the primary (498 ha^{-1}) and logged forest plots (521 ha^{-1}).

On an even larger scale the variation in tree biomass can be considerable. Total yields of different commerical timber groups varied between the logging

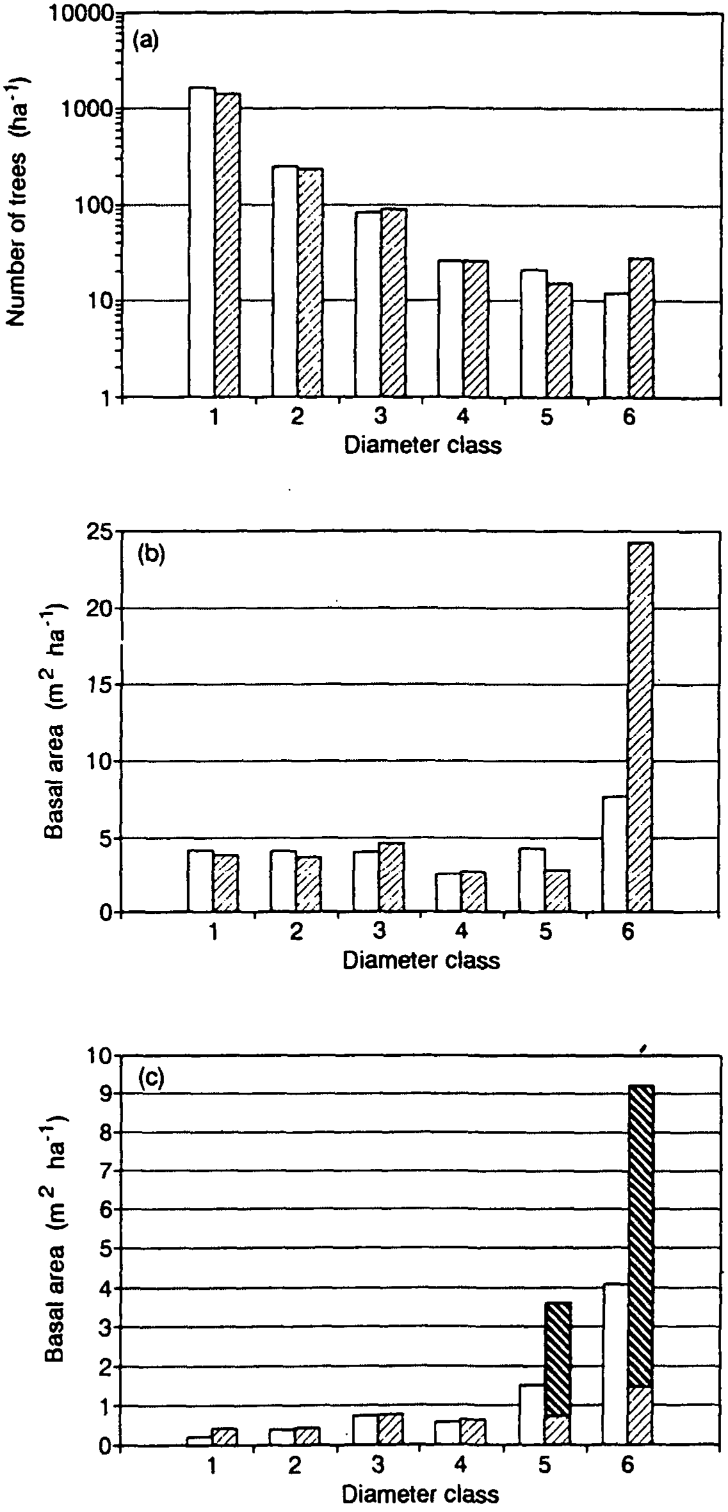


Figure 1. Size class distribution of trees ≥10 cm gbh in 30 sampling areas in each of the primary and logged forest plots; (a) total number of trees, (b) basal area of all trees, (c) basal area of dipterocarp trees only, for the logged forest including that of stumps of logged trees. Diameter (dbh) size classes: 1: 3.2–10 cm; 2: 10–20 cm; 3: 20–30 cm; 4: 30–40 cm; 5: 40–60 cm; 6: >60 cm. ☐ Primary forest plot, ▨ Logged forest plot, ▧ Logged trees in 1978.

Table 1. Means and standard errors of variables studied in 30 sampling areas in each of the primary and logged forest plots. Each sample was a circular area of 314 m^2 (radius 10 m) around each litter trap.

	Primary forest		Logged forest	
	Mean	SE	Mean	SE
Tree density (m^{-2})	0.217	0.005	0.194	0.009
Basal area ($cm^2\ cm^{-2}$)	27.4	2.7	42.2	11.5
Leaf fall ($g\ m^{-2}\ y^{-1}$)	653.1	31.3	619.7	32.1
Species per sampling area	42.5	1.8	39.2	1.5
Families per sampling area	18.9	0.5	19.1	0.5
Altidude (m asl)	215.0	1.3	121.0	2.0

set-ups within the Pacific Hardwood logging coupe 'North Area B' (40–170 $m^3\ ha^{-1}$; Figure 2, cf. Silam Forest Products, 1978) in the Sabah Foundation Concession Area. The set-ups varied in size between 4 and 40 ha. The logged forest plot was located in set-ups 101 and 103 which showed an average timber yield of 100 $m^3\ ha^{-1}$. Yields of commercial dipterocarp timber groups such as white, red and yellow seraya, keruing, kapur and selangan batu (Burgess 1966), contributed to at least 90% of the total timber production.

In the 30 sampling areas in the logged forest plot the high number of cut stumps (*c.* 15 ha^{-1}) indicates severity of the selective logging of 1978. All stumps

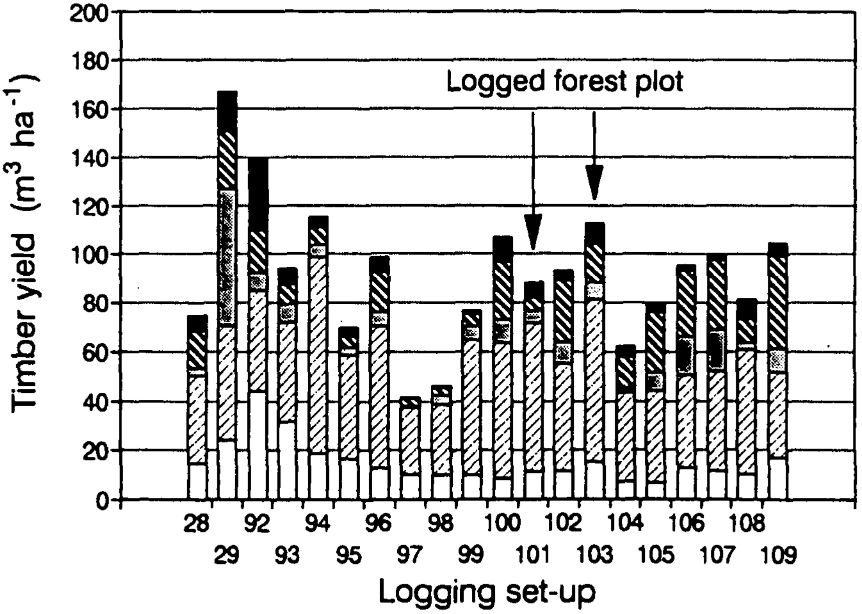


Figure 2. Timber yields of commercial timber groups for 20 logging set-ups in the Pacific Hardwood logging coupe 'North Area B'. The set-ups vary in size between 4 and 40 ha (Source: Silam Forest Products 1978). The logged forest plot was located in set-ups 101 and 103. Timber groups (cf. Burgess 1966, Fox 1970) are indicated as follows: □ white seraya; ▨ red seraya; ▩ yellow seraya; ▧ kapur, keruing and selangan batu, ■ other timber.

were greater than 40 cm dbh. The intensity of logging was quantified as the reduction in trunk basal area, which could be calculated by measuring the total basal area of the stumps. Assuming the girth increment of trees >40 cm dbh to be relatively small over a period of 11 years, the logging is estimated to have caused an 80% reduction in total basal area of the dipterocarp trees (Figure 1c). When the basal area of the logging stumps is included, the sum of the basal area of dipterocarp trees ≥40 cm dbh before logging was *c.* 13 m^2 ha^{-1}, which is twice the basal area of dipterocarps in the primary forest plot.

