PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Interdependence of peat and vegetation in a tropical peat swamp forest

S. E. Page, J. O. Rieley, Ø. W. Shotyk and D. Weiss

Phil. Trans. R. Soc. Lond. B 1999 **354**, 1885-1897
doi: 10.1098/rstb.1999.0529

THE ROYAL SOCIETY

Interdependence of peat and vegetation in a tropical peat swamp forest

S. E. Page[1]*, J. O. Rieley[2], Ø. W. Shotyk[3] and D. Weiss[3]†

[1]*Department of Biology, University of Leicester, University Road, Leicester LE1 7RH, UK*
[2]*School of Geography, University of Nottingham, University Park, Nottingham NG7 2RD, UK*
[3]*Geological Institute, University of Bern, Baltzerstrasse 1, CH-3012 Bern, Switzerland*

The visual uniformity of tropical peat swamp forest masks the considerable variation in forest structure that has evolved in response to differences and changes in peat characteristics over many millennia. Details are presented of forest structure and tree composition of the principal peat swamp forest types in the upper catchment of Sungai Sebangau, Central Kalimantan, Indonesia, in relation to thickness and hydrology of the peat. Consideration is given to data on peat geochemistry and age of peat that provide evidence of the ombrotrophic nature of this vast peatland and its mode of formation. The future sustainability of this ecosystem is predicted from information available on climate change and human impact in this region.

Keywords: tropical peat; swamp forest; geochemistry; hydrology; radiocarbon dating; biodiversity

1. INTRODUCTION

In the tropics peatland occurs in East and South-East Asia, Africa, the Caribbean, Central and South America, wherever rainfall and topography are conducive to poor drainage, permanent waterlogging and substrate acidification. The total area of undeveloped tropical peat is estimated to be between 30 and 45 million hectares (Mha), which is approximately 12% of the global peatland resource (Immirzi & Maltby 1992; Lappalainen 1996). Indonesia contains the largest area of peat in the tropical zone; estimates range from 16 to 27 Mha (Radjagukguk 1992; RePPProT 1990; Rieley *et al.* 1996*a*,*b*). Most of this peat is located at low altitude in the coastal and subcoastal lowlands of Irian Jaya (4.6 Mha), Kalimantan (6.8 Mha) and Sumatra (8.3 Mha).

Lowland tropical peat consists mainly of slightly or partially decomposed trunks, branches and roots of trees within a matrix of almost structureless organic material that also originates from rainforest plants, mostly trees (Rieley *et al.* 1996*b*). The peat is mainly fibrous with low ash and mineral contents, and its thickness varies from 0.5 m to in excess of 10 m (Anderson 1983).

In Indonesia, there are two major categories of peatland—topogenous and ombrogenous. The latter are true peat-forming swamps (organic matter > 50 cm thick), the water and nutrient supplies to which are derived entirely from aerial deposition (rain, aerosols and dust). The surface of these ombrogenous peatlands is usually convex and is above the limit of wet season river flooding. The rain-fed, perched water-table is close to or above the peat surface throughout the year and fluctuates with the intensity and frequency of rainfall. Undisturbed lowland peat swamps support a medium (35–40 m) to low (15–25 m) canopy forest vegetation, although fern, sedge or scrub may dominate on degraded peatlands (Anderson 1963; Rieley & Ahmad-Shah 1996).

The tropical peat swamp forest ecosystem has, until recently, received little attention from ecologists and environmentalists possibly because these forested peatlands fall between the two disciplines of peatland ecology and forest ecology. Most previous studies in South-East Asia have been carried out in coastal peat swamps that formed between 4000 and 5000 years ago on top of marine sediments in low topographic situations (Anderson 1983). In contrast, peat accumulation in the interior peatlands of Central Kalimantan began more than 10 000 years ago (Rieley *et al.* 1992). These peatlands are located up to 200 km inland and occupy entire catchments in more elevated situations (10–30 m above sea level (a.s.l.)) overlying sand, gravel and clay deposits of fluvial origin (Sieffermann *et al.* 1988).

This paper presents information on the forest vegetation and underlying peat within one peat-covered catchment in Central Kalimantan, relating present-day vegetation zonation to differences in the underlying peat. In addition, data are presented on the age of the peat deposit to gain insight into some of the processes involved in the formation of this extensive peat-covered landscape and to predict what its future might be.

2. STUDY AREA AND METHODS

(a) *Study sites and permanent plots*

The main study area is in the upper catchment of Sungai (River) Sebangau in Central Kalimantan, Indonesia. This province has *ca.* 3 Mha of peatland, a large part of which is still covered in peat swamp forest. The Sungai Sebangau catchment (5000 km^2) consists of a large, continuous area of relatively

* Author for correspondence (sep5@leicester.ac.uk).
†Present address: Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139, USA.

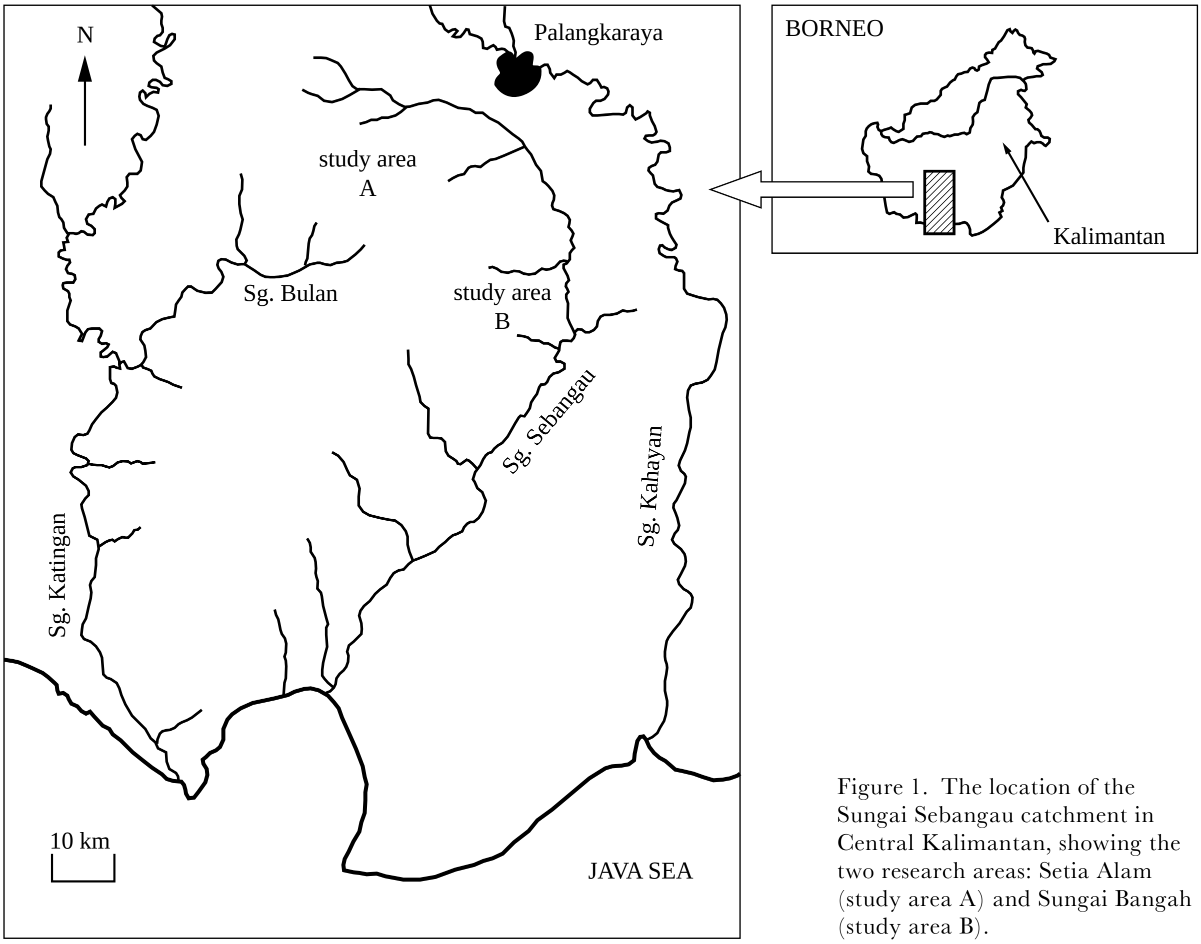

Figure 1. The location of the Sungai Sebangau catchment in Central Kalimantan, showing the two research areas: Setia Alam (study area A) and Sungai Bangah (study area B).