Botanical composition of trees and climbers

The 3869 trees ≥10 cm gbh that were enumerated in the 60 sampling areas (each 314 m^2, total 1.88 ha) in both forest plots belonged to 351 species in 55 families. The number of tree species was higher in the primary forest plot (267 species from 51 families) than in the logged plot (218 species from 50 families). Numbers of species per sampling area (Table 1) were not significantly different between the two forest plots (square-root transformation, $t = 1.438$, $P > 0.10$).

In Table 2, 21 families common to both forest plots are listed in terms of basal area and tree density contribution. These families together represent 93% and 96% of the total basal area, and 86% and 86% of the total tree density in the primary and logged forest plot, respectively. Of these families the Dipterocarpaceae, Euphorbiaceae, Lauraceae, Fagaceae and Meliaceae are important families in both forest plots with regard to their contribution to total basal area and tree density (Table 2). Other important families in the primary forest plot are the Myrtaceae, Oleaceae and Sapotaceae, whilst in the logged forest plot the most important other families are the Leguminosae, Verbenaceae and Alangiaceae. For these 21 families ($N = 21$), tree density ($r_s = 0.851$, $P < 0.001$), numbers of species ($r_s = 0.844$, $P < 0.001$) and leaf fall ($r_s = 0.696$, $P < 0.001$), but not basal area ($r_s = 0.100$, $P > 0.10$), were significantly correlated between the primary and logged forest plots. Numbers of species were significantly correlated with tree density in both primary forest plot ($r_s = 0.852$, $P < 0.001$) and the logged forest plot ($r_s = 0.776$, $P < 0.001$). The highest species richness was recorded in the Euphorbiaceae in the logged forest plot, followed by the Lauraceae, Euphorbiaceae, Annonaceae, Myrtaceae and Meliaceae in the primary forest plot. The number of species of Dipterocarpaceae was similar in both forest plots (Table 2).

The overall floristic similarity of family composition in the two plots was high (PS = 91%), but the number of species common to both plots was lower (PS = 47%; Table 2). Some families such as the Annonaceae, Dipterocarpaceae, Leguminosae, Meliaceae, Sapotaceae and Tiliaceae, had a large overlap in species composition between forest plots (PS > 50%), whereas others such as the Euphorbiaceae, Fagaceae, Moraceae, Myrtaceae and Rubiaceae had a smaller overlap (PS < 50%). This small overlap is probably caused by the lower number of trees per family, owing to the lower number of trees per species.

Of the 267 and 218 tree species in the primary and logged forest, respectively,

Table 2. Tree densities (ha^{-1}), trunk basal areas (m^2 ha^{-1}), leaf fall (g m^{-2} y^{-1}) and the total no. of tree species (trees ≥10 cm gbh) of the first 16 important families in the primary and logged forest plots. Families are ranked in terms of basal area contribution of the first 16 families in the primary forest plot; [1]important in the primary forest plot only; [2]important in the logged forest plot only. The similarity index of Sorensen (%) presents the overlap in taxa between both forest plots.

	Primary forest plot				Logged forest plot				Similarity index
	Density	Basal area	Leaf fall	Taxa	Density	Basal area	Leaf fall	Taxa	(%)
Dipterocarpaceae	149	7.51	219.6	15	203	4.48	94.9	16	58
Euphorbiaceae	637	3.64	41.3	26	684	5.93	85.8	38	34
Myrtaceae	127	2.26	42.8	18	40	0.74	8.4	7	35
Lauraceae	144	2.22	27.4	31	66	2.07	29.6	10	24
Sapotaceae[1]	82	1.42	14.2	4	37	0.29	12.0	6	60
Annonaceae	202	1.09	13.1	18	96	0.51	6.8	12	60
Fagaceae	51	1.05	54.2	11	29	1.20	32.6	8	32
Rubiaceae[1]	72	1.00	0.1	9	61	0.16	0.0	4	15
Tiliaceae	54	0.93	34.3	5	59	0.59	11.2	6	91
Olacaceae[1]	29	0.88	10.2	2	6	0.07	0.1	1	67
Meliaceae	127	0.74	13.6	18	121	1.06	13.0	10	64
Burseraceae	37	0.67	9.1	6	30	1.81	14.3	4	40
Leguminosae	85	0.57	10.6	11	83	12.98	34.6	6	59
Lecythidaceae[1]	30	0.47	9.2	2	23	0.31	3.6	3	80
Apocynaceae[1]	3	0.43	6.3	2	8	0.05	1.1	1	0
Bombaceae	5	0.34	1.7	1	6	1.28	11.6	4	40
Verbenaceae[2]	0	0.00	5.6	1	13	3.2	8.5	5	33
Alangiaceae[2]	8	0.17	2.6	1	34	1.61	1.5	1	0
Moraceae[2]	2	0.00	8.1	8	30	1.19	20.8	4	22
Celastraceae[2]	6	0.00	0.1	1	33	0.73	0.0	1	0
Sterculiaceae[2]	7	0.02	0.8	1	3	0.34	0.0	1	0
Others (incl. unknown species)	312	1.96	45.7	76	272	1.59	57.8	70	0
Total	2171	27.37	570.5	267	1936	42.19	448.1	218	47
Total families				51				50	91

16 species represented 55% and 70% of the total basal areas (Figure 3a,b). Of these 16 species in each plot, three were common to both plots. Within the primary forest plot, six dipterocarp species represented 26% of the total basal area (Figure 3a). In the logged forest plot three dipterocarp species contributed only 3% of the total basal area (Figure 3b). High densities of small and medium-sized trees in the Euphorbiaceae resulted in a fairly high basal area contribution, such as *Mallotus wrayi* (3.6%) and *Aporusa accuminatissima* (3.3%) in the primary forest plot, and *Macaranga hypoleuca* (4.7%) and *M. wrayi* (2%) in the logged forest plot. *Macaranga* is an invasive secondary forest pioneer and not a primary forest gap-pioneer (Whitmore 1989). It is clear from Figure 3b that non-commercial (in 1978) emergent tree species *Koompassia excelsa* (29.8%) and *Alangium ebenaceum* (3.8%) and top and main canopy tree species such as *Teijsmanniodendron bogoriense* (7.5%), *Durio zibethinus* (2.7%) and *Quercus argentata* (2.6%) made high contributions to the total basal area in the logged forest plot. Nowadays, *K. excelsa* and *A. ebenaceum* are commercial species (Y. F. Lee, pers. comm.).

Since their density and contribution to basal area was not measured, the floristic composition of climbers in the two plots is presented on the basis of their contribution to annual leaf fall only. The number of climber species that contributed to leaf fall was higher in the logged forest plot (44 species) than in the primary forest plot (33 species). Overlap in family and species composition of climbers between the two plots follows the same pattern as tree composition. The overlap in family composition is high between the two plots (PS = 78%), for species composition it is lower (PS = 44%).

Species composition of leaf fall

At the 30 sampling points in each of the primary and logged forest plots, the 21 families listed in Table 1 accounted for 89% and 73% of the annual leaf fall, respectively, and 16 species accounted for 58% and 50% of the annual leaf fall, respectively (Figure 3). For these 21 families, leaf fall was significantly correlated with basal area ($r_s = 0.805$, $P < 0.001$ and $r_s = 0.746$, $P < 0.001$, primary and logged plots, respectively) and tree density ($r_s = 0.714$, $P < 0.001$ and $r_s = 0.508$, $P < 0.05$, respectively). The Dipterocarpaceae dominated annual leaf fall (34%) and basal area (29%) in the primary forest. Their contribution to annual leaf fall (15%) and basal area (11%) was much smaller in the logged forest plot. Six species of dipterocarp were ranked among the 16 leading species in the primary plot, contributing 30% of the annual leaf fall (Figure 4a). *Shorea johorensis* and *S. argentifolia* contributed to leaf fall at all 30 primary forest sampling points, although these two species seemed to exclude one another in leaf fall contribution: sampling points where one of the two species dominated in leaf fall (10–40%), the contribution of the other species was small (<2%). In the logged forest plot (Figure 4b), four species of dipterocarp ranked among the 16 leading species but contributed less than 9% of the annual leaf fall. The basal area contribution (29.8%, Figure 3b) of the emergent

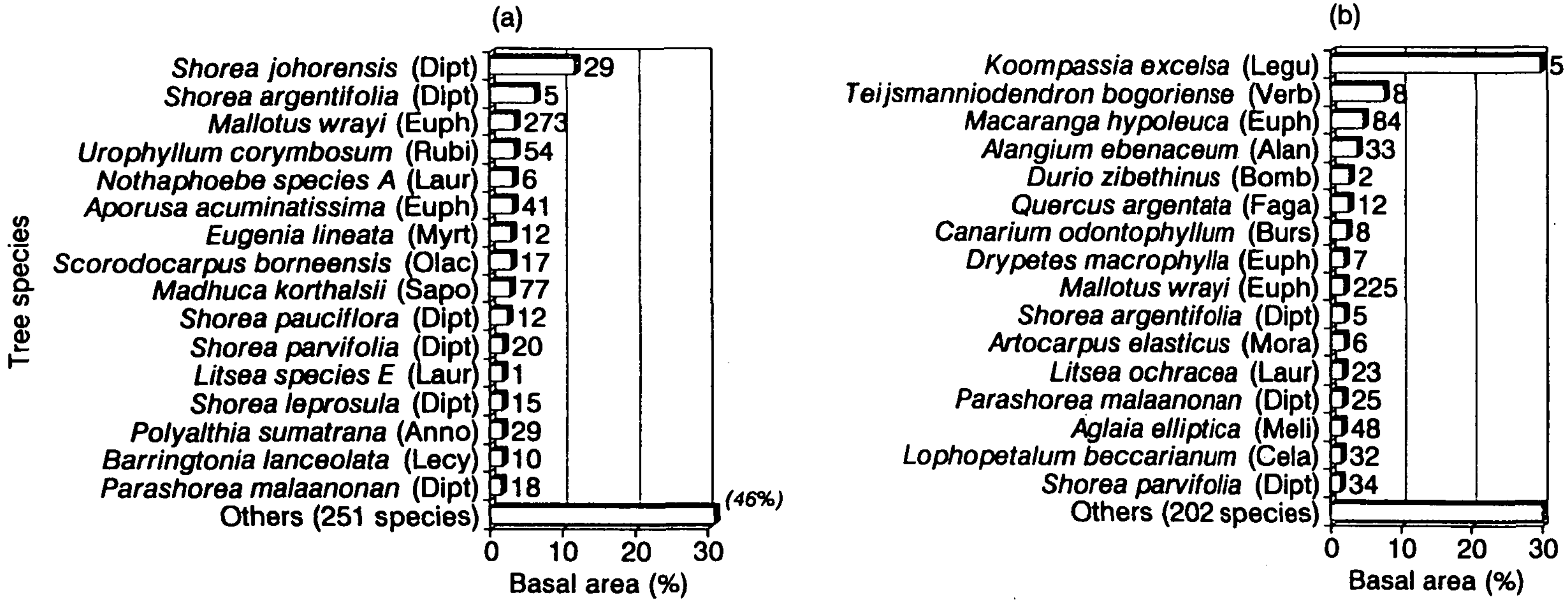


Figure 3. Percentage contribution to total basal area (trees ≥10 gbh) by the 16 leading tree species (abbreviated family names) in 30 sampling areas in each of the primary and logged forest plots; (a) primary forest plot, (b) logged forest plot. The figures on the right of each bar indicate the number of trees (ha^{-1}). Abbreviated family names are the first four letters of those listed in Tables 2, 3 and in the Appendix.

Table 3. Leaf fall (g m^{-2} y^{-1}) and no. of species of climbers and epiphytes in the primary and logged forest plots. Families are ranked according to their contribution to annual leaf fall in the logged forest plot. The similarity index of Sorensen (%) presents the overlap in taxa between both forest plots.

	Primary forest plot		Logged forest plot		Similarity index
	Leaf fall	Taxa	Leaf fall	Taxa	(%)
Climbers					
Leguminosae	43.5	4	37.5	8	67
Graminae	0.7	1	32.0	1	0
Annonaceae	5.1	6	25.3	2	75
Convolvulaceae	0.0	0	17.9	3	0
Rubiaceae	4.8	3	17.1	5	75
Rutaceae	0.0	0	17.0	1	0
Verbenaceae	4.8	1	6.1	1	100
Melastomataceae	0.0	0	2.0	1	0
Apocynaceae	0.0	0	1.8	2	0
Menispermaceae	4.0	1	1.9	4	40
Combretaceae	1.1	2	0.3	1	0
Dilleniaceae	0.6	1	0.2	2	67
Connaraceae	0.5	1	0.0	1	100
Cucurbitaceae	0.0	0	1.6	2	0
Others (incl. unknown species)	17.4	13	7.3	10	43
Total	82.5	33	168.1	44	44
Total families		11		17	79
Epiphytes					
Total	0.28	6	0.57	4	73
Total families		4		4	75

Koompassia excelsa was not associated with a major contribution to leaf fall (4.6%, Figure 4b).

Pioneer trees and fast growing climbers are important contributors to leaf fall in the logged forest plot. Two pioneer species, *Macaranga hypoleuca* and *Euodia confusa*, and four species of climbers *Dinochloa scabrida*, *Spatholobus* species 1, *Artabotrys* species A, *Uncaria* species D, rank among the 16 leading species and together contributed to 34% of the annual leaf fall. In the primary forest plot no pioneer species and only two climber species, *Spatholobus* species 1 and *Artabotrys* species A, ranked among the 16 dominant species and contributed to 8% of the annual leaf fall. Some of the climber species, being present in both the primary and the logged forest plot, such as *Spatholobus* species 1 and an unknown climber species, had a slightly higher contribution to annual leaf fall in the primary forest plot. Other climber species, such as *Uncaria* species D and *Artabotrys* species A, made a very small contribution (<<1%) in the primary forest plot compared with the logged forest plot.