undisturbed peatland, stretching 200 km north from the Java Sea (figure 1). The Sungai Sebangau is a relatively short river and the landscape through which it flows is flat and low lying, rising to only about 30 m a.s.l. at its headwaters. Field research was carried out from 1993 to 1996 using the railway of the logging concession Setia Alam in order to gain access to the interior of this peatland. Information was obtained along several transects established beside the extraction railway and on trails cut through the forest (figure 2). The maximum transect length was 24.5 km from Sungai Sebangau. At this distance the transect was beyond the highest point of the watershed between Sungai Sebangau to the east and Sungai Bulan to the west (figure 1). Study plots were established across the peat dome at an increasing distance from the river to a maximum of 18.3 km (table 1 and figure 2). The plots, each 0.15 ha in area (50 m × 30 m), were located in different forest types within relatively undisturbed forest and beyond the limit of logging activity. The exact locations were chosen following a reconnaissance survey of the transects. Three plots were set up in each of three main forest types, with additional plots in vegetation transition zones. Investigations were also carried out 70 km down river close to Sungai Bangah, a tributary of Sungai Sebangau, where two study plots were established in riverine forest, a forest type that has been destroyed at the main study site by a combination of logging and burning.

(b) *Tree species diversity and forest structure*

In each plot, the diameter of every tree at a standard height (diameter at breast height (1.3 m) above the ground (dbh)) was determined for those trees with a minimum dbh of 7 cm. Maximum canopy height of these trees was obtained, using a clinometer, and their basal circumference (as close to the tree base as possible or immediately above stilt or buttress roots) measured in order to calculate basal areas. The vegetation within the study plots was assigned to a forest type based on differences in habitat and forest structure and by comparison with published accounts of peat swamp forest vegetation.

Characteristics of the trees in each plot were noted to assist in their identification. Local names of trees were assigned; voucher specimens were collected (housed at The Royal Botanic Gardens, Edinburgh), and information on bark and leaf characters, reproductive parts (where available) and other prominent morphological features were cross-referenced to standard works, including Anderson (1972), Ashton (1982), Ng (1978, 1989), Symington (1941) and Whitmore (1972*a*,*b*).

(c) *Peat surface topography, thickness and hydrology*

Surface peat elevation was obtained at intervals of 100 m using a sighting telescope and graduated staff over a distance of 24.5 km from the Sungai Sebangau. Peat thickness was determined every 500 m over the same distance. Data on peat thickness and peat surface levels were also obtained along a transect through the tall interior forest and into the very low canopy forest (see figure 2). At the Sungai Bangah, peat thickness was determined only within the study plots.

The depth of the water-table below the peat surface was measured during the 1993 dry season in ten dipwells inserted into the peat in each of five study plots located in mixed swamp

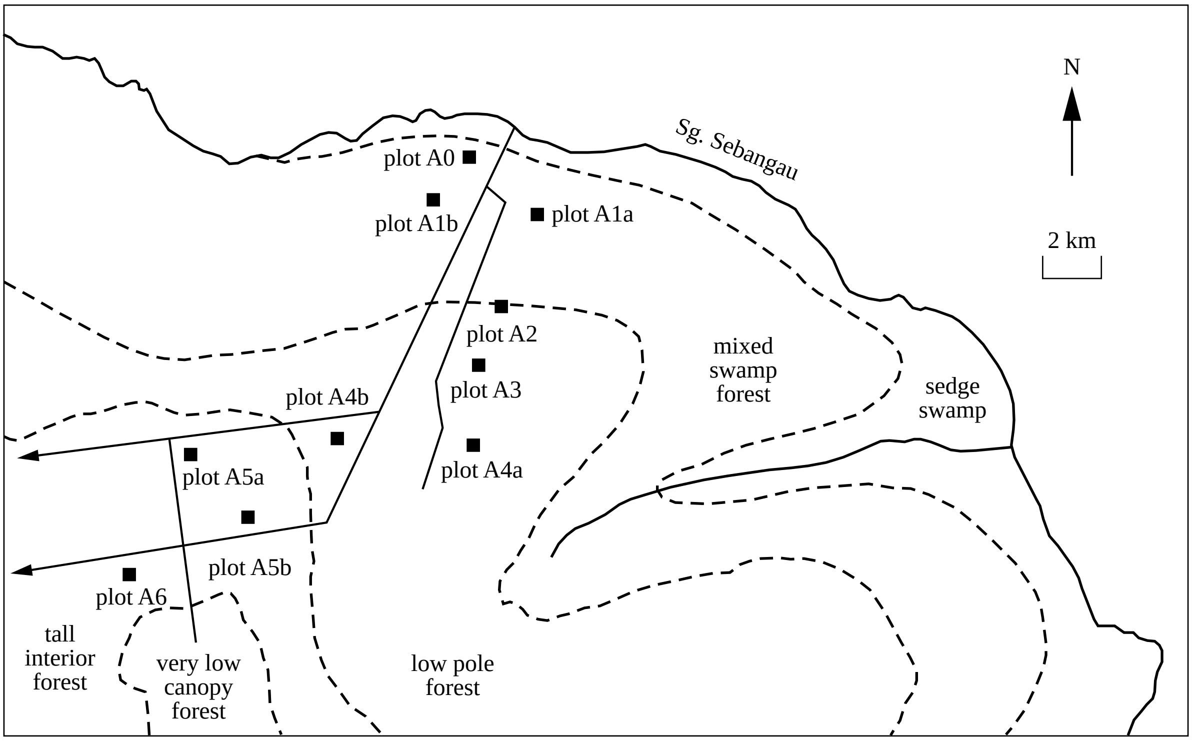

Figure 2. Location of research transects (solid lines) and study plots at Setia Alam in the upper catchment of Sungai Sebangau. Approximate boundaries of principal forest types are indicated (broken lines).

Table 1. *Location, forest type and mean peat thickness for permanent study plots established in peat swamp forest in the Sungai Sebangau catchment*

(Plots B1 and B2 are situated beside Sungai Bangah; plots A0–A6 are situated in Setia Alam concession, see figure 1.)

plot no.	forest type	distance from river (km)	mean peat thickness (m)
B1	riverine	0.4	1.0
B2	transition	0.7	4.0
A0	mixed swamp	1.5	2.8
A1a	mixed swamp	2.6	2.0
A1b	mixed swamp	2.1	3.0
A2	transition	6.5	4.6
A3	low pole	7.7	8.0
A4a	low pole	9.3	9.0
A4b	low pole	10.0	8.7
A5a	tall interior	14.5	9.0
A5b	tall interior	15.0	7.7
A6	tall interior	18.3	9.6

forest, transition forest (mixed swamp–low pole) and low pole forest. During the 1994 dry season the same method was used to measure the depth of the water-table in the tall interior forest.

(d) *Peat chemistry*

Samples of rainwater (collected outside the forest canopy), surface peat water (collected from dipwells) and surface peat (collected beneath the litter layer) were obtained for analysis of pH, conductivity and the major elements calcium, magnesium, potassium, nitrogen and phosphorus. In addition, peat samples were obtained from a continuous peat core. The surface water and peat samples were collected from plots in the mixed swamp, transition (mixed swamp–low pole) and low pole forest types. Ten samples of surface peat water and five samples of surface peat were collected in each plot during the 1993 dry season; four samples of rainwater from separate rainfall events were obtained during the 1996 dry season. Water pH and conductivity were measured in the field after sample collection using field pH and conductivity meters. Cations and anions in the water samples were determined by standard procedures (atomic absorption spectrophotometry (AAS) for cations; nitrate nitrogen by steam distillation; phosphate phosphorus by the molybdenum blue method) (Allen 1974). For the peat samples, pH was measured after sample collection in the field. A subsample of fresh peat was mixed 50:50 with distilled water prior to measurement of pH using a field meter. Prior to further analysis, peat samples were oven dried at 40 °C. Extractable cations were determined by AAS following extraction of 25 g of dried peat by ammonium acetate pH 7. Total phosphorus was obtained by the stannous chloride–ammonium molybdate method and total nitrogen by Kjeldahl digestion followed by steam distillation (Allen 1974). Moisture contents were determined at the time of weighing by further oven drying of subsamples to constant weight and all analysis results were corrected to a dry weight basis.