The botanical composition of monthly leaf fall in the primary and forest plots throughout the study period is presented in Figure 5, according to the structural classification (E, M, U; C; R). Leaf fall of emergent tree species, mainly dipterocarp species, was in the primary forest plot almost twice that in logged forest

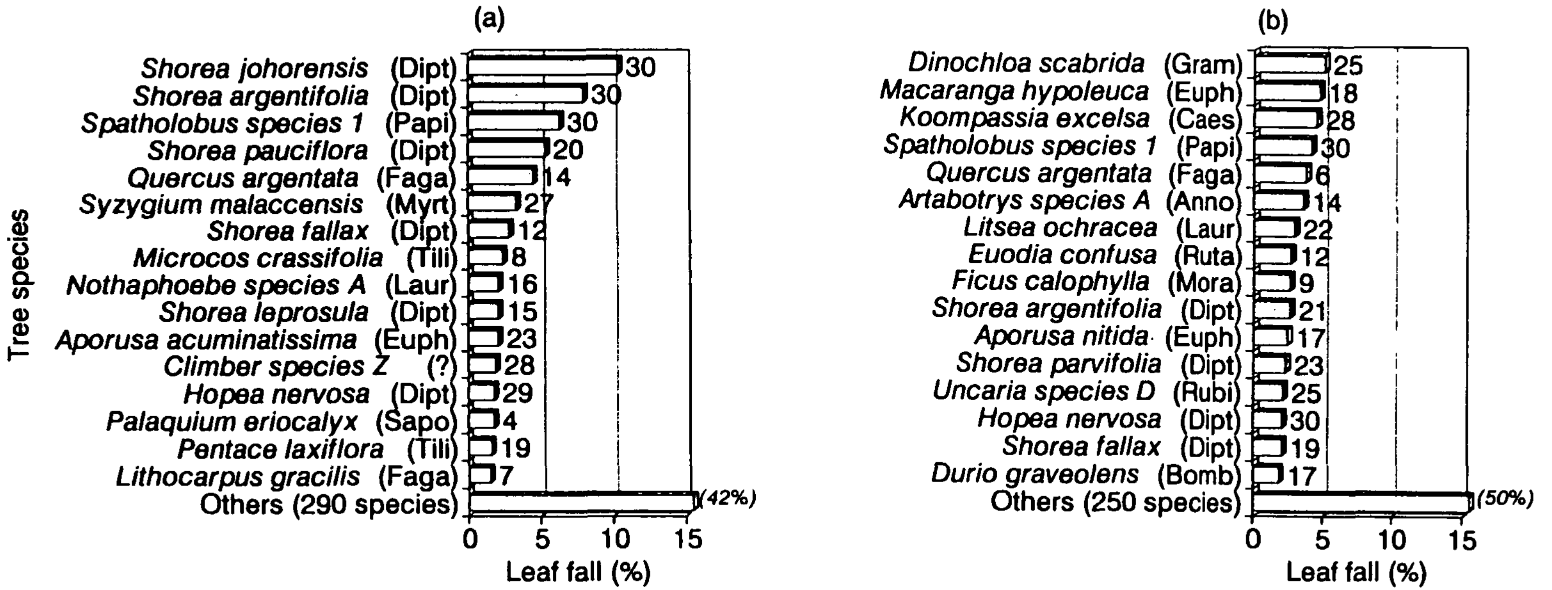


Figure 4. Percentage contribution to the annual leaf fall by the 16 leading tree species (with abbreviated family names) in 30 sampling points in each of the primary and logged forest plots; (a) primary forest plot, (b) logged forest plot. The figures on the right of each bar indicate the number of sampling points to which the species contributed. Abbreviated family names are the first four letters of those listed in Tables 2, 3 and in the Appendix.

plot (Figure 5b). For climbers the converse occurred. Their approximately two times higher contribution to leaf fall in the logged forest plot was due to the high leaf fall contribution by numerous climber species within the families Graminae, Annonaceae, Convolvulaceae, Rubiaceae and Rutaceae (Table 2). Leaf fall by the miscellaneous group was higher in the logged forest owing to the contribution of several fig species. The primary and logged forest plots were similar in the leaf fall contributions of main canopy and understorey species. Percentage contribution of the different structural groups was about constant throughout the study period.

Temporal and spatial variation in leaf fall

Around 110 woody species contributed to leaf fall each month at the 30 sampling points in each of the primary and logged forest plots. In spite of this, leaf shedding patterns of relatively few species, in the primary forest in particular, dominated the composition of the leaf fall throughout the study period (Figure 6). In Figures 6 and 7, respectively, the monthly contributions of the six most important tree families and tree species to leaf fall are shown. In the primary forest the Dipterocarpaceae dominated in leaf fall contribution throughout the study period and determined the monthly fluctuations in leaf fall (Figures 6a, 7a). In the logged forest their contribution was relatively less important (Figures 6b, 7b). Here, the contribution of the Euphorbiaceae and Graminae is constantly high while that of the other families fluctuated throughout the study period.

Emergent and upper canopy tree species, as shown in Figure 7 by *Shorea johorensis*, *S. pauciflora*, *Quercus argentata* and *Nothaphoebe* species A, shed their leaves throughout the year with one or several different peaks of leaf fall. Few large trees, such as *Quercus argentata*, that remained after logging, and the liana species *Spatholobus* species 1 and the fig *Ficus calophylla* (Figure 7b) differed in their period of peak leaf fall, and locally dominated leaf fall.

Since leaf fall was recorded for each sampling point separately, the data allow a comparison of spatial synchronization for species contributing to more than one sampling point. This is exemplified in Figure 8 for six sampling points and four selected species. Synchronization of leaf fall among large individuals of one species resulted in regular peak leaf fall by *Shorea johorensis* (Figure 8a), *Shorea pauciflora* and *Spatholobus* species 1 in the primary forest. Alternating large peaks of leaf fall by different individuals of *Shorea argentifolia* resulted in a dispersed distribution pattern (Figure 8b). In the logged forest plot, leaf fall by *Macaranga hypoleuca* and *Dinochloa scabrida* was continuously high, because the high numbers of small individuals were not synchronized (Figure 8c,d). Synchronization could only be demonstrated for the emergent *Koompassia excelsa*.

Spatial variation in leaf fall was high within both plots. For the 30 sampling points in the primary and in the logged forest plots, respectively, leaf fall was not correlated with trunk basal area ($r_s = 0.257$, $P > 0.05$ and $r_s = 0.160$, $P > 0.10$) or tree density ($r_s = -0.216$, $P > 0.10$ and $r_s = 0.000$, $P > 0.10$) in