In 1995, at a distance of 7.5 km from the river, a peat core 980 cm long was removed for geochemical analysis (0–960 cm wood peat; 960–980 cm interface with alluvial clays–sands). Sampling of the upper 30 cm was accomplished by cutting a 15 cm × 20 cm peat monolith from the peat surface. The rest of the core was obtained using a peat core sampler; sequential 50 cm cores were divided into 20 cm samples. Peat pH was measured soon after sample collection. For subsequent analyses, the peat

Table 2. *Number of trees, total tree basal area and mean tree basal area for selected 0.15 ha study plots located in peat swamp forest in the Sungai Sebangau catchment*

(Basal area per hectare is a calculated figure. Basal areas are for all trees ⩾ 7 cm dbh.)

plot no.	forest type	no. trees	total basal area per plot (cm^2)[a]	mean basal area per plot (cm^2)[b]	basal area ($m^2\,ha^{-1}$)
B1	riverine	157	93 996	599	62.7
A0	mixed swamp	249	74 805	300	49.9
A1a	mixed swamp	269	75 054	279	50.1
A2	transition	375	87 900	234	58.6
A4b	low pole	357	68 886	193	45.9
A5b	tall interior	183	63 251	270	42.2
A6	tall interior	202	86 314	427	57.6

[a] Calculated from basal circumference and not dbh.
[b] Mean basal area = total basal area per plot divided by number of trees in the plot.

Table 3. *Tree height data (number of trees in each height category) for selected 0.15 ha study plots located in peat swamp forest in the Sungai Sebangau catchment*

(Data are presented for all trees ⩾ 7 cm dbh.)

	tree height categories (m)								
plot no.	< 6	6–10	10–14	14–18	18–22	22–26	26–30	30–34	> 34
B1	14	47	35	27	15	12	5	1	1
A0	1	50	92	43	32	22	7	2	0
A1a	4	73	87	47	41	13	4	0	0
A2	5	86	132	86	52	13	1	0	0
A4b	4	41	150	90	52	15	4	1	0
A5b	0	16	41	48	25	18	15	8	12
A6	2	5	37	37	34	33	24	12	18

samples were dried at 105 °C and milled prior to determination of ash content (following combustion at 550 °C) (Andrejko *et al.* 1983) and analysis of a range of elements using conventional wavelength-dispersive X-ray fluorescence spectroscopy.

(e) *Determination of peat age*

Samples of subfossil wood and peat matrix from the main study site were collected for radiocarbon (^{14}C) dating in order to provide information on the age of the peat deposit and its rate of formation. For the collection of wood samples, a soil auger was pushed into the peat until firm resistance to movement was encountered. Pressure was then applied, the auger was turned and a sample of wood collected in the head. Peat samples were obtained using a peat core sampler. Samples were obtained from several locations at increasing distances from Sungai Sebangau and at which peat thickness varied. In addition, the ^{14}C ages of several peat samples from the peat core obtained for geochemical analysis were determined (sample codes B-6917–6922) and several surface and near-surface peat samples from this core were dated using ^{210}Pb analysis (Appleby *et al.* 1988).

3. RESULTS

(a) *Tree diversity and forest structure*

More than 100 trees have been identified to genus or species and other specimens await confirmation (Shepherd *et al.* 1997). Analysis of the study plot data shows that there are distinct differences in forest structure and tree species composition from the river's edge to the watershed. Apart from the tall interior forest, many of the same species of tree are present throughout the forest continuum, although their relative abundance and height changes. The sequence of change is from riverine forest through mixed swamp forest and low pole forest to tall forest in the interior; transitional types can also be recognized (tables 1–4). In addition, a very low canopy forest occupies a discrete area on the highest point of the watershed.

(i) *Riverine forest*

This forest type is intermediate between freshwater swamp forest on inundated mineral soils and peat swamp forest. It is located close to the river (up to 1 km from the edge) and is flooded by river-water during the rainy season. The peat is shallow (up to 1.5 m thick) and, during the dry season, shallow pools are present on the forest floor. The principal canopy tree species is *Shorea balangeran*, which is the only tree to exceed a height of 35 m. Other canopy trees, including *Calophyllum* spp., *Campnosperma coriaceum* and *Combretocarpus rotundatus*, achieve heights between 25 and 35 m. The sedge *Thorachostachyum bancanum* is characteristic of the ground vegetation. Most of this forest in the upper Sungai Sebangau catchment has been destroyed as a result of logging and burning and has been replaced by low-growing sedge swamp.

Table 4. *Tree dbh data (number of trees ⩾ 7 cm dbh in each dbh category) for selected 0.15 ha study plots located in peat swamp forest in the Sungai Sebangau catchment*

(Data are presented for all trees ⩾ 7 cm dbh.)

	tree dbh categories (cm)											
plot no.	7–12	12–17	17–22	22–27	27–32	32–37	37–42	42–47	47–52	52–57	57–62	> 62
B1	68	29	16	11	16	6	6	2	0	0	1	2
A0	137	55	24	15	7	6	1	1	1	0	1	1
A1a	162	61	23	8	5	3	0	1	0	2	2	2
A2	225	87	38	15	4	3	1	0	1	0	1	0
A4b	238	67	34	8	4	2	2	0	0	0	0	2
A5b	97	38	12	11	8	9	4	2	0	0	2	0
A6	88	43	28	15	8	11	6	2	1	0	0	0

(ii) *Transition forest (riverine–mixed swamp forest)*

This occupies a very narrow zone (*ca.* 1.0–1.5 km from the river) on peat up to 2 m thick. It occurs up to the limit of riverine flooding and is influenced mostly by water outflow from the interior peat catchment. The principal canopy tree is *Shorea balangeran*.

(iii) *Mixed swamp forest*

This forest type extends up to 4 km from the margin of the peat dome into the interior. It is located beyond the limit of river flooding on peat that increases from 2 to 6 m in thickness. The forest is tall and stratified, with an upper canopy at a height of 35 m, below which there is a closed layer between 15 and 25 m and then a more open layer of smaller trees 7–12 m in height. The trees grow on large hummocks formed by root plates, interspersed with hollows that fill with water during the rainy season. Many of the trees have stilt or buttress roots; pneumatophores are frequent. Typical trees of the middle and upper canopies include *Aglaia rubiginosa*, *Calophyllum hosei*, *C. lowii*, *C. sclerophyllum*, *Combretocarpus rotundatus*, *Cratoxylum glaucum*, *Dactylocladus stenostachys*, *Dipterocarpus coriaceus*, *Dyera costulata*, *Ganua mottleyana*, *Gonystylus bancanus*, *Mezzetia leptopoda*, *Neoscortechinia kingii*, *Palaquium cochlearifolium*, *P. leiocarpum*, *Shorea balangeran*, *S. teysmanniana* and *Xylopia fusca*.

(iv) *Transition forest (mixed swamp–low pole forest)*

There is a slow gradation from mixed swamp to low pole forest between 4 and 6 km from the river. The upper and middle canopies are composed of a range of species similar to those of the mixed swamp forest, although densities of *Calophyllum* spp., *Combretocarpus rotundatus* and *Palaquium cochlearifolium* are greater. The forest canopy reaches a maximum height of 25–30 m. Few trees exhibit buttressing or stilt roots; pneumatophores are abundant on the forest floor. Pandans (*Pandanus* and *Freycinetia* spp.) form an almost continuous ground cover.

(v) *Low pole forest*

This forest occurs between 6 and 11 km from the river on peat that is from 7 to 10 m thick. The water-table is permanently high and the forest floor is very uneven. The trees grow on island-like hummocks that are separated by deep, water filled hollows in which the water persists throughout the dry season. Pneumatophores are abundant and there is a dense mat of tree roots in the surface peat. Only two canopy layers are discernible. The upper is open and reaches a maximum height of 20 m; the lower occurs at a height of 12–15 m and is more closed. The principal canopy species are *Combretocarpus rotundatus*, *Calophyllum fragrans*, *C. hosei* with lesser amounts of *Campnosperma coriaceum* and *Dactylocladus stenostachys*. Pandans form a dense, continuous ground cover and *Nepenthes* spp. are abundant.