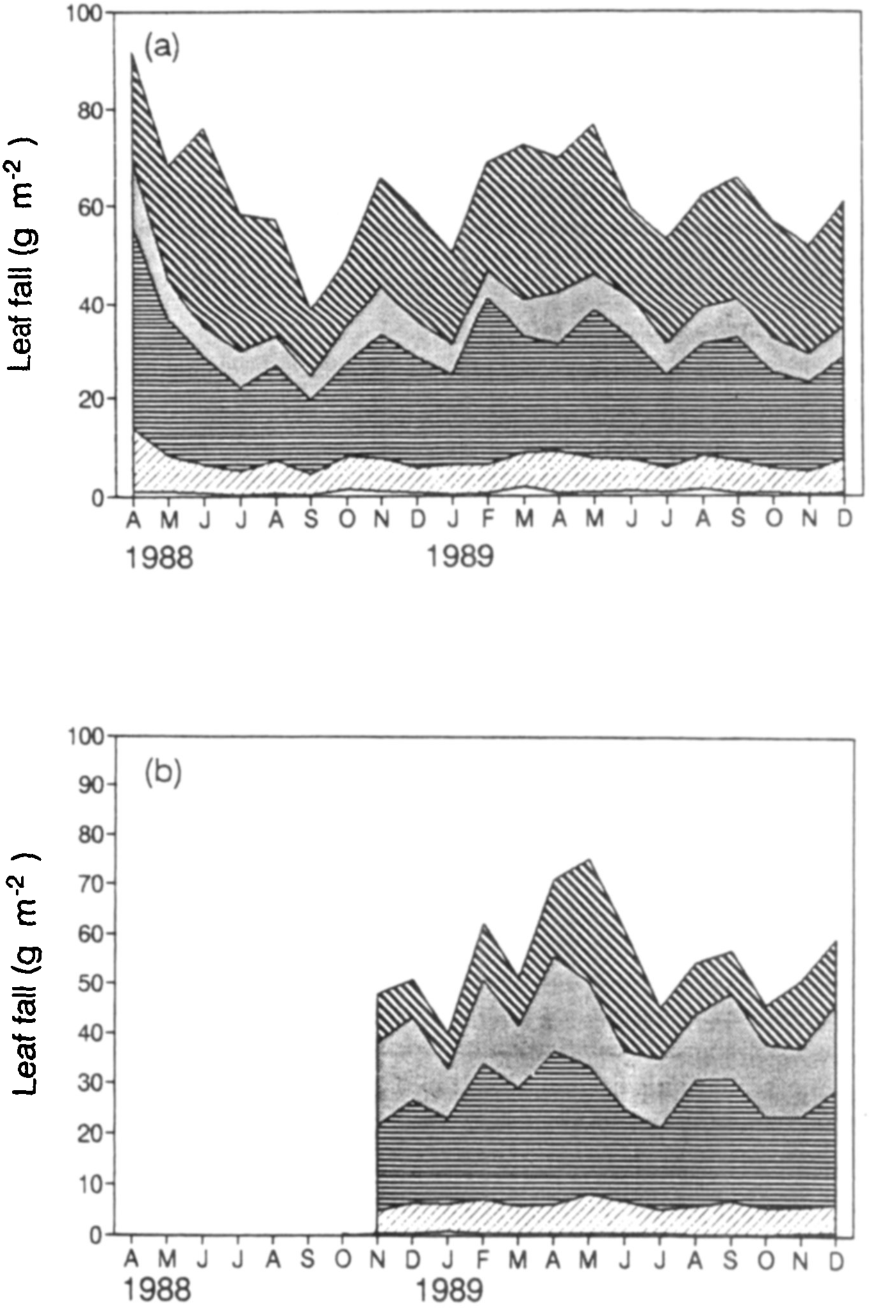
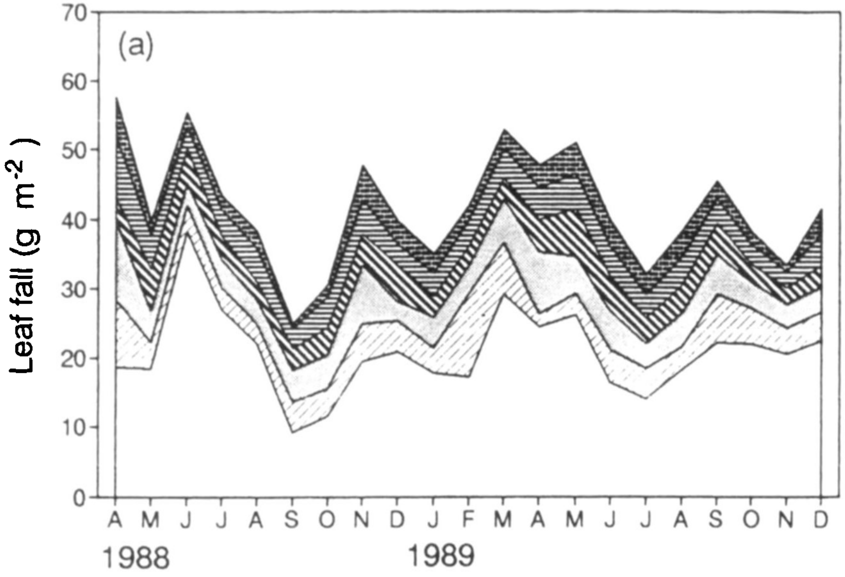


Figure 5. Monthly leaf fall of species, classified according to their position in the forest canopy, at 30 sampling points in each of the primary and logged forest plots; (a) primary forest from April 1988 to December 1989, (b) logged forest plot from December 1988 to December 1989. Contributions to annual leaf fall for the period December 1988–December 1989 were distributed over five structural groups in primary and logged forest plots, respectively, as follows: ▧ emergent species (39%, 22%), ▒ climber species (13%, 27%), ▤ main canopy species (37%, 38%), ▨ understorey species (10%, 10%), ☐ miscellaneous (epiphytes, figs) (1%, 3%).



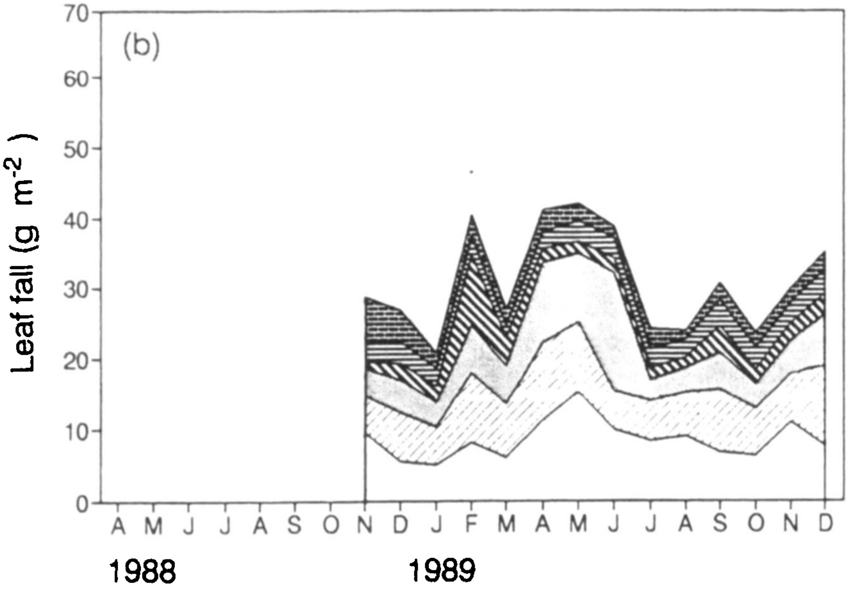
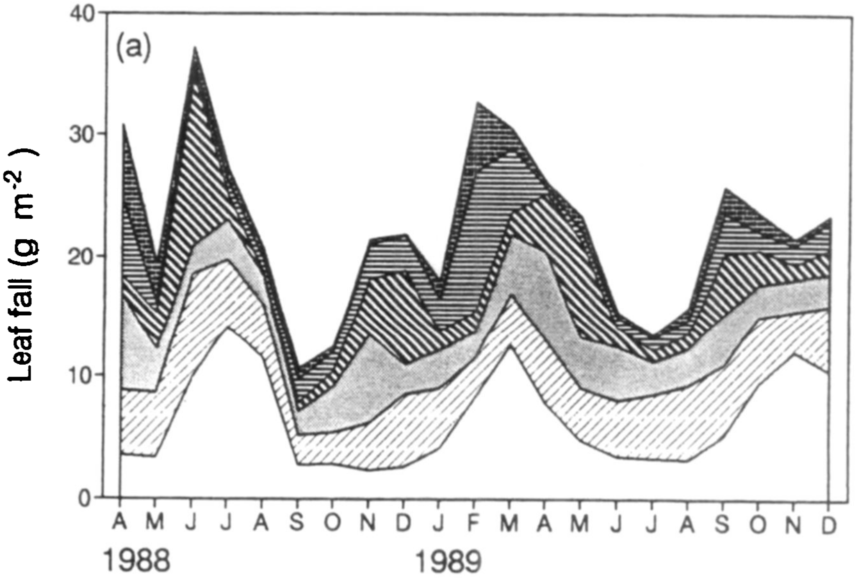


Figure 6. Monthly leaf fall of the six most important families at 30 sampling points in each of the primary and logged forest plots; (a) primary forest from April 1988 to December 1989, (b) logged forest from December 1988 to December 1989. The six families indicated for the primary forest plot are (from bottom to top): Dipterocarpaceae, Fagaceae, Leguminosae, Myrtaceae, Euphorbiaceae, Tiliaceae; indicated for the logged forest plot are (from bottom to top): Dipterocarpaceae, Euphorbiaceae, Leguminosae, Fagaceae, Annonaceae, Graminae.



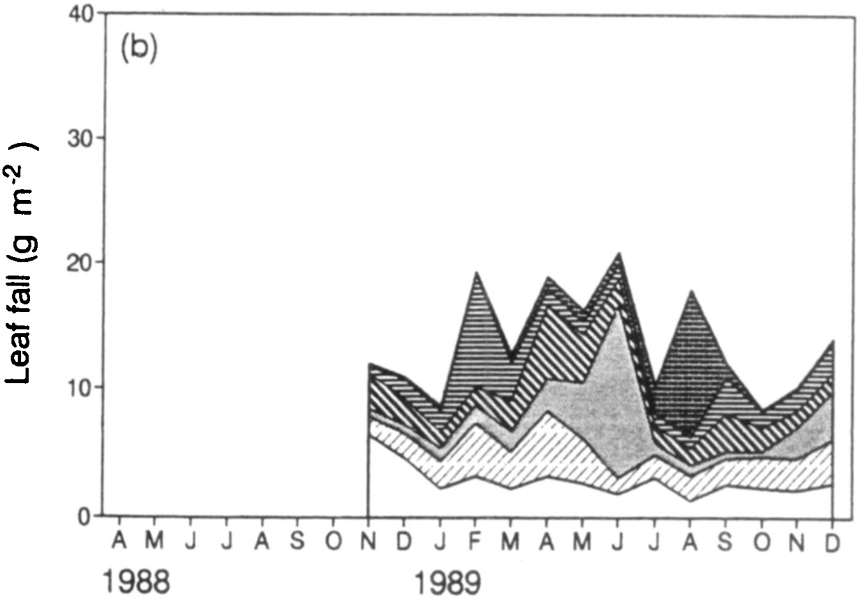


Figure 7. Monthly leaf fall of six important species at 30 sampling points in each of the primary and logged forest plots; (a) primary forest from April 1988 to December 1989, (b) logged forest from December 1988 to December 1989. The six species indicated for the primary forest plot are (from bottom to top): *Shorea johorensis*, *Shorea argentifolia*, *Spatholobus* species 1, *Shorea pauciflora*, *Quercus argentata*, *Nothaphoebe* species A; indicated for the logged forest plot are (from bottom to top): *Dinochloa scabrida*, *Macaranga hypoleuca*, *Koompassia excelsa*, *Spatholobus* species 1, *Quercus argentata*, *Ficus calophylla*.

the corresponding sampling areas. For the Dipterocarpaceae, leaf fall at the 30 sampling points was correlated with trunk basal area in the primary ($r_s = 0.749$, $P < 0.001$) and in the logged forest plot ($r_s = 0.495$, $P < 0.005$), respectively, but not with tree density ($r_s = 0.005$, $P > 0.10$ and $r_s = 0.300$, $P > 0.05$, respectively). At the 30 sampling points in the logged forest plot, leaf fall of *Macaranga* spp was correlated with basal area ($r_s = 0.825$, $P < 0.001$) and with tree density ($r_s = 0.756$, $P < 0.001$) in corresponding sampling areas, as density and basal area were highly correlated with each other ($r_s = 0.947$, $P < 0.001$).

The majority of tree species contributed less than 1% to the total annual leaf fall, owing to their small biomass or to their low densities or both. Although these species contributed to the diversity of leaf fall, their patterns in leaf fall were not quantified.

DISCUSSION

Botanical composition of trees

Size class distribution, densities of trees and the number of families were similar in the primary and logged forest plots. The total number of tree species was higher in the primary forest plot while the number of climber species was higher in the logged forest plot. Although there was a large overlap in family composition, tree species composition differed considerably between the two forest plots, indicating differences in vegetation composition that already existed before the logging of 1978.

Our 30 primary forest areas were located in one of the two 4 ha enumerated plots used by Newbery *et al.* (1992) to analyse the vegetation composition (≥ 10 cm gbh) of primary dipterocarp forest in the Danum Valley. Differences in forest composition between his two replicate plots were very small, especially in comparison with other locations in primary dipterocarp forest studied by Fox (1972) and Nicholson (1979), and other researchers in Borneo and Peninsular Malaysia (Newbery *et al.* 1992). Variation in total basal area, in tree density and in tree family composition between these different research locations exceeded the differences between our primary and logged forest plots.

Spatial variation in forest composition resulted in high spatial variation in trunk basal area between the 30 sampling areas in each forest plot. Although tree trunk basal area was higher in the logged forest plot it was extremely variable within the plot due to the presence of some *Koompassia excelsa* trees $>>$ 60 cm dbh, that had remained after logging.

Trunk basal area and density of dipterocarp trees ≥ 40 cm dbh were, respectively, 5.8 $m^2\ ha^{-1}$ and 11 ha^{-1} in the primary forest plot, and were higher than the respectively 2.1 $m^2\ ha^{-1}$ and 8 ha^{-1} in the logged forest plot. However, they were smaller than the respectively 11.0 $m^2\ ha^{-1}$ and 19 ha^{-1} in the whole 4 ha primary forest plot in which 30 sampling areas were randomly located (D. M. Newbery, pers. comm.). A high number of dipterocarps ≥ 40 cm dbh in the 4 ha plot (*c.* 86%) was located outside the 30 randomly chosen sampling areas.