(vi) *Tall interior forest*

This forest occupies much of the most elevated part of the peatland dome, from 12 km (where there is a sharp transition to it from low pole forest) to beyond the end of the 24.5 km transect. The peat water-table inside this forest type is below the surface throughout the year. There are few obvious hummocks and hollows and hardly any of the trees have prominent pneumatophores. The upper canopy reaches a maximum height of 45 m, below which two further layers can be distinguished at 15–25 m and 8–15 m. Canopy trees include *Agathis dammara*, *Calophyllum hosei*, *C. lowii*, *Cratoxylum glaucum*, *Dactylocladus stenostachys*, *Dipterocarpus coriaceus*, *Dyera costulata*, *Eugenia havelandii*, *Gonystylus bancanus*, *Gymnostoma sumatrana*, *Koompassia malaccensis*, *Mezzetia leptopoda*, *Palaquium cochlearifolium*, *P. leiocarpum*, *Shorea teysmanniana*, *S. platycarpa*, *Tristania grandifolia*, *Vatica mangachopai*, *Xanthophyllum* spp. and *Xylopia* spp. *Pandanus* spp. are absent except under gaps in the canopy.

(vii) *Very low canopy forest*

This very open, low canopy forest was discovered, at the end of the 1996 survey season, on the highest point of the catchment between the two river systems where it occupies a discrete area of about 13 km × 6 km, surrounded by tall forest. This area has a permanently high water-table and is characterized by very large pools, up to 200 m across and 1 m in depth, interspersed with forest-covered islands. Few of the trees exceed 1.5 m in height and the commonest species are *Calophyllum* spp., *Combretocarpus rotundatus*, *Cratoxylum* spp., *Dactylocladus stenostachys*, *Litsea* spp., *Ploiarium alternifolium* and *Tristania* spp. Pneumatophores are abundant with many protruding high above the surface of the pools; those of *D. stenostachys* exceeding 1.5 m in height. Owing to the open canopy, more light reaches the forest floor than in all other forest types and, consequently, there is a greater diversity and

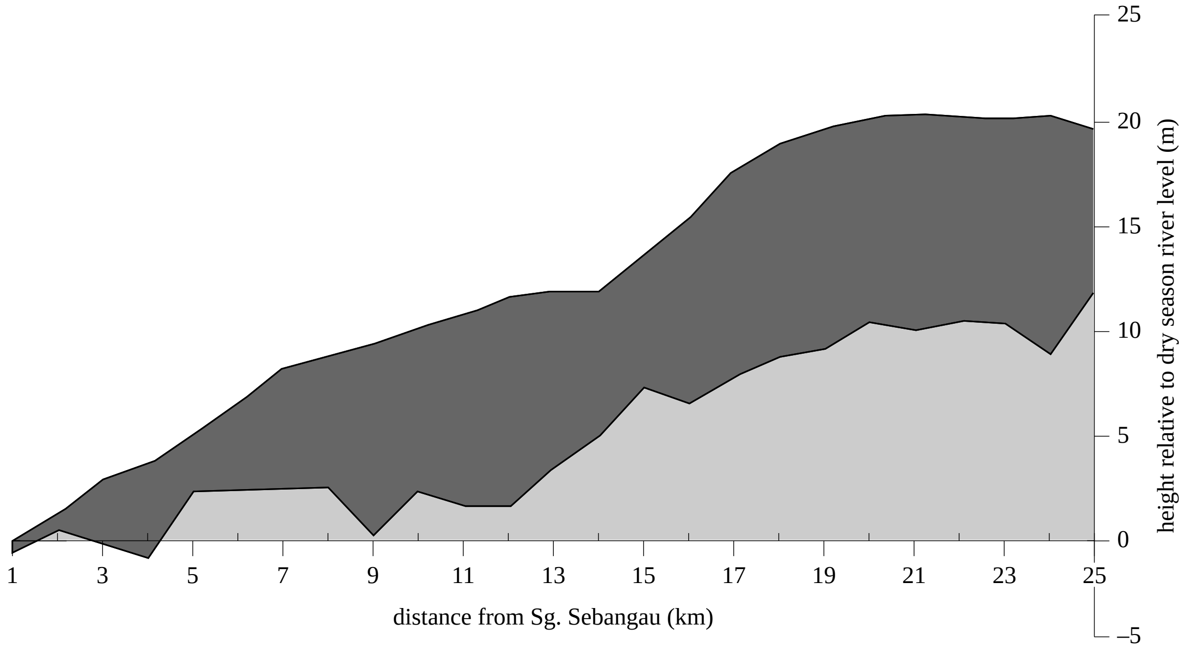

Figure 3. Peat surface elevation, peat thickness and mineral ground topography along a 24.5 km transect from Sungai Sebangau (vertical scale exaggerated).

cover of bryophytes on the peat surface. There is a lack of *Pandanus* spp. and the sedge *Thorachostachyum bancanum* is the most frequent vascular plant of the forest floor.

(b) *Tree enumeration data: comparison of forest structure and tree species composition*

Summary data from seven study plots illustrate the main differences between the forest types and the main trends in forest change from the river to the centre of the peatland dome (tables 2–4). There is a trend of increasing numbers of trees per plot from the riverine forest, through mixed swamp forest to low pole forest. In contrast, the density of trees in the tall interior forest is greater than in riverine forest but less than in mixed swamp forest (table 2). Tree height and girth (tables 3 and 4) decrease from the riverine forest to the low pole forest but then increase markedly in the tall interior forest. Twenty-three per cent of trees in the tall interior forest have a height greater than 26 m, compared with only 1% in the low pole forest and 3% in the mixed swamp forest plots. In general, total basal area per plot (table 2) decreases from the riverine forest through mixed swamp forest to low pole forest with a subsequent increase in the tall interior forest. The highest total basal areas were in the riverine forest (62.7 $m^2\ ha^{-1}$), mixed swamp–low pole transition forest (58.6 $m^2\ ha^{-1}$) and tall interior forest (57.6 $m^2\ ha^{-1}$).

In the very low canopy forest, owing to difficulty of access and lack of time, only a temporary plot could be established in order to provide some comparative data. The trees in this area were considerably smaller, both in height and girth, than in the other forest types. The large pools on the peat surface reduced the tree density to less than that in the low pole forest (about 150 trees per 0.15 ha compared with 357). More than 70% of the trees had a dbh of less than 12 cm and a large number of small trees (less than 7 cm dbh) were present. Most trees were less than 15 m in height.

(c) *Peatland characteristics*

(i) *Surface and bottom topography: peat thickness*

A composite profile through the peatland from the river to the watershed shows the surface levels, bottom topography and thickness of the intervening peat (figure 3). Changes in peat thickness, surface elevation and surface gradient are summarized in table 5.

The peatland exhibits a domed profile. The highest point on the watershed is approximately 20 m above the dry season water level of the Sungai Sebangau at a distance of 21 km onto the dome. For the first 12 km, peat thickness increases gradually to a maximum of 10 m. Over the same distance, the underlying mineral ground maintains a more or less constant level, although there are several small depressions. At a distance of 12 km from the river there is a marked increase in the surface elevation of the peatland, mirrored by an increase in the base level of the mineral ground. The gradient of the peat surface is very low between 5.5 and 12.5 km from the river (1:1628), with a surface elevation increase of only 4.3 m over 7 km; this is the zone occupied by low pole forest. Between 12.5 and 16 km there is an increase in the gradient (1:625) that coincides with the sharp transition zone from low pole to tall interior forest. After this, the gradient declines (1:1482) and reduces further over the watershed where it is almost flat (1:4091). The data on peat thickness and surface topography obtained along the transect through the tall interior forest into the very low canopy forest show that the latter forest type is at a slightly higher altitude and that the peat is still thick, maintaining an average of 11 m.

(ii) *Hydrology*

The maximum water-table drawdown below the peat surface at the end of the dry season is shown in table 6. The water-table was highest, at an average of 24 cm below the surface, in the low pole forest, with a decrease to nearly 40 cm in the mixed swamp forest nearer to the

Table 5. *Changes in peat thickness, peat surface elevation and peat surface gradient along a 24.5 km transect from Sungai Sebangau to its watershed in Central Kalimantan. Forest types are also indicated*

distance from Sungai Sebangau (km)	mean peat thickness (m)	cumulative change in surface elevation from Sungai Sebangau (m)	gradient	main forest type
0–1.5	1.2	+1.7	1:882	riverine
1.5–5.5	3.7	+7.6	1:678	mixed swamp
5.5–12.5	8.4	+11.9	1:1628	low pole
12.5–16	8.3	+17.5	1:625	tall interior
16–20	10.5	+20.2	1:1482	tall interior
20–24.5	9.5	+19.1	1:4091	tall interior
overall	7.8	+20.2	1:990	—

Table 6. *Peat water-table levels recorded at the end of the 1993 dry season (1994 dry season for plot A5b) ($n = 10$) in study plots located in peat swamp forest in the upper catchment of the Sungai Sebangau*

plot no.	forest type	depth of water-table below peat surface (cm ± s.d.)
A0	mixed swamp	39.0 ± 4.2
A1a	mixed swamp	39.0 ± 4.5
A2	transition	34.3 ± 3.7
A3	low pole	23.7 ± 3.4
A4a	low pole	24.0 ± 2.8
A5b	tall interior	150.0 ± 7.6

river. The tall interior forest is markedly different from the other forest types, with a mean water-table 150 cm below the peat surface. Observations in the rainy season indicated that the water-table in the tall interior forest never rose above the peat surface, remaining at a depth of 20–30 cm, whilst in the other forest types the water-table was at or above the peat surface at that time.

(d) *Peat chemistry*

(i) *Surface peat and surface water*

Surface water is acidic (average pH 3.6) with a very low electrical conductivity (average 50 $\mu S\,cm^{-1}$); all ions are present in very low concentrations (table 7). In comparison, rainwater has a higher pH of 5.9 but a lower conductivity of 41 $\mu S\,cm^{-1}$ than surface peat water. Electrical conductivity decreases from the mixed swamp forest to the low pole forest plots and there is a similar trend, with some variations, for potassium, calcium, magnesium and nitrate nitrogen. The most marked decrease is shown by phosphate phosphorus.

Surface peat pH (average 3.1) is consistently lower than surface water pH and the concentrations of extractable ions are low (table 8). These features are common to most ombrotrophic peatlands (Shotyk 1988). The most obvious trends are increases in extractable calcium and magnesium and total phosphorus between the mixed swamp forest and the low pole forest plots.

(ii) *Peat core*

The average pH of peat samples from the top 100 cm is 3.0 ± 0.3 (± s.d.), in the middle of the core (400–500 cm) it is 2.9 ± 0.2, and for the bottom section (800–940 cm) it is 3.7 ± 0.1 (table 9). The average pH for the whole core (0–940 cm) is 3.2 ± 0.4. The top 3 cm of the core have an ash content of 1.04%, declining to 0.35% at a depth of 9–12 cm. Most of the rest of the core, to a depth of 840 cm, has a very low ash content and, except for two samples, is less than 1%. Samples from the peat–mineral transition zone (840–920 cm) have a higher ash content, rising to 5%. The average ash content from the surface to a depth of 840 cm is very low (0.49 ± 0.24%).

Calcium decreases markedly within the top 90 cm of the profile (from 2398 $\mu g\,g^{-1}$ in the first 15 cm to 58 $\mu g\,g^{-1}$ at 90 cm). Apart from two small peaks at 650 cm (120 $\mu g\,g^{-1}$) and 750 cm (154 $\mu g\,g^{-1}$), calcium remains relatively constant throughout the lower part of the profile (averaging about 50 $\mu g\,g^{-1}$). There is a less pronounced decrease in magnesium within the top 190 cm of the profile, otherwise values remain more or less constant throughout. Potassium exhibits a strong decrease within the top 130 cm of the profile (from 1366 $\mu g\,g^{-1}$ at the surface to 62 $\mu g\,g^{-1}$ at 130 cm) and remains relatively constant throughout the rest of the profile (averaging 15 $\mu g\,g^{-1}$). Phosphorus decreases from the peat surface to a depth of 190 cm (256 $\mu g\,g^{-1}$ at the surface to 24 $\mu g\,g^{-1}$ at 190 cm); below this depth it is distributed relatively evenly within the profile.

(e) *Radiocarbon dating of peat*

The radiocarbon age of peat and wood samples is summarized in table 10; results are expressed as uncalibrated ^{14}C years before present (yr BP) ± s.d. The data are arranged in order of increasing distance from Sungai Sebangau and are grouped into two age groups, 'young peat' (< 2000 yr BP) and 'old peat' (> 6000 yr BP); peat of intermediate age was not found in this study. The depth of peat from which samples were taken for ^{14}C determination ranged from 0.9 to 10 m and the radiocarbon ages obtained varied from 390 ± 210 to 10320 ± 50 yr BP. The base of the peat core (at a depth of 940 cm) was dated to 18 300 ± 50 yr BP (sample reference B-6922).

4. DISCUSSION

(a) *Variation in forest vegetation*

The vegetation of the Sungai Sebangau catchment consists of a continuum of forest types from the river to the centre of the peatland dome. The sequence is

Table 7. *Chemical analysis data (mg l*$^{-1}$ *± s.d.) for surface peat water samples (n = 10) collected in five study plots located in peat swamp forest in the Sungai Sebangau catchment*

(Conductivity is measured in µS cm^{-1}. Rainwater was collected outside the forest canopy (*n* = 4).)

	plot no. and forest type					
	plot A0 mixed swamp	plot A1a mixed swamp	plot A2 transition	plot A3 low pole	plot A4a low pole	rainwater
pH	3.9 ± 0.5	3.4 ± 0.3	3.4 ± 0.4	3.5 ± 0.4	3.6 ± 0.3	5.9 ± 0.3
conductivity	54 ± 9	53 ± 6	51 ± 6	50 ± 4	44 ± 5	41 ± 5
K	0.82 ± 0.07	0.73 ± 0.04	0.31 ± 0.04	0.65 ± 0.08	0.30 ± 0.02	0.14 ± 0.01
Ca	0.71 ± 0.03	0.38 ± 0.01	0.41 ± 0.02	0.38 ± 0.02	0.51 ± 0.03	0.37 ± 0.02
Mg	0.12 ± 0.02	0.06 ± 0.01	0.06 ± 0.01	0.09 ± 0.01	0.07 ± 0.01	0.10 ± 0.01
NO_3-N	0.07 ± 0.01	0.12 ± 0.03	0.08 ± 0.01	0.09 ± 0.0	0.08 ± 0.01	0.12 ± 0.02
PO_4-P	2.69 ± 0.12	2.81 ± 0.19	0.93 ± 0.07	0.33 ± 0.05	0.50 ± 0.04	0.04 ± 0.01

Table 8. *Chemical analysis data (pH, extractable K, Ca and Mg, and total nitrogen and phosphorus ± s.d.) for surface peat samples (n = 5) collected from beneath the litter layer in five study plots located in peat swamp forest in the Sungai Sebangau catchment*

(Values are µg g^{-1} dry weight for all elements except nitrogen which is expressed as a percentage.)

	plot no. and forest type				
	plot A0 mixed swamp	plot A1a mixed swamp	plot A2 transition	plot A3 low pole	plot A4 low pole
pH	2.9 ± 0.3	3.2 ± 0.2	3.1 ± 0.2	3.2 ± 0.4	3.2 ± 0.3
K (extractable)	134.9 ± 10.2	124.7 ± 11.4	120.2 ± 11.9	129.6 ± 9.8	119.9 ± 7.6
Ca (extractable)	21.6 ± 1.3	35.0 ± 2.1	22.3 ± 1.6	48.0 ± 3.3	50.6 ± 3.9
Mg (extractable)	20.5 ± 1.7	25.0 ± 1.8	37.0 ± 2.2	40.4 ± 2.7	39.6 ± 2.1
N (total)	1.8 ± 0.1	1.0 ± 0.1	1.9 ± 0.2	1.4 ± 0.2	0.8 ± 0.1
P (total)	278 ± 31	272 ± 22	373 ± 32	340 ± 29	339 ± 24

comparable to those described by Anderson (1983) and Stoneman (1997) from Sarawak and Brunei, and Brady (1997) from Sumatra. There are, however, several important differences. Anderson and Brady both describe a sequence of change in which relatively species-diverse mixed swamp forest is replaced by species-poor medium and low pole forest associations. According to Anderson, the ultimate forest type that replaces low pole forest in the centre of some Sarawak peat swamps is a savannah-like forest. This occurs on dry peat and has a very open canopy, with a tree height of usually less than 15 m. In the Sebangau catchment, although there is a sequence from mixed swamp forest to low pole forest on thicker peat, there are further changes beyond the latter to tall, relatively diverse forest overlying much of the watershed and, in one location, very low canopy forest with large open water pools. Savannah forest was not encountered. The presence of the tallest forest on the thickest peat is surprising since it was believed previously that peat more than 3 m thick could support only low pole forest (Sieffermann *et al.* 1988). This interpretation was used to conclude that the tall interior forest, known from aerial photographs and early satellite images, must be growing on mineral soil, probably tropical podzol. It is, in fact, located on peat up to 13 m thick. How can this apparent anomaly be explained?