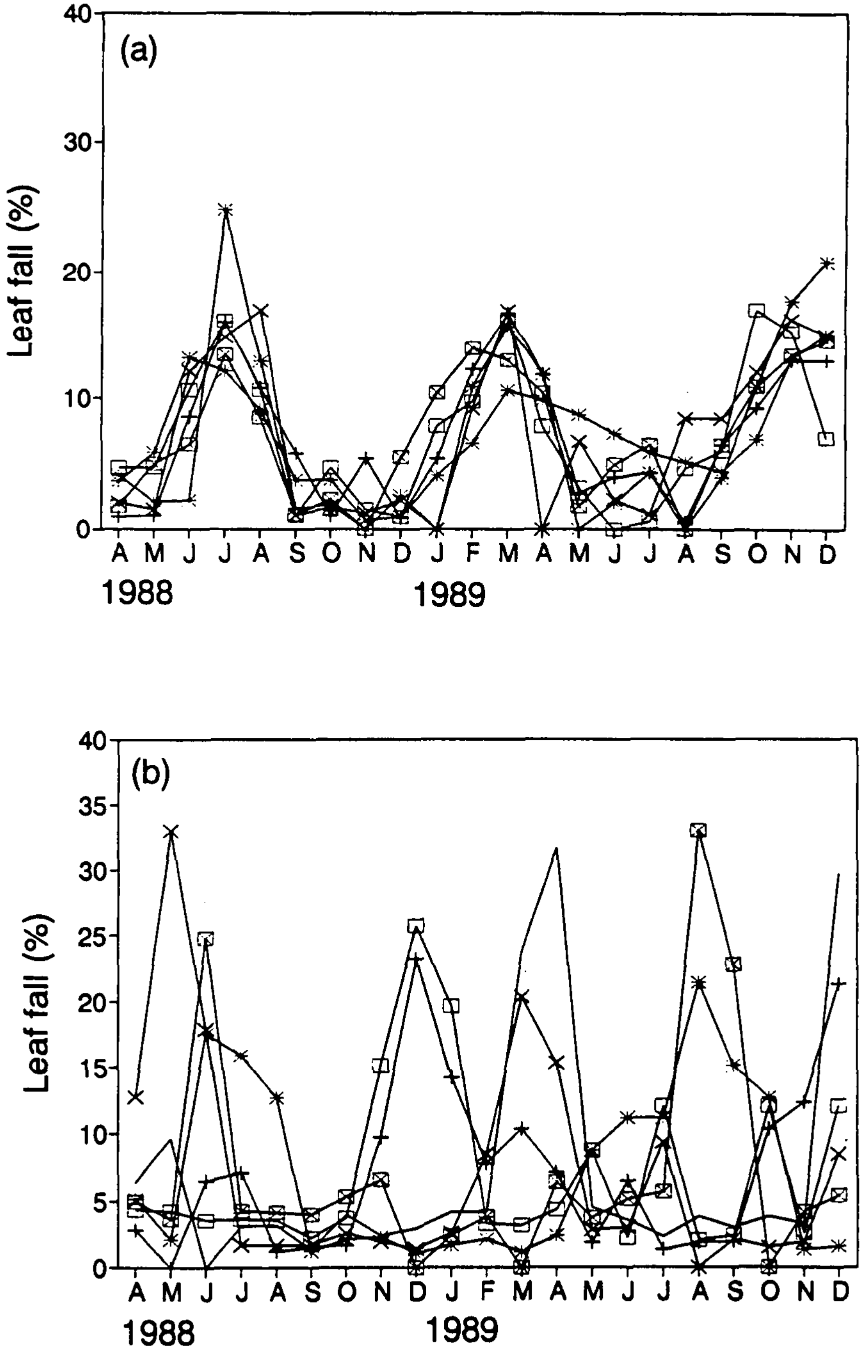


Figure 8. Monthly leaf fall of four woody species at six different sampling points (expressed as a percentage of the total annual leaf fall of a particular species at a particular sampling point) in the primary forest plot during the period April 1988–December 1989, and in the logged forest plot during the period December 1988–December 1989: (a) primary forest plot: *Shorea johorensis*, Dipterocarpaceae; (b) primary forest plot: *Shorea argentifolia*, Dipterocarpaceae; (c) logged forest plot: *Macaranga hypoleuca*, Euphorbiaceae; (d) logged forest plot: *Dinochloa scabrida* (Graminae).

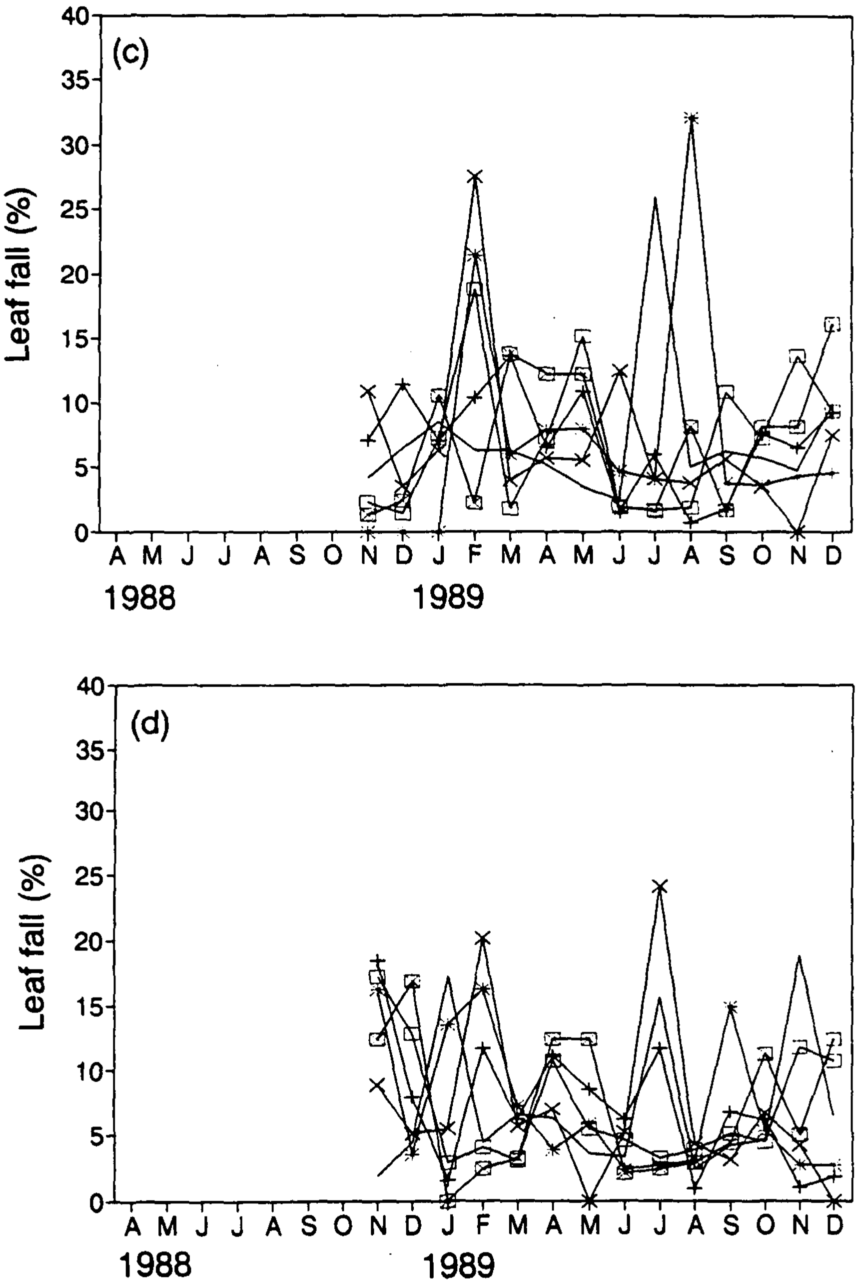


Figure 8 continued.

The total surface area of our 30 sampling areas was 0.94 ha, or 23.5% of the total plot, and most unusual with regard to the dipterocarps. Obviously, the dimension of sampling areas used in our study were such that the estimates for total trunk basal area in the forest plots have only an indicative value. The basal area contributions of the numerous tree families and tree species are used here to indicate roughly which taxonomic groups dominate tree biomass and leaf fall, in comparison with other tropical forest sites.

The severe selective logging in 1978 was confirmed by the high number of stumps of logged trees, and by locally high densities of secondary pioneer species such as the euphorb *Macaranga* spp and several secondary forest climber species (Kartawinata *et al.* 1989, Whitmore 1984). Logging reports concerning the concession area in which our logged forest plot was located, confirmed the intensive removal of dipterocarp trees that resulted in yields of *c.* 100 m^3 ha^{-1} of dipterocarp timber (Silam Forest Products 1978). This value is within the range reported for selective logging elsewhere in Borneo (Fox 1972, Hurst 1990, Kartawinata *et al.* 1989, Nicholson 1979). The number of small dipterocarp trees <10 cm dbh was relatively high in the logged forest compared with the primary forest, and indicated good regeneration of the Dipterocarpaceae 12 years after logging.

Botanical composition of leaf fall

The primary and logged forest plots differed considerably in species composition of leaf fall. In the logged forest, dipterocarps showed a lower contribution to basal area and leaf fall. At sampling areas adjacent to former skid tracks in particular, leaf fall was dominated by several exclusive pioneers such as *Macaranga hypoleuca* (T. B. A. Burghouts, pers. obs.). While the contribution to leaf fall by emergent tree species was lower than in the primary forest, the contribution by climbers and pioneer tree species was relatively higher. Leaf fall contributions of main canopy species and of understorey species were equal in both forest plots.

Most of the leaf litter collected could be identified to the woody species present within a 10 m radius round the litter trap. Occasionally, large emergents that were located outside the boundary of the sampling area contributed to the leaf fall within areas, because of a widely dispersed leaf fall. Measured quantities of leaves of single tree species varied considerably depending on the distance between trees and traps. According to Lowman (1984) amounts of litter are not always negatively correlated with the distance from the parent tree. The aims of our study render spatial and temporal variation of leaf fall of more interest (also Burghouts *et al.* 1992 and Burghouts & Burijnzeel, in prep.) than the relation between leaf biomass and trunk basal area. For the latter, it would have been necessary to study tree-specific leaf fall and species-specific leaf life spans (Chabot & Hicks 1982).

The density of lianas $\geqslant 2$ cm gbh in the primary forest plot was remarkably high (882 ha^{-1}) when compared with other lowland forest sites in Borneo (Campbell & Newbery 1993), yet their contribution to leaf fall was only half that in the logged forest plot. Natural succession in primary rainforest is marked by a rise in the number of small gaps created when one or several trees die and fall over (Whitmore 1984). Correspondingly there is a small but significant increase in the abundance of lianas which multiply vegetatively in response (Campbell 1990). Budowski (1970) and Hall & Swaine (1981) could relate the successional status of the forest to the size and height of the lianas present and Gentry (in Hegarty 1989) suggested that liana density and stand maturity were negatively correlated. In forest which is disturbed due to logging, large gaps are formed and climbers proliferate rapidly and in large numbers over the remaining vegetation. Ogawa *et al.* (1965) and Kira & Ogawa (1971) found that trees supporting a higher mass of climber leaf correspondingly produced a lower amount of tree leaf. The higher contribution to leaf fall in the logged forest is probably due in part to this and to the general increase in the abundance of climbers in this area.

Temporal and spatial variation in leaf fall

In seasonal tropical forests mass leaf fall occurs in the dry or in the wet season. Many tree species are deciduous (Koriba 1958, Lieberman 1982) and are triggered by moisture stress, by low light intensities or by high humidities (Addicott 1978, Chabot & Hicks 1982, Frankie *et al.* 1974). The periodicity of leaf fall depends on seasonality in climatic patterns. Spatial variation in leaf fall then largely depends on the distribution and biomass of trees and tree species.

In the relatively uniform wet tropical climate of south-east Asia, leaf fall is high throughout the year (Whitmore 1984). In Burghouts *et al.* (1992) temporal variation in total leaf fall was small compared with the spatial variation in a primary and a logged dipterocarp forest plot in the Danum Valley in Sabah, Malaysia. Mosaics of accumulating freshly fallen leaf litter indicated that different trees occasionally shed their leaves at higher rates. Only a few tree species renew their leaf biomass in an annual cycle, e.g. *Koompassia excelsa* (Whitmore 1984). Of the evergreen tree species most species seem to add on a new flush-generation of leaves more or less simultaneously with the shedding of the previous flush-generation. Others remain evergreen all the time and habitually maintain two or more coexisting flush-generations (Longman & Jenik 1974, Ng 1984). The periodicity of leaf fall and the synchronization of leaf fall between trees or between taxonomic groups determine the mosaic of litter on the forest floor. The latter contributes to the patchiness of the forest floor, which is assumed to be an important determinant of niche diversification for seedlings (Molofsky & Augspurger 1992, Sydes & Grime 1981) and forest floor organisms in general (Heatwole 1961, Swift & Anderson 1989, Tilman 1988).

Cycles of leaf renewal can be of variable lengths (Chabot & Hicks 1982) and are not necessarily synchronized among individuals, as shown in Holttum (1940) and in the present study. In the primary forest plot leaf fall was dominated by a relatively low number of large emergent and upper canopy trees. Therefore a major part of leaf fall occurred in generally large peaks, synchronized or alternating among the individual trees, and followed a regular periodicity. In the logged forest plot, leaf fall was dominated by the contribution of climbers and high numbers of relatively small pioneer trees. Leaf fall by these species was not synchronized between the numerous individuals but was more evenly distributed in time. It can be concluded that patchiness of the leaf litter layer and also the regularity with which this patchiness changes, are more pronounced in the primary forest plot. This agrees with Burghouts *et al.* (1992) who showed that the abundance of forest floor arthropods was also more patchy in the litter layer of the primary forest plot than in the logged forest plot.

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APPENDIX

List of species (families) appearing in text and figures, ranked in alphabetical order. Structural classification: E: emergent; M; main canopy; U: understorey; C: climber.

Aglaia elliptica Bl. (Meliaceae); M
Alangium ebenaceum (Clarke) Harms (Alangiaceae): M-E
Aporusa accuminatissima Merr. (Euphorbiaceae); U-M
Aporusa nitida Merr. (Euphorbiaceae); U-M
Artabotrys species A (Annonaceae); C
Artocarpus elasticus Bl. (Moraceae); M-E
Barringtonia lanceolata (Ridl.) Payens (Lecythidaceae); U-M
Canarium odontophyllum Mig. (Burseraceae); M
Dinochloa scabrida??? (Graminae); C
Drypetes macrophylla (Bl.) Pax & Hoffm. (Euphorbiaceae); M
Durio graveolens Becc. (Bombacaceae); M-E
Durio zieethinus Murray (Bombacaceae); M
Eugenia lineata DC Merr. & Perr. (Myrtaceae); M
Euodia confusa Merr. (Rutaceae)
Ficus calophylla Bl. (Moraceae); M
Hopea nervosa King (Dipterocarpaceae); M-E
Koompassia excelsa (Becc.) Taub. (Leguminosae); E
Lithocarpus gracilis (Korth.) Soepadmo (Fagaceae); M-E
Litsea ochracea (Bl.) Boerl. (Lauraceae); M
Litsea species E (Lauraceae); M
Lophopetalum beccarianum Pierre (Celastraceae); U-M
Macaranga hypoleuca (Rchb. f. & Zoll.) Muell. Arg. (Euphorbiaceae); M
Madhuca korthalsii (Perre) Lam. (Sapotaceae); M
Mallotus wrayi King ex H. f. (Euphorbiaceae); U
Microcos crassifolia Burn. (Tiliaceae); M
Nothaphoebe species A (Lauraceae); E
Palaquium eriocalyx H J Lam. (Sapotaceae); M
Parashorea malaanonan Bl. (Dipterocarpaceae); E
Pentace laxiflora Merr. (Tiliaceae); M-E
Polyalthia sumatrana (Miq.) Kurz (Annonaceae); M
Quercus argentata Korth. (Fagaceae); M
Scorodocarpus borneensis (Bail.) Becc. (Olacaceae); M-E
Shorea argentifolia Sym. (Dipterocarpaceae); E
Shorea fallax Meij. (Dipterocaarpaceae); E
Shorea johorensis Foxw. (Dipterocarpaceae); E
Shorea leprosula Miq. (Dipterocarpaceae); E
Shorea parvifolia Dyer (Dipterocarpaceae); E
Shorea pauciflora King (Dipterocarpaceae); E
Spatholobus species 1 (Leguminosae); C
Syzygium malaccensis (L.) Merr. & Perr. (Myrtaceae); M
Teijsmanniodendron bogoriense Koords. (Verbenaceae); M
Uncaria species D (Rubiaceae); C
Urophyllum corymbosum (Bl.) Korth. (Rubiaceae); U