Assuming that tropical ombrotrophic peatlands have a mode of formation broadly similar to that of temperate bogs, the wettest part of the peatland should occur on the highest part of the dome (Ingram 1983). During peatland development, a vegetation succession takes place from mixed swamp forest to low pole forest, which is reflected in the zonation from the periphery to the centre of the peat dome (Anderson & Muller 1975). These changes in forest type appear to be concomitant with variations in the hydrology and thickness of the peat (i.e. to development of a permanently high water table within a mass of thick peat). Differences between peat swamp forest types are also influenced by variations in nutrient availability (ombrotrophic as opposed to minerotrophic) in the surface of the peat and the efficiency of nutrient cycling and uptake (between the atmosphere, surface peat and vegetation) within the ecosystem. These processes achieve a state of dynamic equilibrium as peat accumulation proceeds and forest types develop over time. In his palynological investigations, Morley (1981) demonstrated that a sequence of vegetation change, from mixed swamp forest to low pole forest, had occurred in the Sungai Sebangau peatland several thousand years ago at a distance of 5.5–8 km from the river. Closer to the river, the shallower peat was formed entirely by mixed swamp forest vegetation without succession to low pole forest.

Table 9. *Summary of geochemical data for a 9.8 m peat profile collected in peat swamp forest at a distance of 7.5 km from the Sungai Sebangau*

(Values for major elements are $\mu g\, g^{-1}$ dry peat; ash content is expressed as percentage of dry peat. Results are averages over intervals of least change; n.d., not determined.)

depth (cm)	Mg	Ca	K	P	pH	ash
0–3	712	2398	1366	256	2.3	1.04
3–6	705	1341	837	238	2.9	0.71
6–9	527	1571	620	199	3.0	0.46
9–12	228	294	467	161	n.d.	0.35
12–15	551	367	481	168	3.0	0.37
15–30	470	583	288	143	3.1	0.39
30–90	401	165	149	115	n.d.	0.50
90–190	403	43	49	49	2.9	0.52
190–290	189	27	12	25	3.0	0.29
290–390	169	36	13	31	3.0	0.38
390–490	166	42	15	34	2.9	0.40
490–550	152	49	14	33	3.1	0.23
550–570	177	60	16	36	3.2	1.09
570–650	195	63	14	34	3.6	0.57
650–670	228	120	18	32	3.9	1.11
670–750	186	67	16	32	3.1	0.55
750–770	172	154	19	31	3.3	0.83
770–830	170	72	21	33	3.5	0.59
830–840	388	57	57	67	3.0	0.42
840–920	158	86	16	42	3.7	3.64
920–940	70	47	30	103	3.9	5.18
940–960	292	25	677	238	4.1	57.9
960–980	569	42	1229	311	4.5	86.2

The transect studied by Morley extended only for 8 km from the river and he may have been unaware of the existence of the tall interior forest.

(b) *Interdependence of forest types and peat characteristics*

(i) *Peatland topography and peat thickness*

It is evident that the changes in vegetation described in this paper coincide, at least in part, with increasing height of the surface of the peat dome and thickness of peat. Marginal mixed swamp forest is located on shallow peat (< 2 m) while low pole, tall interior and very low canopy forest are all on thick peat (*ca.* 10 m). The three last named types all occur on the flattest areas whilst the steepest gradients support transition forest between one type and another. Surface topography and peat thickness, however, cannot influence the vegetation directly but operate through changes that they bring about or promote in other characteristics of the peatland, especially hydrology, chemistry and organic matter dynamics (balance between peat accumulation and peat degradation).

(ii) *Hydrology*

The fundamental role of water in the development and maintenance of ombrogenous peatlands is well established (Ivanov 1981) and an adequate supply, determined by the balance of rainfall and evapotranspiration, is critical to their sustainability. In addition, the nature of the peat itself, in terms of its ability to retain and store water, is important and determines the relative height of the peatland water-table (Ingram 1978). The hydraulic conductivity of peat near to the surface (i.e. the acrotelm layer in which there is fluctuation of the water-table) determines the speed at which water moves laterally through the peat after rainfall. It influences, therefore, the speed with which the water-table drops to its ambient level (Bragg 1997). The hydraulic conductivity of the acrotelm of tropical peat appears to be much higher than that of temperate peat (Takahashi & Yonetani 1997).

In common with other ombrotrophic peatlands, the Sungai Sebangau peatland should be regarded as a single ecohydrological unit in which the hydrology of one part has an influence on adjacent areas. During the dry season the peat water-table is highest in the very low canopy and low pole forests, lower in the mixed swamp forest and considerably lower in the tall interior forest. The different peat surface altitudes and gradients, although relatively small, have a strong influence on local hydrological conditions. It was observed, for example, that water overflowed from the pools at the edge of the very low canopy forest into the surface peat of the tall interior forest that surrounds it at a slightly lower level. In the latter forest, water is never present at the peat surface but substantial movement of water (whether from rainfall or subsurface flow from higher parts of the peat dome) occurs laterally through the deep (up to 1.5 m) acrotelm downslope into the low pole forest. The low pole forest receives water from both rainfall and lateral water movement from higher elevations and these, together with a lower surface gradient in this part of the dome, maintain a high water-table at or above the peat surface for nine to ten months of the year. These conditions are conducive to the development of the more depauperate low pole forest. During the rainy season, surface water movement occurs from the

Table 10. *Age of peat in the upper catchment of Sungai Sebangau determined by radiocarbon dating of wood and peat samples*

	distance from river (km)	thickness of peat (m)	depth of sample (m)	nature of organic material assayed	age of peat (uncalibrated ^{14}C yr BP ± s.d.)	sample reference
young peat	1	3	3	wood	760 ± 210	KB1
	2	2	2	wood	1140 ± 250	KB2
	3	3	2	wood	1760 ± 250	KB3
	3.2	3.5	1.2	wood	390 ± 210	KB10
	6	> 4	1.2	wood	400 ± 130	KB7
	6	> 4	0.9	peat	400 ± 150	KB8
	7.5	9.8	1.3	peat	1450 ± 40	DW1
	10	10	1.7	wood	1300 ± 50	RAV1/1
old peat	4	> 4	3	wood	6920 ± 160	KB4
	5	> 4	2.5	wood	6830 ± 270	KB5
	5.5	> 4	3	wood	6580 ± 240	KB9
	6	> 4	3	wood	7030 ± 270	KB6
	7.5	9.8	2.4	peat	6070 ± 40	DW2
	7.5	9.8	6.2	peat	9060 ± 100	DW3
	7.5	9.8	6.6	peat	10 320 ± 50	DW4
	10	10	4.5	wood	8450 ± 60	RAV1/2
	10	10	10	wood	9600 ± 60	RAV1/3
	14.5	8.7	2.8	wood	6670 ± 50	JR1/1

low pole forest downslope towards the marginal mixed swamp forest and the river. At the end of the rainy season, surface flow ceases, except after occasional heavy rainfall events, but lateral water movement through the acrotelm continues until the maximum dry season draw-down within the low pole forest is achieved. The marginal peat swamp forest eventually receives all of the water that moves out from the centre of the peatland dome. The riverine forest, or in its absence sedge swamp, is the last recipient of this radial water flow and during the rainy season these areas are also inundated with river flood-water.

(iii) *Surface peat and peat water chemistry*

The differences in the forest vegetation cannot be explained readily by reference to the chemical analysis data for either surface peat or peat water. The chemical analysis data for surface peats indicate a trend from the marginal forest to the low pole forest of an increase in several elements, especially extractable calcium and magnesium and total phosphorus. The hydrochemical data, however, indicate a trend from the marginal forest to the low pole forest of decreasing levels of most of the ions measured, i.e. levels are highest towards the periphery of the peat swamp and lowest in the interior. The movement of water across the peatland dome must also be considered since this mass flow brings with it a constant supply of nutrients in low concentration that the trees can use for their growth. The mixed swamp and riverine forest zones are the final recipients of all the water flowing off the interior of the peatland and this, in part, may explain the greater height and girth of the canopy trees in these areas compared with the low pole forest. In addition, the roots of trees in the riverine forest probably may also penetrate through the shallow peat to the underlying mineral ground whilst, during the rainy season, this forest type also receives river floodwater containing dissolved nutrient elements. Thus, the ecological factors determining vegetation zonation on this peatland appear to be similar to those operating on ombrotrophic peatlands in temperate regions, i.e. vegetation growing towards the periphery of the peatland dome receives an increased water flow and, consequently, an increased rate of supply of dissolved nutrient elements and dissolved oxygen (Ingram 1967; Sparling 1967).

(iv) *Peat core geochemistry*

The low ash values for most of the core indicate that this part of the Sungai Sebangau peat deposit has been ombrogenous for most of the last 10 000 years. This was also the conclusion of the palynological study carried out by Morley (1981) that showed ombrogenous peat formation began abruptly over a topogenous freshwater swamp.

The peat core chemical analysis data reveal a strong accumulation of several elements, namely calcium, potassium and phosphorus, in the upper 150 cm of the profile, although values are very low compared with mineral soils. The surface enrichment of elements important in plant mineral nutrition may indicate their bioaccumulation in the surface peat as a result of long-term nutrient uptake and cycling. Over the millennia that this peatland has been in existence plant nutrients have been localized within the forest biomass and the surface acrotelm layer of peat. In the latter, some decomposition has occurred with consequent nutrient release. For this single peat core the highest concentration of elements is in the top 15 cm although there is evidence of some bioaccumulation down to 150 cm, which is probably the maximum extension downwards of the tree roots.

(v) *Age of peat in the upper Sungai Sebangau catchment*

Radiocarbon dating provides strong evidence of two different age sequences in the peat. There is 'young' peat less than 2000 years old that was obtained in bottom and near bottom samples from cores taken close to the Sungai Sebangau (up to 3 km) and from the upper peat of cores obtained further onto the peatland dome (up to 10 km). The age of this young peat varies from around 400 yr BP at depths of about 1 m to between 1140 and 1760 yr BP from 2–3 m. In contrast, several samples taken from beyond 4 km onto the dome provide much older ages, in excess of 6000 yr BP, at depths of only 2.5–3 m below the surface. Similar old ages have been reported previously for Central Kalimantan peats (Sieffermann *et al*. 1988; Neuzil 1997). There is also evidence that, in some locations, young peat overlies old peat. For example, dates of peat samples from the core abstracted at 7.5 km from the river reveal that the age of the peat near to the surface (1.3 m) is 1450 yr BP. Further down, at 2.4 m, it is already 6070 yr BP, whilst at 6.6 m it is 10 320 yr BP. These dates indicate that the surface peat, down to about 2 m, is young peat overlying old peat that makes up most of the peat profile. There is also evidence from ^{210}Pb analysis of surface peat samples from this location to suggest that the young peat is accumulating currently at a rate of up to 20 cm per 100 years (P. Appleby, personal communication).

It is notable that none of the samples for which data are presented produced ages intermediate between the young peat of less than 2000 yr BP and the old peat of more than 6000 yr BP. The pattern of peat formation in the Sebangau catchment has, therefore, been complex although the result is a visually uniform peat-covered landscape. As a result of the earlier phase of formation (commencing more than 10 000 yr BP), peat developed on undulating interfluves, covering extensive areas with a mantle of peat, possibly up to 15 m thick. This peat continued to accumulate until about 5000 yr BP after which peat formation slowed down and eventually stopped. Since the peat close to the surface is old, it is assumed that degradation of this older peat has been taking place for at least the last 2500 years. Evidence suggests it is continuing to disappear at the present time at an average rate of about 10 cm per 100 years (Sieffermann *et al*. 1988). This older peat must have formed under much wetter climatic conditions than prevail today, possibly without the seasonality of wet and dry seasons that now prevails.

In contrast, the peat closer to the river started to form only within the last 2000 years following changes to the mineral ground hydrology caused by sea level and land surface changes and possibly capture of the headwaters of Sungai Sebangau by the adjacent Sungai Katingan. The last event would have changed Sungai Sebangau from a fast-flowing, alluvial river, to a much shorter river with reduced velocity and sediment load (Morley 1981). These changes would have provided suitable conditions for ombrogenous peat formation to commence in the river flood plain. Subsequently, the younger peat of the valley merged with the older, high peat on the watershed.

(vi) *Dynamic ecological processes and the sustainability of tropical peat swamp forest: past, present and future*

The fact that the peatland in the upper catchment of Sungai Sebangau consists of peat formed in two widely different periods of time provides a further insight into the relationship between the present-day forest types and the underlying peat. It also enables the future sustainability of this ecosystem to be predicted.

Tropical peat swamp forest is a dual ecosystem. Its development and maintenance is dependent upon the ecological functions and processes of each component, forest and peatland, and the way in which these interrelate at the principal point of contact, i.e. within the acrotelm. This dual ecosystem is very sensitive to changes that take place to this shallow superficial layer. On the one hand the acrotelm is the surface protective layer of the peatland supplying partially decomposed plant material to the lower catotelm that forms the bulk of the peat deposit and thereby adding to the thickness of accumulating peat. On the other hand, the acrotelm is the rooting zone for the forest vegetation and it is where limited organic matter decomposition is releasing nutrients that become available for subsequent plant uptake. The extent of the acrotelm is determined by the maximum depth to which the peat water-table falls during the dry season that in turn is dependent on the hydraulic conductivity profile of the acrotelm (Bragg 1997).

From the preliminary research carried out on the Sungai Sebangau peatland it is evident that the most important factors in determining the organic matter accumulation potential of the peat, and the biodiversity and structure of the forest it supports, are hydrological intactness and nutrient availability. The former creates the conditions necessary to maintain a viable peatland system while the latter determines the nature of the forest that can grow upon it. In general, the tallest forest should be found on the marginal areas that receive mass water flow from the interior. During pronounced dry seasons, the water-table in the marginal swamp forest may decline to a low level allowing air to enter the acrotelm thereby promoting some aerobic decomposition of organic material and nutrient release (Brady 1997). In contrast, the wettest parts of the peatland system, where peat is actively accumulating, provide a lower nutrient capital to support forest biomass. The apparent anomaly in this model is the presence of the tall forest overlying more than 10 m of peat on the watershed.

In the tall interior forest, the age of peat near to the surface (2.8 m) is 6670 years suggesting that most, if not all of the peat in this watershed position is old and that the surface is degrading. Sieffermann *et al*. (1988) and Neuzil (1997) also proposed a similar scenario from their studies of high peat elsewhere in Central Kalimantan. If, as seems likely, peat degradation has been taking place for at least 2500 years then, in the past, the thickness of peat may have been about 1.5 m greater than at present. Since then, there has been a slow but constant release of nutrient elements stored in the peat that have become available for uptake by the vegetation. This higher nutrient availability has been sufficient to support a more biologically diverse and productive forest than elsewhere in this peatland landscape. At the present time, therefore, the low pole and mixed swamp forests are located on a young peat surface that is still accumulating peat, whilst the tall interior forest is located on an old peat surface in which the organic matter is oxidizing slowly.

Tropical peat swamp forest, in common with all ecosystems, is in a dynamic relationship with its environment and any persistent change, particularly in climatic wetness, will have implications for its long-term stability. Peat formation on the highest parts of the peatland dome cannot be sustained by the present climate of Central Kalimantan and any increase in the frequency and length of the dry season will promote more surface oxidation and a faster rate of peat degradation. It could also reduce the rate of peat accumulation where this process is still occurring. Conversely, the restoration of a wetter climate could greatly extend the life of this ecosystem and promote renewed or more rapid rates of peat accumulation. The caveat to this latter statement is that there is increasing pressure on the peatlands of Central Kalimantan for land development and human settlement that could lead to the complete loss of this ecosystem in the short to medium term, regardless of climate change.

This paper is based (in part) on material collected whilst two of the authors (S.E.P. and J.O.R.) were participants in the Royal Society's South-East Asia Rain Forest Research Programme (Programme publication no. A/283). Their research was supported also by the British Council, Jakarta and the UK Government's Darwin Initiative. W.S. and D.W. are grateful to the Wander Foundation, University of Berne, for financial support. All authors would like to thank Professor R. G. Sieffermann and Dr M. Fournier (both formerly of Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM), Paris) for assistance with and discussions on radiocarbon dating, Steve Reese of the Radiocarbon Laboratory, University of Berne, for the ^{14}C age dates of the peat core samples, Dr Andrij Cheburkin, Geological Institute, Ukrainian Academy of Sciences, Kiev, for XRF spectroscopy analyses, Dr Peter Appleby, University of Liverpool, for ^{210}Pb age dating, Dr P. A. Shepherd for his contribution to vegetation survey, Dr G. Argent (The Royal Botanic Garden, Edinburgh) and Dr J. A. R. Anderson for assistance with tree identification, and numerous students from the Universities of Nottingham, Leicester, Hokkaido and Palangka Raya for their help with fieldwork.

REFERENCES

Allen, S. E. (ed.) 1974 *Chemical analysis of ecological materials*. Oxford, UK: Blackwell.

Anderson, J. A. R. 1963 The flora of the peat swamp forests of Sarawak and Brunei including a catalogue of all recorded species of flowering plants, ferns and fern allies. *Garden. Bull. (Singapore)* **29**, 131–228.

Anderson, J. A. R. 1972 *Trees of peat swamp forest of Sarawak*. Sarawak: Forest Department.

Anderson, J. A. R. 1983 The tropical peat swamps of western Malesia. In *Mires: swamp, bog, fen and moor. B. Regional studies* (ed. A. J. P. Gore), pp. 181–199. Amsterdam: Elsevier.

Anderson, J. A. R. & Muller, J. 1975 Palynological study of a Holocene peat and a Miocene coal deposit from NW Borneo. *Rev. Palaeobot. Palynol.* **19**, 291–351.

Andrejko, M. J., Fiene, F. & Cohen, A. D. 1983 Comparison of ashing techniques for determination of the inorganic content of peats. In *Testing of peats and organic soils* (ed. P. M. Jarret), pp. 5–20. Philadelphia, PA: ASTM.

Appleby, P. G., Nolan, P. J., Oldfield, F., Richardson, N. & Higgitt, S. 1988 ^{210}Pb dating of lake sediments and ombrotrophic peats by gamma assay. *Sci. Total Environ.* **69**, 157–177.

Ashton, P. S. 1982 Dipterocarpaceae. *Flora Malesian* **9**, 237–552.

Brady, M. 1997 Effects of vegetation changes on organic matter dynamics in three coastal peat deposits in Sumatra, Indonesia. In *Biodiversity and sustainability of tropical peatlands* (ed. J. O. Rieley & S. E. Page), pp. 113–134. Cardigan, UK: Samara Publishing.

Bragg, O. M. 1997 Understanding ombrogenous mires of the temperate zone and the tropics: an ecohydrologist's view. In *Biodiversity and sustainability of tropical peatlands* (ed. J. O. Rieley & S. E. Page), pp. 135–146. Cardigan, UK: Samara Publishing.

Immirzi, C. P. & Maltby, E. 1992 *The global status of peatlands and their role in the carbon cycle*. Wetlands Ecosystems Research Group, Report 11. Exeter, UK: University of Exeter.

Ingram, H. A. P 1967 Problems of hydrology and plant distribution in mires. *J. Ecol.* **55**, 711–724.

Ingram, H. A. P. 1978 Soil layers in mires: function and terminology. *J. Soil Sci.* **29**, 224–227.

Ingram, H. A. P. 1983 Hydrology. In *Mires: swamp, bog, fen and moor. B. Regional studies* (ed. A. J. P. Gore), pp. 67–158. Amsterdam: Elsevier.

Ivanov, K. E. 1981 *Water movement in mirelands* (translated by A. Thomson & H. A. P. Ingram). London: Academic Press.

Lappalainen, E. (ed.) 1996 *Global peat resources*. Jyväskylä, Finland: International Peat Society.

Morley, R. J. 1981 Development and vegetation dynamics of a lowland ombrogenous peat swamp in Kalimantan Tengah, Indonesia. *J. Biogeogr.* **8**, 383–404.

Neuzil, S. G. 1997 Onset and rate of peat and carbon accumulation in four domed ombrogenous peat deposits in Indonesia. In *Biodiversity and sustainability of tropical peatlands* (ed. J. O. Rieley & S. E. Page), pp. 55–72. Cardigan, UK: Samara Publishing.

Ng, F. S. P. 1978 *Tree flora of Malaya*, vol. 3. Kuala Lumpur: Longman.

Ng, F. S. P. 1989 *Tree flora of Malaya*, vol. 4. Kuala Lumpur: Longman.

Radjagukguk, B. 1992 Utilisation and management of peatlands in Indonesia for agriculture and forestry. In *Proceedings of the International Symposium on Tropical Peatland. Kuching, Sarawak, Malaysia, May 1991*, pp. 21–27. Malaysia: Ministry of Agriculture, MARDI.

RePPProT 1990 *A national overview from the regional physical planning programme for transmigration. UK Overseas Development Administration and Directorate BINA Programme*. Jakarta: Ministry of Transmigration.

Rieley, J. O. & Ahmad-Shah, A. A. 1996 The vegetation of tropical peat swamp forests. In *Tropical lowland peatlands of Southeast Asia* (ed. E. Maltby, C. P. Immirzi & R. J. Safford), pp. 55–73. Gland, Switzerland: IUCN.

Rieley, J. O., Sieffermann, R. G. & Page, S. E. 1992 The origin, development, present status and importance of the lowland peat swamp forests of Borneo. *Suo* **43**, 241–244.

Rieley, J. O., Page, S. E. & Setiadi, B. 1996*a* Distribution of peatlands in Indonesia. In *Global peat resources* (ed. E. Lappalainen), pp. 169–178. Jyväskylä, Finland: International Peat Society.

Rieley, J. O., Ahmad-Shah, A. A. & Brady, M. A. 1996*b* The extent and nature of tropical peat swamps. In *Tropical lowland peatlands of Southeast Asia* (ed. E. Maltby, C. P. Immirzi & R. J. Safford), pp. 17–53. Gland, Switzerland: IUCN.

Shepherd, P. A., Rieley, J. O. & Page, S. E. 1997 The relationship between vegetation and peat characteristics in the upper catchment of Sungai Sebangau, central Kalimantan, Indonesia. In *Biodiversity and sustainability of tropical peatlands* (ed. J. O. Rieley & S. E. Page), pp. 191–210. Cardigan, UK: Samara Publishing.

Shotyk, W. 1988 Review of the inorganic geochemistry of peats and peatland waters. *Earth Sci. Rev.* **25**, 95–176.

Sieffermann, R. G., Fournier, M., Truitomo, S., Sadelman, M. T. & Semah, A. M. 1988 Velocity of tropical peat accumulation in central Kalimantan, Borneo. In *Proceedings of the Eighth International Peat Congress, Leningrad, USSR*, vol. 1, pp. 90–98. Leningrad, USSR: International Peat Society.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Sparling, J. H. 1967 The occurrence of *Schoenus nigricans* L. in blanket bogs. I. Environmental conditions affecting the growth of *Schoenus nigricans* L. in blanket bogs. *J. Ecol.* **55**, 1–13.

Stoneman, R. 1997 Ecological studies in the Badas peat swamps, Brunei Darussalam. In *Biodiversity and sustainability of tropical peatlands* (ed. J. O. Rieley & S. E. Page), pp. 221–230. Cardigan, UK: Samara Publishing.

Symington, C. F. 1941 *Foresters' manual of Dipterocarps*. Malayan Forest Records, No. 16. Kuala Lumpur: Caxton Press.

Takahashi, H. & Yonetani, Y. 1997 Studies on microclimate and hydrology of peat swamp forest in central Kalimantan. In *Biodiversity and sustainability of tropical peatlands* (ed. J. O. Rieley & S. E. Page), pp. 179–187. Cardigan, UK: Samara Publishing.

Whitmore, T. C. (ed.) 1972*a* *Tree flora of Malaya*, vol. 1. Kuala Lumpur: Longman.

Whitmore, T. C. (ed.) 1972*b* *Tree flora of Malaya*, vol. 2. Kuala Lumpur: Longman.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES