ORGANIC MATTER DYNAMICS OF COASTAL PEAT DEPOSITS IN SUMATRA, INDONESIA

by

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ABSTRACT

Organic matter dynamics were investigated in the surface peat layer (acrotelm) in study sites traversing three raised ombrotrophic peat deposits, containing up to 3, 6 and 12 m, respectively, of peat located on the east coast of Sumatra, Indonesia. The three deposits were uniform in climate, topography, surficial geology and were under continuous forest cover. Increased peat depth and distance from the edge of the deposit was associated with important changes in species composition, structure and morphology. To account for the differences in peat depth, I hypothesized that the relative importance of: 1) peat age, 2) organic matter decomposition and 3) litter additions, in controlling peat accumulation varies among the three deposits.

Age differences, using ¹⁴C dating, did not account for variable peat accumulation. Peat at the clay-peat interface was approximately 4000 to 4500 years old in each study site, while acrotelm peat ranged from 45 to 660 years old. The relatively recent age of the acrotelm layer suggested that peat accumulation in the study sites was either at steady state or expanding. Older peat in this layer would have indicated surface degradation of the raised peat deposits. Small roots and root fragments in the acrotelm of the deep peat deposit were considerably younger than the matrix of amorphous peat.

Samples of acrotelm peat were incubated under aerobic conditions for 30-day periods in glass jars. There were no significant differences in peat respiration rates between samples at different moisture levels. Significantly higher respiration rates, however, were measured in acrotelm peat from the 12 m deposit compared with the same layer in the 9 and 6 m sites in the same deposit and in the sites on the 3 and 6 m deposits. Buried cotton strips disappeared at the same rate at all study sites. However, the disappearance of leaf litter from mesh bags was most rapid in the 3 m site and slowest in the 12 m site. Decay rates were mainly controlled by varying organic matter quality due to species composition differences across the gradient of increasing peat depth. Several chemical parameters were significantly correlated with indices of litter and peat decay in the following order of importance: soluble C fraction > lignin:N > C:N > P. Litter quality in the study sites was generally low compared to other tropical forests on nutrient poor soils.

Organic matter additions varied between the three peat deposits. Rates of small and fine litterfall declined significantly while small and fine root mass was increased across the gradient of increasing peat depth. Preliminary measurements of root growth into mesh bags of root-free peat indicated higher production of small roots in the

acrotelm of the 9 and 12 m peat sites. A continuous 20–40 cm thick mat of fine and small roots present in the 12 m site restricted aboveground litter fall from being preserved in the peat matrix below the root mat. The presence of the root mat suggested that aboveground organic additions contribute less to peat accumulation with increasing peat depth.

High water table levels were important in controlling peat accumulation and decay in the 3 and 6 m peat sites, while resource quality appeared more important in the 9 and 12 m sites. The results suggested that the increases in peat mass among the study sites were attributed mainly to increased additions of fine and small roots at the base of the acrotelm, rather than slower rates of aboveground litter decay at the top of the acrotelm.

The study concludes that several of the assumptions of the two-layer model for accumulation in *Sphagnum* peatlands do not apply directly to the deposits of woody peat in East Sumatra. The results were consistent, however, with a key assumption of the *Sphagnum* peat model that continued accumulation of peat is due to an increase in the mass entering the catotelm layer. The greater input of small roots of poor resource quality appeared to be the most important process contributing to peat accumulation among the study sites. The high root inputs, however, also appeared to promote the cessation of peat accumulation in the 12 m peat deposit. This and further studies should provide a better basis for more selective management of vegetation (species composition, stand structure, tree morphology, etc.) and environmental (moisture, temperature) variables in Sumatran peat deposits.

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CHAPTER 1

INTRODUCTION*

1.1 BACKGROUND

Although not generally recognized in scientific circles before the end of the 19th century, tropical peatlands cover large coastal areas in Southeast Asia. Peatlands, mainly in Malaysia, Papua New Guinea and Indonesia, range in area from 20 to 33 million hectares (Mha) (Immirzi *et al.* 1992). Indonesia contains about 20 Mha of mainly coastal peatlands, divided among Sumatra (8 Mha), Kalimantan (7 Mha) and Irian Jaya (5 Mha) (RePPProT 1988, 1990) (Figure 1–1). Over 8 Mha of Indonesia's coastal peatlands contain peat thicker than 2 m (Euroconsult 1984). Raised peat deposits of 10 to 17 m are found in Sumatra (Brady and Kosasih 1991, Diemont and Supardi 1987, Supardi *et al.* 1993), Kalimantan (Riely *et al.* 1992) and Irian Jaya (Brady *et al.* 1995). Anderson (1959) and Whitten *et al.* (1984) mention peat accumulations of 20 to 30 m, but did not provide details.

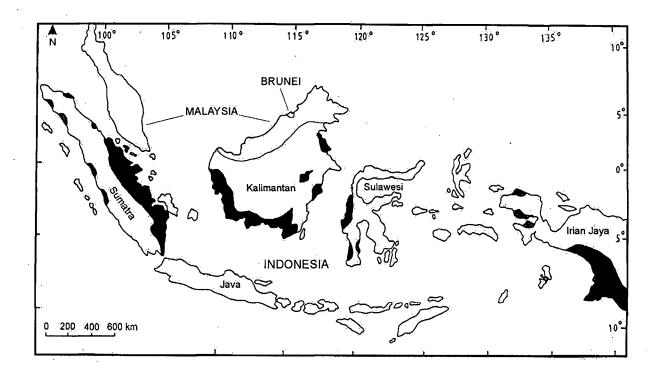


Figure 1-1. Approximate predisturbance boundaries of peatlands in Indonesia (after Collins et al. 1991).

^{*}Footnotes are given at the end of the Chapter.

The raised peat deposits in Southeast Asia contain mainly ombrogenous peat of recent origin. Much of the coastal peat in Southeast Asia began accumulating between 3500 and 5000 years before present (yBP). In Kalimantan, older deposits of up to 9000 yBP are located at slightly higher elevations and inland from the younger peat deposits on the coast (Sieffermann *et al.* 1988). Similar to the definition used for this peat type in the northern hemisphere (Moore and Bellamy 1974), ombrogenous tropical peatlands and peat are characterized by: a markedly convex surface; are rain-fed, with a raised water table (relative to the water table elevation in the local topography surrounding the peat deposit); are not subject to flooding from adjacent water sources such as rivers or tidal inundation; do not contain streams and rivers that flow from one side of the deposit to the other; have a soil pH of less than 4; and undergo a loss on ignition of more than 75% (Anderson 1964b, Andriesse 1974, 1988).

The physical and chemical properties have been described for lowland peat in Sumatra (Polak 1941, 1952, Suhardjo and Widjaja-Adhi 1976, Esterle *et al.* 1992), Borneo (Anderson 1961, 1964a, Driessen and Rochimah 1976) and Peninsular Malaysia (Coulter 1950, Tay 1969). Peat consists of the partially decomposed remains of the former forest. Well preserved woody materials are commonly found within the matrix of dark brown amorphous material. The overall properties of tropical peat are a result of several factors, including wood content, degree of decomposition, mineral admixtures (Ismail 1985), stratification and compaction (Bouman and Driessen 1985), which determine bulk density, hydraulic conductivity and water holding capacity (Driessen 1977).

Tropical peat is characterized by a low nutrient content and high acidity. The chemistry of peat is affected by many factors, including the nature of the original plant material, the supply of inorganic solutes, the activities of plants and animals including microorganisms, environmental conditions, and finally, the age and history of the peat (Clymo 1983, Given and Dickinson 191978). Peat contains the full range of chemical compounds found in the parent material. The inorganic geochemistry of undisturbed peat in East Sumatra has been characterized by lowash, low-sulphur, low-pH and low nutrient systems into which the flow of inorganic constituents is highly restricted (Neuzil *et al.* 1993). The organic fraction of peat consists largely of lignin, humic substances, and smaller amounts of hemicellulose, cellulose, proteins, waxes tannins and resins (Polak 1941, 1952, Coulter 1950). Lignin contents of 65–76% of dry mass have been reported in ombrogenous peat deposits in Sumatra (Hardon and Polak 1941) and Peninsular Malaysia (Coulter 1950), while lignin in peats of the northern hemisphere does not generally exceed 60% (Clymo 1983). Peat from East Sumatra was analyzed using nuclear magnetic resonance (¹³C NMR) techniques

to determine bulk organic chemical characteristics (Hatcher *et al.* 1989). The peat was found to be homogeneous with depth below the litter layer and showed similar characteristics when compared to ombrogenous peat from a deposit in New Hampshire, USA (Cameron 1987). Both contained substantial amounts of lignin derived from vascular plants and large amounts of aliphatic, noncarbohydrate materials most likely derived from algae or cuticular waxes (Cameron *et al.* 1989).

Tropical peatlands have been classified several ways for different purposes (IUCN *In press*).

Classifications have considered geographic location and topographic position (Rieley *et al.* 1992, Sieffermann *et al.* 1988); trophic status (Coulter 1957); vegetation communities (Anderson 1983); depth; nature of underlying strata; degree of decomposition and chemical properties (Driessen 1977, Soils Research Institute 1976); and fibre and maceral content (Esterle and Ferm 1994). Most classifications have been developed as tools for land-use planning and peatland development.

1.1.1 Peatland Development

Until the mid-1900s, the coastal peatlands of Indonesia remained largely forested (Endert 1920, Polak 1938, van de Koppel 1938). Flooding and intractable conditions made the peatlands relatively inaccessible, and compared to adjacent mineral soils they were generally considered of low potential for agriculture (Coulter 1957, Kostermans 1958, Polak 1950). Little was known about the coastal peatlands other than information from surveys and inventories for small-scale forest harvesting (Sewandono 1937) and horticulture (Polak 1938, 1950). The peatland forests in peninsular Malaysia and Sarawak were also harvested for timber. In Indonesia and Malaysia, foresters began collecting basic silvicultural data (Anderson 1959, 1961b, 1963, Wyatt-Smith, 1959, 1963a,1963b, Brunig 1961, 1969). Much of the information on peat swamp forest composition and structure collected in the 1950s and 1960s remains among the most up to date (IUCN *in press*).

With the growth of Indonesia's population in the 1960s and 1970s came increasing demands for timber and other forest products, food production, settlement areas and energy production (Hill 1991). The demands increased pressure for land development, particularly in marginal areas including coastal peatlands. Here, large tracts of unexploited land were less affected by the bureaucratic, political and cultural issues surrounding land title and ownership that affect settled regions throughout Indonesia (Donner 1987, Hanson and Koesoebiono 1979, World Bank 1990). In response to development pressures during the 1970s and 1980s, extensive tracts of coastal lowlands

and peatland in Sumatra and Kalimantan were exploited for government controlled agricultural and forestry projects (Whitten *et al.* 1987a).

One of the world's largest transmigration programs was responsible for the resettlement, between 1974 and 1989, of over 600 000 families from the populated islands of Java and Bali to Indonesia's outer Islands (Dick 1991). Government-sponsored settlement units ranging in area from 20 000 to 50 000 ha were established in newly cleared and drained swamplands, mainly in Sumatra (World Bank 1988). By 1989, about 1.3 Mha of coastal swampland had been opened. In addition, a similar or greater number of unsponsored transmigrant families (Swakarsa) moved into the lowlands and opened forested areas adjacent to the government schemes (Hanson 1981, World Bank 1988). Also during this period, forest concessions of up to 0.5 Mha in size were established in the coastal peatlands and timber was harvested under the Indonesian selective system (Donner 1987, Sutter 1989, World Bank 1990). At a smaller scale of use, peatlands were also opened for tree crop and timber estates (Sutter 1989, Review Indonesia 1992), and peat sod mining (Ministry of Mines and Energy 1987). A detailed account of the transmigration and forestry activities in Indonesia's coastal peatlands is provided in Appendix 1.

By the mid-1980s the difficulties of large-scale agricultural and forestry development of Indonesia's coastal peatlands became widely known. Acceptable rates of agricultural production were difficult to achieve, particularly in the deeper peat deposits (Ismunadji and Supardi 1984, World Bank 1988). In response, many farmers abandoned their land and left the transmigration settlements (GOI 1983, Hardjono 1986). Several settlements were abandoned entirely and were relocated to more suitable areas (Whitten *et al.* 1987a). Also during this period commercial logging exhausted much of the accessible peat swamp forests (Hardjono 1991, GOI/IIED 1985). Illegal or secondary logging of cut-over swamp forest remains common in regions still dependent on established sawmills, plywood and pulp industries (Danielson and Verheugt 1990, Brady and Kosasih 1992).

The rate of large-scale peatland conversion in Indonesia slowed during the latter half of the 1980s. Several factors contributed to the reduction. These included the high costs of government-sponsored swampland conversion (World Bank 1990) combined with low agricultural production (Driessen and Sudjadi 1984), and the limited success of transmigration schemes (Euroconsult 1984). In addition, conflicts with forestry concessions increased (Dick 1991, Myers 1991ab), and the emergence of numerous environmental impacts gained international attention

(Caufield 1985, Secrett 1986, Whitten *et al.* 1987a). Moreover, by 1985 overall self-sufficiency in rice production was achieved, which somewhat reduced the pressure to develop new agricultural lands.

New government policies focused attention on the redevelopment and improvement of existing settlements rather than opening new land (Ministry of Transmigration 1988). Also, programs were developed to encourage higher rates of spontaneous transmigration. At the same time, nation-wide environmental management and conservation policies were introduced that affected peatland development. Regulations were introduced that require more detailed development planning and a stronger focus on integrated resource management (Panayotou and Ashton 1992).

1.1.2 Environmental Effects of Peatland Development

During the 1980's it also became widely understood that forest clearing and peat drainage were causing serious environmental effects (Secrett 1986, World Bank 1988). Forest harvesting exposed the peat surface to direct sunlight leading to high surface temperatures and loss of surface peat moisture (Driessen and Sudjadi 1984). Slow or arrested forest regeneration following logging has been observed in peatlands in Sumatra (Kostermans 1958, Brady and Kosasih 1991), Kalimantan (Riswan 1981, Kartawinata and Vayda 1984) and Malaysia (Kochummen and Ng 1977). In peat areas cleared and drained for agricultural crops, farmers had to contend with severe hydrological and edaphic conditions including drought (Woods 1987, Leighton and Wirawan 1985), fire (Anderson 1983, Brady 1989, Malingreau *et al.* 1985), degradation and flooding (Chambers and Abdullah 1977, Chambers 1979, Elshof 1990), low fertility (Chew *et al.* 1978, Driessen and Sudewo 1977), acid sulphate toxicity (GOI 1983, Pons and van Breeman 1981), weeds and pests (Andriesse 1988, Koswara and Rumawas 1984), and disease (Caufield 1985).

During the 1970's and 1980's research on the effects of peatland conversion was limited mainly to broad-based land surveys and crop variety and fertilizer trials. Extensive baseline surveys recorded broad features of regional hydrology, chemical and physical soil properties and vegetation, including important descriptions of the structure and composition of peat forest types². The surveys provided basic information for the selection of forest sites to be converted to agriculture. They did not address the main factors controlling the peat-forming systems. Horticultural research in converted peatlands focused mainly on crop variety testing and fertilizer trials. Agricultural crop varieties were grown and maintained under controlled conditions at test farms in Sumatra and Kalimantan³.

Most studies described yields of different crop varieties on thin (1–2 m) peat under controlled conditions. The variety of peatland uses described above are reflected in the considerable variation in the classification and description of tropical peat as described above.

1.1.3 Growing Resource Demands and Peatland Sustainability

While the rate of swampland conversion declined in the late 1980s and early 1990s, Indonesia's population grew at a rate of 1.6% annually. The reliance on natural resources continued to increase. In absolute terms, the value added of primary commodities increased by 91% over the past 20 years and has been projected to increase by another 50% by the year 2010 (World Bank 1994). National planning targets call for an increase of 2.5% annually in agricultural production (BPS 1991). Almost 100 000 ha of new land must be put into agriculture to meet the targets. Despite these measures, increasing consumption and declines in production have led to the resumption in 1995 of rice imports (Arasu 1996). Demands for increased food production have required the government to reconsider policies on swampland development. In September 1995, it was announced that 1 Mha of peatlands in Central Kalimantan will be converted to agricultural production (FEER 1995). A recent nation-wide survey sponsored by the Ministry of Transmigration identified approximately 7 Mha of forest land outside Java considered suitable for conversion for settlements, cash crops, fruit trees, industrial crops, plantation forests, inland fisheries and aquaculture production (RePPProT 1990).

The forestry sector is also under increasing pressure to manage Indonesia's peatlands sustainably (Dick 1991). By the year 2000, annual demand for wood in Indonesia may double from it's 1990 level to 72 million cubic meters (FAO 1990a). In addition to the rising timber demands, the Indonesian forestry sector is under pressure to demonstrate that forests are being managed sustainably. The Ministry of Forestry has committed to meeting the provisions of the International Tropical Timber Organization (ITTO) for certification that wood product exports are from sustainably managed forests (ITTO 1990). As a result of these and other factors, the extensive tracts of swamp forest that were logged in the 1970s are receiving increased attention. The next harvesting period of the 40-year rotation approaches early in the next century.

The nature of the development pressures described above will require that Indonesian peatlands be increasingly exploited for multiple functions and uses. Single resource uses such as forestry or agriculture within a peat deposit, as occurred in the 1970s and 1980s, will become less common. In addition to multiple resource

exploitation, the new laws and policies provide the framework to ensure that conservation, biodiversity and environmental functions are to be retained in and around developed peatlands. However, the information acquired to date, mainly through baseline surveys and horticultural trials, does not provide the ecological understanding necessary for multiple use management of peatlands (Braatz 1993, Panayotou and Ashton 1992). Further, ecological understanding and management of peat-forming systems are complicated by the high spatial diversity found in Indonesian peatlands, relative to that of adjacent lowland forests on mineral soil (Anderson 1983). The diversity is characterized by large differences in peat depth and vegetation composition found within the coastal peat deposits of Sumatra, Kalimantan and Irian Jaya.

1.2 NATURE OF THE PROBLEM

Large areas of coastal peatlands contain relatively shallow peat, of 0.2 m to 1.5 m in thickness (Euroconsult 1984). The thin deposits of peat are being developed rapidly for agriculture and forestry. The potential to preserve the thin peat deposits is low. Other deposits, however, including coastal peat throughout the region and the higher elevation peats along inland river valleys in Central Kalimantan, are up to 17 m in depth. Recent retrospective studies, using radiocarbon dating techniques, have provided evidence that peat in the older (~9000 yBP) high deposits in Kalimantan is no longer accumulating and that the deposits may be degrading (Sieffermann 1990, Rieley *et al.* 1992, Neuzil *In press*). It has not been determined which of the coastal deposits of younger peat continue to accumulate peat, which have reached a steady state, and which are undergoing net decomposition. An understanding of the peat-forming process in the coastal deposits is needed as their land-use potential remains undefined. Knowing whether these deposits continue to accumulate peat, are in steady state or are degrading would influence their land-use status for single or multiple use purposes, or for conservation and protection.

The use of retrospective studies and radiocarbon dating to determine the current and future status of peatforming systems is limited by several important assumptions about the peat matrix during aging and by their limited
explanatory value. The historical studies should be complemented with a processed-based understanding of peatforming processes. The present study demonstrates that indicators used to evaluate and predict peat processes
should be based on an understanding of the factors (in addition to age) that control peat accumulation. To be useful
to planners and managers, such indicators should provide understanding of the edaphic, hydrological and botanical
components of the peat-forming system that can be practically managed.

1.2.1 Allogenic and Autogenic Factors of Peat Accumulation

Peat accumulation has been attributed to the two primary variables of water and ionic supply (Tallis 1983). Changes in these variables are either externally induced (allogenic) or self-induced (autogenic), and result chiefly from modifications to the hydrology or surface topography of peat deposits. It is well known that allogenic factors such as precipitation, radiation, temperature and local hydrology have influenced the development and differentiation of peatlands (Barber 1981, Moore and Bellamy 1974). The distribution, height and shape of raised peat deposits in Europe (Granlund 1932), the Soviet Union (Ivanov 1975) and North America (Damman 1977, Vitt 1994) have been strongly related to regimes of surplus moisture. The zonation of raised peat deposits corresponding to temperature isopleths is thought to be stronger at the northern limit of their range (Damman 1986, Almquist-Jacobson and Foster 1995).

In Southeast Asia, the lowland peat-forming systems are almost exclusively coastal and influenced by a hot and mostly humid climate (Anderson 1983). Variation in local hydrology of the peatlands is likely to be of greater influence than is climate. Most of the coastal peatlands are located in deltaic areas where the thinner peats (1–2 m) are subject to flooding from adjacent rivers, while the deeper peats (<3 m) receive rainwater only. The importance of geomorphology and local hydrology on the spatial distribution of tropical peat deposits has been demonstrated on the islands of Sumatra (Cecil *et al.* 1993, Esterle and Ferm 1994) and Borneo (Winston 1994).

Similar to temperate peatlands, once tropical peats have accumulated to a depth above which they are not affected by flooding from adjacent rivers, they may respond less to allogenic factors, and more to autogenic processes associated with their own composition and hydrology. There are several autogenic processes that control peat-forming systems, each operating at different scales of organization (Clymo 1983). Large-scale processes include the plant community dynamics associated with the catena⁴ of forests from the edge to the centre of each raised peat deposit. Smaller-scale processes involve organic matter fixation and decay within layers of peat. These biological processes in turn affect important abiotic factors of the peat-forming system such as water movement through peat.

There are several published studies of plant communities in the coastal peatlands of Indonesia and Malaysia. Most include surveys of vegetation composition, canopy height and peat depth. Anderson (1961b, 1963, 1964b, 1976a, 1983) provided detailed vegetation studies of peat deposits in Borneo, and Wyatt-Smith (1959, 1961,

1963a) described the peat swamp forests in Peninsular Malaysia. Endert (1920), Sewandono (1937, 1938), Kostermans (1958), Laumonier (1980), Silvius et al. (1984), Whitten et al. (1984) and Brady and Kosasih (1991), described peat swamp forests along the east coast of Sumatra. Many of the surveys recognized a sequential, often concentric pattern of forest types across raised peat deposits that can be loosely related to increasing peat depth. Among the raised peat deposits, the forest types share certain common features of species composition and structure. Tree species of Campnosperma, Gonystylus, Shorea, Palaquium and Dyera are commonly found on thin peats (1–6 m) throughout Indonesia. Thicker deposits of peats (6–15 m) often contain species including Tristania, Calophyllum, Cratoxylon, Combretocarpus, Shorea, and Diospyros. Several species of Pandanus, Nepenthes and Freycinetia are common in the understory.

Anderson (1961b) described, in perhaps the most detail published, a catenary sequence of forest types in the peat swamp forests of Sarawak and Brunei. He distinguished a concentric pattern of six forest types that differed in composition and structure over a gradient of peat depth and location. Stands on thin layers of peat at the edges of peat deposits showed high rates of growth, species richness and standing biomass. With increasing peat depth, tree heights, diameters, and species numbers declined, while stem density increased. On the deepest (10–17 m) peat in the central expanse of peat deposits, the forest types were characterized by a low canopy of pole-sized trees. These forest types have been referred to as "Padang forest".

The factors that govern these changes in forest types are not well understood, but have been attributed to declines in nutrient and moisture availability in the deeper peat (Anderson 1961b, Brünig 1971, Whitmore 1984a). Few plant roots can reach down to the underlying soil layers, and sediment-laden river waters rarely flood the higher elevation peat (Cameron *et al.* 1989, Driessen 1977). As a result, nutrients enter the peat swamps mainly through precipitation and dust fall. The seminal work of J.A.R. Anderson in the 1960's and 1970's in Sarawak suggested that declining soil nutrition is the single most important factor determining the declining stature of forest stands in deeper peat. Tree height and diameter changes are supported by numerous vegetation surveys. In Sumatra, Suhardjo and Widjaja-Adhi (1976) demonstrated a clear trend of declining soil macronutrients and tree stature towards the central expanse of peat deposits in Riau. There are, however, no published field studies on forest nutrient and organic matter dynamics which explain how plant and soil processes lead simultaneously to increased peat accumulation and declining forest stature (Brunig 1990).

Our current understanding of organic matter fixation and decay processes in tropical peatlands has come mainly from retrospective studies. Age (¹⁴C) profiles combined with texture and fragment analyses have been used to reconstruct plant communities and the environmental conditions of deposition within peat profiles. Anderson (1961b) was one of the first to use age profiles to calculate peat accumulation rates in the Baram River peatlands of Sarawak. Over about 4000 years (4 kyr), net accumulation rates decreased upsection from 4 to <2 mm a⁻¹. Sieffermann (1988) and Sieffermann *et al.* (1988) published studies of historical trends of peat accumulation in Kalimantan peatlands. They calculated net accumulation rates near Palangkaraya by comparing ¹⁴C ages at different peat depths. Using the age vs' depth curve, they concluded that maximum rates of accumulation near the base of the deepest peat deposits were about 2 mm a⁻¹, with lower accumulation rates towards the surface of deposits. Diemont and Supardi (1987) and Supardi *et al.* (1993) found a similar pattern of rates decreasing upsection in deep peat deposits located in Riau Province, Sumatra.

Neuzil (*In press*) summarized peat accumulation rates recorded from tropical ombrogenous deposits. The rates were derived from ¹⁴C retrospective data and assume there is no further decay of peat below the water table. Average rates within deposits ranged from 0.9 mm a⁻¹ in the Kalimantan "high peat" to 3.1 mm a⁻¹ for deep (10–15 m) deposits in Sumatra. Thinner deposits of similar basal age (3–4 yBP) occur in Sumatra and Kalimantan and reflect slower peat accumulation rates. For comparison, the range of tropical peat accumulation rates exceeds the range of average temperate and boreal peat accumulation rates (<0.8 mm a⁻¹) by a factor of about three to five.

The use of ¹⁴C ages to calculate peat accumulation rates assumes no further decay of, or plant inputs to buried peat layers. Clymo (1984) summarized the evidence showing that decay occurs throughout the peat deposit. He cautioned that age-depth profiles do not fully explain the processes involved in peat accumulation. Few age studies have analyzed the surface layers in peat-forming systems and the ages of the different fragments contained in these layers. It is not known why different rates of accumulation occur in peat deposits of similar age, and which peat deposits continue to accumulate peat, which are in steady state, and which are degrading.

Historical patterns of peat accumulation in Indonesia have recently been studied using coal petrographic techniques (Cameron *et al.* 1989, Esterle and Ferm 1994, Grady *et al.* 1993). Geochemical, environmental and climatic conditions have been reconstructed by comparing megascopic (larger plant parts), microscopic (particle size, maceral⁵ content) and chemical (*e.g.*, sulphur, ash) characteristics of peat. Vertical sequences of peat were analyzed from deposits in Sumatra (Esterle and Ferm 1994) and Kalimantan (Moore and Hilbert 1992, Dehmer

1993). The studies show how peat layers differ both in texture, because of species changes, and in the degree of decay as determined by texture analysis⁶. The petrographic studies focus on the spatial variability of peat types buried within deposits and their relationships to stratigraphic variations in ancient coal types.

Retrospective studies, using ¹⁴C ages and petrographic techniques, have advanced our understanding of tropical peat-forming systems. However, they are imperfect reconstructions of plant communities and environmental conditions of peat deposition. The studies do not reveal the process by which plant matter is arranged within the peat mass. Furthermore, different plant communities may have dissimilar processes of peat formation. For example, Covington and Raymond (1989) studied root/shoot ratios in mangrove peat. Their results suggested that high root/shoot ratios were due to the presence of a root mat that prevents the input of aerial debris to peat. In contrast, previous palynological studies of mangrove peat linked the high root/shoot ratios to changes in salinity and tidal effects. As another example, Shearer and Moore (1995) analyzed fragments of peat from Kalimantan and could not find angiosperm xylem tissue, leaves, cuticle, reproductive organs, seeds and stems. They attributed the absence of plant components to high rates of decomposition in aerial litter above the peat surface.

Reconstruction studies reveal the nature of material which remains in peat after the decay process is at an advanced stage. They also provide some information on the conditions of decay, but do not provide an understanding of the processes of organic matter fixation and decay before, during and after the preservation of plant material as peat. For example, plant matter buried in the upper layers of peat is subsequently affected by water table fluctuations (Moore and Shearer 1993) and ingrowth of plant roots (Wallen 1986, 1993), and the effects continue until the last stages of the formation of waterlogged peat.

1.2.2 Process Models of Peat Fixation and Decay

The processes of organic matter fixation and decay have been studied in detail in temperate and boreal zones. Most studies have focused on *Sphagnum*-dominated peat-forming systems. Known since Newton's day (Clymo 1983), peat accumulates as a result of the imbalance between processes controlling organic matter fixation (plant litter and sloughed root production), and decay. The simplest quantitative model of peat accumulation is shown by the equation,

$$x = \frac{p}{k} \left(1 - e^{-kt} \right) \tag{1}$$

where x is the accumulated mass of peat measured from the surface downwards, p is the rate of addition of plant dry mass, k is the decay rate, and t is the age of peat at a given depth relative to that at the surface.

Organic matter decay is defined here according to Swift *et al.* (1979), as the sum mass loss resulting from catabolism, comminution and leaching of water-soluble materials. Although different plant materials decay at different rates and patterns, the negative exponential model of decay is commonly used in the peat accumulation model. A linear model predicts complete disappearance and is not plausible in a peat-forming system. More complex models (*e.g.*, quadratic) are likely to better explain the disappearance of some organic materials, but may not be important as partially decayed matter is eventually incorporated into the peat layer. Decay rates have been reviewed for temperate peatlands by Heal *et al.* (1978), for tundra peats by Heal *et al.* (1975, 1981) and Flanagan and Bunnell (1980), and for peatlands in general, by Clymo (1983). Published decay rates of tropical peat could not be found.

Another important observation earlier in this century was the structural and functional differences between surface and subsurface peat layers. Ivanov (1981) defined the boundary between the 0–50 cm surface layer of live plants, litter and aerobic peat, and the thicker mainly anaerobic layer of peat proper, as the mean depth of the minimum water table in summer. The two layers have been referred to, respectively, as 'acrotelm' and 'catotelm' (Ingram 1978) and are used here. In the entire peat mass, there is a sharp transition between the faster rates of decay (10⁻²–10⁻³ a⁻¹) found in the aerobic layer and slower rates of decay (10⁻⁴–10⁻⁵ a⁻¹) in the subsurface anaerobic peat layer. Clymo (1983) reviewed the few studies of decay rates in the catotelm of temperate peatlands. These rates range from one to ten percent of decay rates in the acrotelm layer.

Moisture saturation and low oxygen concentration have generally been considered the dominant factors inhibiting decomposition of peat. However, at larger spatial scales, Ingram (1982) demonstrated that peat-forming systems are constrained by the groundwater mound theory— where unconstrained by local topography, the lateral and vertical dimensions of peat deposits are controlled by hydrological factors such as rates of recharge and hydraulic conductivity. Other factors controlling peat accumulation and decomposition include temperature, surficial geology, nutrients, organic matter quality, allelopathy and plant physiology (Gore 1983). Clymo (1983) used the two layer concept to expand the basic model of peat growth,

$$x_{total} = x_A(t_C) + x_C(\infty)$$
 (2)

where x_{total} is the total mass of peat, x_A is the mass of the acrotelm layer with a characteristic time t that matter stays in the aerobic zone before being immersed in the rising catotelm layer, and $x_C(\infty)$ is the steady state mass in the anaerobic zone.

The two-layer model (eq. 2) has been used successfully to predict historical rates of peat accumulation in several *Sphagnum*-dominated raised peat deposits in temperate and tundra regions (reviewed by Clymo 1984, 1987, 1993). Clymo's model of *Sphagnum* peat accumulation is based on several assumptions about plant and hydrological conditions in both the acrotelm and catotelm layers including:

- vegetation inputs to the acrotelm are unchanged from year to year and productivity is relatively constant during peat accumulation,
- the acrotelm is between 20-50 cm thick and remains constant in depth and mass during peat accumulation,
- about 80-90% of the dry matter in the acrotelm is lost to decay before entering the catotelm,
- the boundary between the acrotelm and catotelm is always at approximately the same depth below the peat surface,
- a decrease in the depth of the acrotelm layer is associated with a decrease in the amount of decay before
 preservation and an increase in the amount of plant mass entering the catotelm layer, and is the most important
 means by which the total depth of peat can be increased,
- no fresh plant material is added to peat in the acrotelm or catotelm once below the peat surface,
- decay processes occur in the catotelm and are similar to those in the acrotelm, but are slower because of anaerobic conditions and smaller temperature fluctuations.

1.2.3 Tropical Peat Accumulation

The two-layer model (eq. 2) has not been applied to tropical peatlands. Holocene peat deposits are found on coastal plains in both temperate (Moore and Bellamy 1974) and tropical (Andriesse 1988) regions. Peat deposits in both regions are similar in size with radii extending from several to tens of kilometers. However, there are large differences in the climate and vegetation between the regions. Annual rainfall rates may be comparable between the regions (1500–3000 mm), but tropical peat accumulates in conditions of higher and more constant air temperature. The important effects of increasing temperatures on soil microbial activity and organic matter decay are well

documented (Damman 1986, Tate 1977, 1980, Swift et al. 1979). The effects of higher and more constant temperatures on plant and litter production also occur, but do not appear to be as well established (Vogt et al. 1986).

Botanically, tropical peatlands contain a greater diversity of species and lifeforms than found in temperate regions. The coastal peatlands are predominantly forested and possess a catena of forest types associated generally with increasing peat depth (Anderson 1983). As a result, the underlying peat originates from woody matter of mixed composition and morphology, rather than from *Sphagnum*-dominated vegetation. Recent detailed studies have shown large spatial differences in peat texture and composition within deposits. Esterle and Ferm (1994) described the physical changes in surface peat along a gradient of increasing peat depth in a deposit along the Batang Hari River in Sumatra. The peat changed from sapric-textured peat of high wood content in the shallow (3 m) peat, to fibric-textured peat of high root content in the deep (8 m) peat. The changes suggest slower decay rates in the surface layers of the deep peat deposit. Similarly, using geochemical analyses, Dehmer (1993) inferred slower decay rates in the surface layers of a deep (12 m) peat deposit in Kalimantan. Measures of actual decay rates, however, have not been published for peatlands in Southeast Asia.

Slower decay and increased preservation in the fibric surface layer of the thicker peat deposits are consistent with the two-layer model (eq. 2) of accumulation for *Sphagnum* peat. Winston (1994) compared the theoretical predictions of the model with surveyed profiles of tropical peat deposits. The model was calibrated to predict the maximum height and lateral extent of peat domes in Sarawak. The assumptions were that water tables rise and decay rates decline with increasing peat accumulation and anaerobic decay.

Although some palynological and geochemical studies of preserved peat in the catotelm layer suggest a link in deeper peat deposits between rising water tables and increased surface preservation, this effect has not been tested in the acrotelm peat layer. Water table levels have not been monitored across peat deposits. Moreover, results of recent petrographic analyses of Indonesian peat contradict the rising water table effect. Grady *et al.* (1993) analyzed the maceral content⁷ of peat from different layers of a deep deposit near Siaksriindrapura, Riau. He assumed that increased fungal degradation⁸ of plant cells in peat is evidence of higher oxygen levels in peat during degradation. The results of the maceral study suggested that the root-dominated fibric peat found in deep deposits is more aerobic than that in wood-dominated sapric peat found in thin deposits. Even in this situation, the water table rises as peat accumulates and the catotelm is below the water table year round. The maceral evidence implies that

peat accumulation in deeper peat deposits may be associated more with drier surface or acrotelm conditions and changes in plants, rather than with a rising water table as assumed by Clymo's two-layer model (eq. 2) and the results both of Esterle and Ferm (*ibid.*) and Dehmer (*ibid.*).

In the present study, I attempt to resolve the contradictory interpretations provided by the different analyses of preserved peat. This is accomplished by providing a better understanding of the fixation and decay processes of organic matter located in the zones of active peat preservation—the aerial litter layer, the acrotelm layer, and at the acrotelm-catotelm boundary—which cannot be fully assessed using the petrograhic techniques and historical analyses described above. Because of the important climatic and botanical differences between temperate and tropical peatlands, it is uncertain whether the assumptions of the two-layer model (eq. 2) for *Sphagnum* peat are valid for peat accumulation in tropical peatlands. Some of the model's assumptions may apply directly, but some may need to be modified or eliminated. Finally, the model may require new assumptions to adequately account for peat accumulation in tropical peatlands.

1.3 STUDY QUESTIONS

The need to manage peatlands requires that planners and resource managers better understand the main components and processes of peat-forming systems. These include vegetation, hydrology and soil. In the past this understanding has come from experience in temperate peatlands where peat accumulation processes are relatively well understood. Observed rates of *Sphagnum* peat accumulation have been explained by theoretical and quantitative models. The management implications derived from the models have focused mainly on water table control.

The *Sphagnum*-based models have not been applied to tropical peatlands where accumulation rates are several times faster, average ground temperatures are much higher, peat originates largely from trees and the hydrological conditions remain unstudied. In addition, increased peat accumulation is associated with changes in forest composition, physiognomy and structure. Although the hydrology component is likely to be important in tropical peats, the importance of the other components remains unknown. Before the model of *Sphagnum* peat accumulation can be applied to tropical peatlands two general questions should be answered:

1) How do allogenic (climate, hydrology) and autogenic (vegetation) factors vary with increasing depths of tropical peat? and

2) What are the effects of increasing peat depth on the three main components of Clymo's peat accumulation model?

In the present study I examine five questions related to the model components of age, plant matter additions and decay in the coastal peat deposits of East Sumatra:

- How much does peat age vary in acrotelm layers of different peat deposits? Which of the Sumatra peat deposits continue to accumulate peat, which are in steady state, and which are undergoing net decomposition?
- The *Sphagnum* model assumes that 10 to 20% of dry matter in the acrotelm is incorporated into the catotelm.

 But, do decay rates of aerial litter, acrotelm and upper catotelm layers vary with increasing peat depth? If so, which environmental and edaphic factors have the greatest effect(s) on decay processes?
- The *Sphagnum* model assumes that deeper peat deposits contain a higher water table and thinner acrotelm layer. Does the acrotelm layer in tropical peat change in depth with increasing peat accumulation?
- The Sphagnum model assumes that the addition of organic matter to peat is constant. How do the vegetation changes associated with increasing peat depth affect the quality, quantity and location of litter additions to tropical peat?
- How can an improved understanding of peat accumulation processes be used for the planning and management
 of multiple use activities in the coastal peat deposits of East Sumatra?

The costs of not improving our understanding of tropical peats are increasing. Large areas of peatland in Sumatra and Kalimantan were developed in the 1970's and 1980's. The occupied areas of these peatlands remain underutilized, while large areas have been abandoned with little current value for agriculture, forestry, recreation or conservation purposes. Moreover, plans call for the continued conversion of virgin peatlands for various new development schemes. As more peatlands are destroyed, those remaining under forest cover will require more intensive management for multiple uses.

A better understanding of how peat accumulates in tropical peatlands would allow managers to identify which peat deposits can be developed and managed, and those that should be protected. Deposits in which peat is actively accumulating or in steady state may be given higher conservation status than those that are degrading and undergoing changes towards conditions found in surrounding forests on minerotrophic soils. To date, this type of

criterion has not been used in Indonesian land use planning. A model of tropical peat accumulation may reveal other management strategies in addition to water table control—the sole management tool currently used. Preliminary results from the present investigation suggest that peat deposits of increased depth may be influenced by other factors that affect peat independently from the effects of water.

1.4 OBJECTIVES AND DESIGN OF THE STUDY

The studies and surveys reviewed in Section 1.2 show that vegetation and moisture conditions change with increasing peat depth in tropical peatlands. Although a quantitative model has been developed for *Sphagnum* peat accumulation in temperate regions, none has been devised for tropical peatlands. Because the main components of the tropical model are peat age, decay, and plant matter additions, a separate model is proposed for the present peats. For this, the overall objectives of the present study were to determine: 1) how the components of the model vary with increasing peat depth; and 2) to what extent the model assumptions for *Sphagnum* peat accumulation are valid for tropical peatlands.

Three raised peat deposits located on the east coast of Sumatra, Indonesia were studied (Figure 1–2). The central expanses of the three peat deposits are 3, 6 and 12 m in depth, respectively. The peat deposits were selected because they have soil, hydrological and vegetation characteristics that are representative of other coastal peatlands in Sumatra of similar peat depth (Table 1-1)⁹.

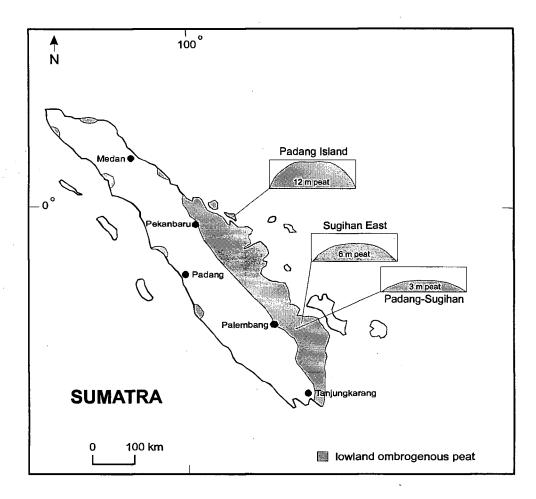


Figure 1-2. Coastal peatlands in Sumatra and location of the three peat deposits of 3, 6 and 12 m depth.

Table 1–1. Location, size and characteristics of the raised peat deposits in Sumatra selected for study.

	Conditions			
Study area name	Area of peat deposit (ha)	Max. peat depth* (m)	Vegetation cover	Drainage regime
1. Padang-Sugihan	89 300	3	primary forest	unmanaged
2. Sugihan East	~160 000	6	primary forest	unmanaged
3. Padang Island	~100 000	12	primary forest	unmanaged

^{*}Approximate depth of peat at study areas in central expanse area.

Field and laboratory investigations of the three peat deposits were undertaken to: 1) document vegetation composition and structure of forest types associated with increasing peat depth; 2) measure the amplitude and frequency of water table and ground temperature fluctuations, and the edaphic conditions in peat deposits of increasing depth; 3) determine ¹⁴C ages of peat constituents in acrotelm and catotelm layers; 4) describe the current

degree of humification in acrotelm and upper catotelm layers and measure variation of decay rates under field and laboratory conditions; 5) estimate relative quantitative (mass) and qualitative (organic matter chemistry) contributions of aboveground and belowground plant matter to acrotelm and catotelm peat layers; and 6) identify management interventions that incorporate an understanding of the allogenic and autogenic factors controlling peat accumulation.

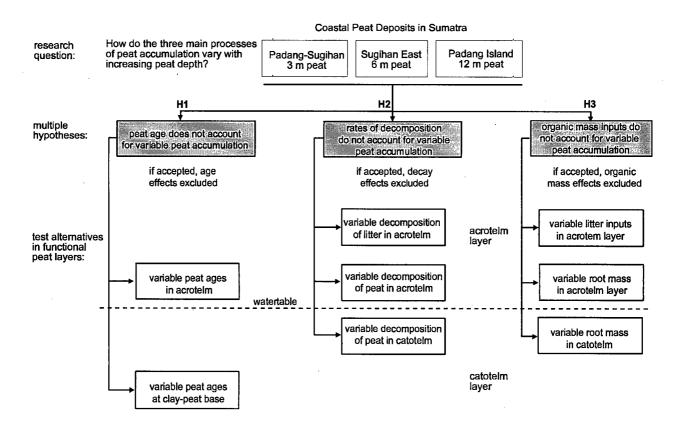


Figure 1–3. Diagram of peat study framework used to organize series of alternative and competing hypotheses that explain changes in peat accumulation processes associated with increasing peat depth.

Multiple working hypotheses (Chamberlain 1890, Platt 1964), organized according to the framework in Figure 1–3, address each component of the two-layer peat model (eq. 2), including peat age, decay, and plant matter. The framework incorporates the vertical layering of peat above and below the water table in the central expanse of the three deposits. The hypotheses related to peat age, decay, and plant matter may or may not be mutually exclusive. The order in which they are shown in Figure 1–3 reflects the increasing uncertainty, due to methodological limitations, of being able to accept or reject the null hypotheses. For example, excluding age effects

in the catotelm may be more certain than excluding root additions in the same layer. This is because aging techniques using ¹⁴C are more well developed than techniques for measuring root additions which involve production and mortality (Kurz and Kimmins 1987).

The present study was not concerned with questions related to the potential upper limits of tropical peat accumulation, or to the lateral dimensions of peat deposits. Much of this is covered by Winston (1994), who addressed issues of vertical and lateral growth potential in tropical peatlands. He compared theoretical predictions of the *Sphagnum* peat model (eq. 2) with observed profiles of peat deposits in Sarawak. The model predictions corresponded well with observed profiles. However, as discussed in Section 1.2 above, many of the assumptions about vegetation and moisture used as boundary conditions for the model have not been verified by field studies.

Study areas were located in forest types occupying the central expanse ¹⁰ of the three raised peat deposits. The areas were selected to represent the most advanced stage of development on each deposit as reflected by maximum peat depth. The field studies were constrained by several factors including: 1) lack of background information and published studies on organic matter dynamics in tropical peat ecosystems, 2) distances between peat formations, 3) difficult access to the central expanse of the three peat deposits because of tidal restrictions, long walking distances, inclement weather, forest fires and animal hazards, and 4) limited time and funds to collect intraseasonal and intra-annual data from all study sites.

During and following the field studies, the description, sampling and monitoring activities in the study areas were supported with laboratory studies to further assess the components of the peat accumulation model (Figure 1–4). In particular, hypotheses related to the decay component of the model were further examined under simpler and more controlled conditions than in the field. To further assess the allogenic and autogenic controls on organic matter decay, peat samples from the study sites were incubated in the laboratory at different levels of moisture, temperature and substrate additions that reflected the range of site conditions recorded during the field studies. Further, decay potential was related to the age and organic chemistry of peat constituents in samples from surface and subsurface layers (Figure 1–4). Combining the field studies with the laboratory experiments ensured that the study results are applicable in the real world from which the hypotheses that are to be tested were derived (Hairston 1989).

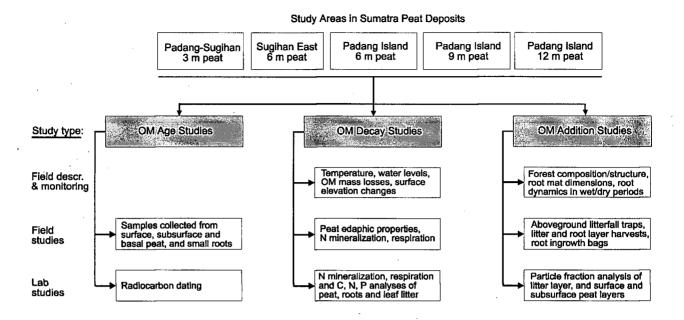


Figure 1–4. Flow chart illustrates the field and laboratory components of the peat accumulation study.

1.5 ORGANIZATION OF THE STUDY

The study is divided into seven chapters. Chapter two explains the field and laboratory study methods. Climate conditions, vegetation characteristics, and the environmental and edaphic conditions of peat in the study areas are presented in Chapter Three. Results of the main studies on peat age, decay and plant additions are presented in Chapter Four. A discussion and synthesis of the vegetation and environmental controls on organic dynamics is provided in Chapter Five. The findings of the study are used to identify planning and management strategies consistent with maintaining the ombrogenous conditions of coastal peatlands subject to multiple use.

The Bibliography lists published and unpublished material from Sumatra and other peatland areas of Indonesia and Southeast Asia. Numerous unpublished Indonesian-language reports are listed with English translations by the author. These reports contain valuable biophysical descriptions and laboratory results of environmental baseline information collected in the 1960's and 1970's for many peatlands that have since been altered by commercial logging, or converted for agricultural development.

FOOTNOTES

¹Relevant legislation includes: Regulation no. 29 (1986) and 51 (1993) concerning environmental impact assessment, Law no. 5 (1990) concerning ecosystem conservation and protection, Regulation no. 27 (1991) concerning the protection and conservation of swampland, Law no. 24 (1992) concerning spatial planning and the provision of a framework to identify conservation areas, and Regulation no. 64 (1993) concerning swampland reclamation procedures.

²Examples of baseline surveys include: Institute Pertanian Bogor 1969a, 1969b, 1975, 1976a,b,c&d, 1978b&c, 1980c, 1982, 1984, MPW 1977, Soeriaatmadja 1978, SRI 1973,1976, Suhardjo and Widjaja-Adhi 1976, UNSRI 1982b, Zahri 1982.

³Examples of horticultural research in peatlands include: Anwarhamand and Sulaiman 1984, Basa *et al.* 1983, Institute Pertanian Bogor 1977, 1978a, 1980a&b, IRRI 1984a&b, Noeerjamsi and Hidayat 1974, Partohardjono and Basa 1985, Polak and Soepraptohardjo 1951, Rochim and Basa 1983, Rumawas 1984, Sastrosoedarjo 1985.

⁴Anderson (1961b) used the term "catenary stages" to refer to the sequential pattern of forest types found in raised

peat deposits in Sarawak. The term is borrowed from soil science and refers to soils comprised of the same parent material that differ in soil-water relations along a transect or gradient.

⁵Complex organic compounds found in peat and coal and identified by colour, translucency and other optical properties, and the degree of fragmentation and degradation (Esterle *et al.* 1989).

⁶Peat has been classified according to stages of decay. The Von Post scale recognizes ten (H1-H10) stages. The scale has been narrowed to three classes of increasing decay (fibric, mesic and sapric types). Farnham and Finney (1965) defined the three classes quantitatively by analysis of fibre content and size.

⁷A petrographic technique first developed to study coal.

⁸Indicated by higher levels of inertinite (high O/C ratio) and degraded huminite maceral groups. The greater degradation of huminite cellular debris is interpreted to be the result of fungal activity that increases in response to increasingly aerobic conditions (Grady *et al.* 1993).

⁹As could be derived from the published surveys and studies reviewed above.

¹⁰The inner flat area of raised peat deposits.

CHAPTER 2

METHODS

2.1 SELECTION OF THE STUDY SITES

Five study sites were located in the central expanse of three raised peat deposits on the east coast of Sumatra (Figure 1–2). The sites were selected to represent advanced stages of development in each deposit as reflected by maximum peat depth and distance from the lagg¹. Preliminary vegetation surveys performed for this study showed that the central expanse of the Padang–Sugihan (3 m peat) and the Sugihan East (6 m peat) deposits in South Sumatra contained mixed forest types (Table 2–1, Figure 2–1). Surveys of the deep peat (12 m) deposit on Padang Island in Riau revealed a catena of three main forest types. Mixed forest occurred on the lagg and rand² areas. Tall and low pole forest types were found in deeper peat (9–12 m), with the latter occurring towards the central expanse of the peat deposit (Figure 2–2). Before detailed studies commenced, several peat deposits near the three study areas were also surveyed (Figure 2–1 and Figure 2–2). The adjacent deposits were used as reference areas to determine whether the study areas were representative of peatland conditions in the region. The five study sites described above are referred to hereinafter by acronyms according to their location and peat depth: PS3, SE6, PI6, PI9 and PI12 (Table 2–1).

Table 2-1. Characteristics of study sites.

No.	Peat deposit	Province	Location in peat deposit	Max. peat depth (m)	Distance to lagg (km)	Dominant forest type	Study site symbol
1	Padang-Sugihan	South Sumatra	Central expanse	3	12	mixed	PS3
2	Sugihan East	South Sumatra	Central expanse	6	15	mixed	SE6
3a	Padang Island	Riau	Outer rand	6	8	mixed	PI6
3b	Padang Island	Riau	Inner rand	9	10	tall pole	PI9
3c	Padang Island	Riau	Central expanse	12	12	low pole	PI12

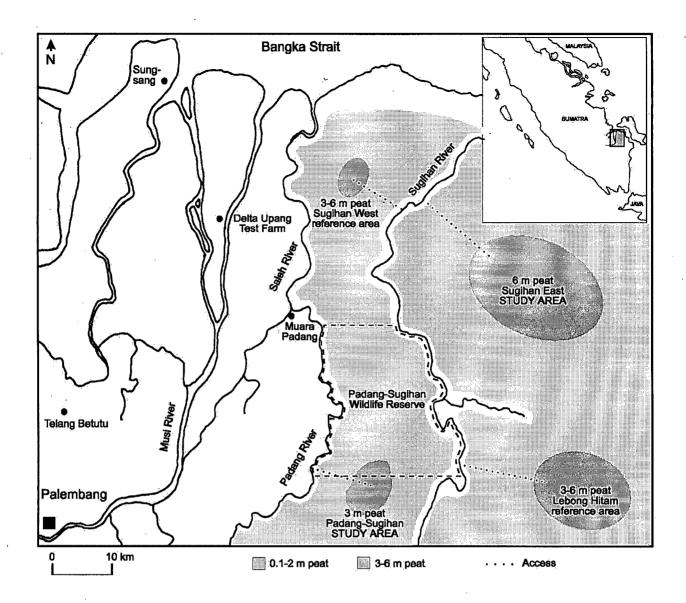


Figure 2–1. Location of study sites in South Sumatra. Reference areas are peat deposits with similar features. Boundaries of shallow and deep peat deposits are approximate, based on field surveys and interpretation of aerial photographs. Not all peatlands are shown.

2.1.1 Padang Sugihan Peat Deposit

The PS3 study site was located in the southern portion of the Sugihan-Padang Elephant Reserve (Suaka Marga Padang-Sugihan) in Musi-Banyuasin Regency, South Sumatra Province (Figure 2–1). The area was blanketed with peat measuring up to 3 m thick and covered by a mixed-species forest type reaching 40 m in height. The shape of the forest canopy was highly irregular. This forest type in Sumatra has been referred to as "chablis" by Laumonier (1980) and Huc and Rosalina (1981).

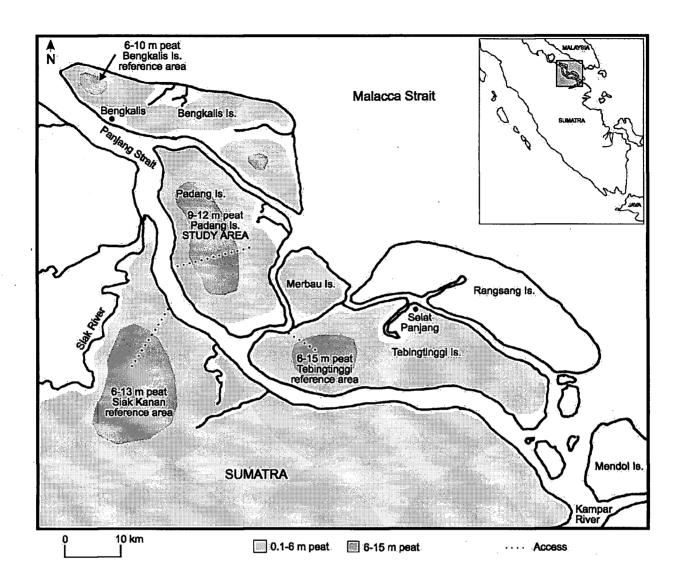


Figure 2–2. Location of study sites in Riau, Sumatra. Reference areas are peat deposits with similar features. Boundaries of shallow and deep peat deposits are approximate, based on field surveys and interpretation of aerial photographs. Not all peatlands are shown.

Preliminary surveys during the study showed that dominant tree species include *Gonystylus bancanus*, *Shorea leprosula*, *Palaquium* spp., *Ganua motleyana*, *Campnosperma auriculata*. A dense shrub canopy dominated by *Licuala spinosa* and *Salacca* spp. lies between 4 and 6 m in height. The vegetation and soil conditions in the PS3 study area are similar to those described in published surveys (Thorenaar 1924, 1927, Bianchi 1941, Kostermans 1958, Laumonier 1980, Whitten *et al.* 1984) of the adjacent reference areas (Figure 2–1). The comparison indicated

that the PS3 study site was similar to the mixed chablis forest on the central expanse of other medium depth peat deposits found elsewhere in the region.

Prior to being gazetted as a wildlife reserve in 1983, the Padang–Sugihan area was classified by the Forestry Ministry as production forest. It was surveyed for commercial timber value in 1970 and 1971 (Department of Agriculture 1970, 1971a). The forest was selectively logged from the early to the mid 1970's. The cutting appears to have been highly selective as existing stumps of the harvested trees are widely dispersed (average of 2 to 4 stumps per ha) and many large trees remain standing. The small canals dug through the forest to haul out logs were also widely dispersed, but could still be identified.

In the late 1970's the area was reclassified for transmigration development. Extensive soil, peat depth, hydrology and vegetation surveys were made of the unmanaged forest prior to development (Institute Pertanian Bogor 1982). The survey data show that the original conditions in the peat swamp were similar to the existing soil, vegetation and hydrology conditions of the reference areas at Sugihan West and Lebong Hitam (Figure 2–1). Initial settlement construction activities included the excavation of seven 15 m wide primary drainage canals linking the Sugihan and Padang Rivers (92 km total). Approximately 670 km of smaller secondary canals were excavated perpendicular to the primary canals for peat drainage. Further descriptions of the settlement preparation activities are described by MacKinnon and Setiono (1983) and Nash and Nash (1985a and 1985b).

The Padang–Sugihan area was reclassified again in 1983. The forest concession was canceled and the forest (77000 ha) then became the Padang–Sugihan Wildlife Reserve. During "Operasi Ganesha" in December 1982, 232 elephants were herded into the reserve from recently established transmigration settlements in the region (MacKinnon and Setiono 1983). By the mid 1980's, the reserve contained over 400 elephants (Nash 1985a). It also became a refuge for Sumatran tigers and other wildlife (Nash 1985b). The forests of the reserve have been surveyed by Mukhtar (1986), Nash and Nash (1985a, 1985b) and RePPProT (1988).

Access to the sites was by small boat at high tide along a 22 km abandoned drainage canal (no. 7). A 2 km trail was cleared from the canal to the study area. During periods of low water, access to the area was by foot from the Padang River (Figure 2–1).

2.1.2 Sugihan East Peat Deposit

The SE6 study site was located approximately 35 km east of the Sugihan River in the central expanse of a large peat deposit, hereinafter referred to as Sugihan East (Figure 2–1). The extensive area (approximately 400 000 ha) east of the Sugihan River and north of the Lebong Hitam River was predominantly forested and blanketed with peat ranging from 1 to 6 m thick. Peat depths had not been surveyed in the deposit prior to this study. As a result, the peat depths shown in Figure 2–1 were inferred from the forest types recorded by the Ministry of Forestry inventories of the area (Department of Agriculture 1971b, Department of Forestry 1987). During the present study a peat depth of 6 m was measured at the SE6 study site.

The peat forests of South Sumatra were first described by Endert (1920) in his "Flora of Palembang."

Hildebrand (1949) provided an extensive collection of locally used vernacular names for the tree species. Forests in the region were inventoried for commercial harvesting in the early 1970's (Department of Agriculture 1970, 1971b).

Although the surveys were extensive, they are of limited use for ecological studies as only trees of greater than 35 cm stem diameter were recorded. The surveys are valuable though, as they contain historical descriptions of general site conditions such as flooding, fires and other disturbances.

The SE6 study site was located in a mixed forest community characterized by an uneven-canopied (40–50 m) forest. Preliminary surveys during the present study showed that the forest is dominated by *Gonystylus* bancanus, Shorea leprosula, Palaquium sp., Ganua motleyana, Campnosperma auriculata and Dyera costulata. The presence of Pandanus spp. and Cyrtostachys lakka in the subcanopy reflect increased peat depth compared to the PS3 study site.

Access to SE6 was by small boat along a 10 km long canal (no. 27) from the Sugihan River to a logging camp (PT Hutrindo). A logging railway was used to travel 25 km from the camp to the central expanse of the Sugihan East peat deposit (Figure 2–1). Replicate study plots were located in intact forest 2 km east of a selective logging operation.

2.1.3 Padang Island Peat Deposit

The deep peat study areas were located on Padang Island in Bengkalis Regency, Riau Province (Figure 2–2). The island covers an area of approximately 120 000 ha, of which 60 to 70% consists of peat up to 12 m thick (measured). Deeper peat (perhaps to 15 m) may exist, but was not accurately measured during the present study.

On the west side of the island, peat has accumulated over unripened marine clays and alluvium to a recorded depth of 12 m above sea level (asl) within a distance of 1200 to 2000 m from the shoreline. The peat deposits extend nearly to the shoreline on the western coast where there is an abrupt transition from mixed peat forest to mangrove forest. Where the mangroves have been destroyed by logging or sago plantations and subsequent shoreline erosion has occurred, cliffs of peat often 2 to 4 m high have been exposed at the shoreline. These vertical walls of peat are maintained by wave action in the Lalang Strait. Because it is generally believed that coastal peat accumulation occurs only in the rain-fed environments behind mangrove forest, the western shoreline of Padang island probably at one time extended further into the Strait than at present (Bird and Onkosongo 1980). This type of shoreline erosion was also observed along the north coast of nearby Bengkalis Island (S. Neuzil, personal communication, 1996). In Sarawak, Anderson (1964b) observed that coastal erosion on the Rejang Delta exposed 2 m of peat along the coast. Elevation surveys (Lasmo 1992a, 1992b) show that changes in peat depth are considerably more gradual on the eastern side of Padang Island. Peat is present at the shoreline, but rises to the maximum depth over a much longer distance (5000–6000 m) than on the west side of the island.

Preliminary surveys for this study showed that forest composition and structure change noticeably from a mixed forest type at the outer margins of the peat deposit, to a stunted pole forest type on the central peat expanse. The forests of Padang Island were first surveyed by Sewandono (1937, 1938). He inventoried forest volume and composition, and divided the forest into two main types. These consisted of mixed and pole forests, with several sub-classes of each. The Indonesian Forestry Department, in preparation for commercial logging, made forest volume surveys on Padang Island in the 1970's (Department Pertanian 1974). However, as trees in the pole forests were below the minimum harvestable size (35 cm dbh), the stands on the central peat expanse were not included in the surveys.

Recent satellite images reviewed during the study indicated that 60 to 70% of Padang Island and 80 to 90% of the central peat expanse was forested (Brady and Kosasih 1991). The continued presence of undisturbed forest

has been due mainly to poor fertility of the peat for agriculture and stunted tree growth that limits commercial forestry. Commercial harvesting has historically been limited to sago (*Metroxylon* spp.) plantations established in the shallow peats directly behind the mangrove fringe that grows on the coast around most of the island. However, harvesting has also occurred on the island in the mixed forests along the coastlines behind the mangrove.

Sewandono (1938) described the use of a "Pangglong" railway system around the turn of this century for harvesting and transporting small diameter poles for construction purposes in Singapore.

Three main forest types were distinguished during preliminary field surveys for this study. The forest types occurred roughly along gradients of increasing peat depth and distance from the central expanse. Extending from the shoreline to the central expanse, they are: 1) mixed species forest (PI6) on the 1–6 m thick rand peat behind the mangrove fringe; 2) tall pole forest (PI9) of *Calophyllum sundaicum*, *C. ferrugineum*, *C. costulatum* and *Campnosperma auriculatum*, on the outer edge of the central expanse or inner edge of the rand; and 3) low or stunted pole forest (PI12) of *C. ferrugineum*, *Tristania obovata*, *Eugenia* spp. in the central expanse. Forest types of similar composition and structure were also found in the three peat reference areas located on deep peat in deposits adjacent to the Padang Island peat deposit (Figure 2–2). The reference areas have been described by others (Anderson 1976b, Diemont and Supardi 1987, Supardi *et al.* 1993). Access to the study sites was by walking along a 15 km trail cleared between the three forest types (Figure 2–2).

2.2 FIELD SCHEDULE

Field studies took place from 1986 to 1994. Because of travel constraints between study areas in South Sumatra and those in Riau Province, it was not possible to conduct field studies in both regions simultaneously. As a result, data were collected at each study site for a minimum of two wet seasons and two dry seasons. Wet seasons were defined as three consecutive months with over 100 mm rainfall per month, while dry seasons have monthly rainfall less than 100 mm for three consecutive months. During the field periods the study sites in South Sumatra Province and Riau Province were subject to similar periods of heavy rainfall and to two El Nino-related droughts (1987 and 1991). Climate conditions of the study areas are further discussed in Chapter Three.

2.3 STUDY VARIABLES

The principal assumption underlying the study was that comparisons among a carefully selected sequence of study areas in the three peat deposits of increasing depth could be used to demonstrate patterns of change in the acrotelm peat layer as defined in Chapter 1. For the purposes of the study, the acrotelm peat layer in each site was 40 cm thick, divided into a top (0–20 cm) and base (20–40 cm) layer. The acrotelm top was mostly unsaturated, but occasionally flooded by rising watertable levels during annual wet periods. The acrotelm base was mostly saturated, but occasionally unsaturated during extended dry periods. The depth of the two layers were decided upon during preliminary field visits based on waterlevels and peat saturation.

As organic matter dynamics and age are the main determinants of peat depth, the study focused on the biotic, physical/environmental and chemical factors that control organic matter accumulation and decay in the acrotelm layer over time. The study was organized into separate analyses of: 1) study area conditions, and 2) organic matter dynamics as follows:

- 1) Site Description Study (Chapter Three). Characteristics of the study areas Trends in the following variables along a gradient of increasing depth in peat deposits:
 - Regional climate patterns;
 - plant species composition, aboveground forest structure (density, dominance and distribution), and
 stand development history;
 - patterns of peat water levels, moisture and temperature fluctuations; and
 - edaphic factors of peat bulk density, pore space and water holding capacity.
- 2) Organic Matter Dynamics Studies (Chapters Four and Five):

Organic matter ages – Trends in organic matter ¹⁴C age with changes in peat depth and vegetation.

Organic matter decay – Trends in the following variables with changes in peat vegetation, and environmental and edaphic conditions:

- edaphic factors (of bulk density, particle size fractions) to estimate the degree of organic matter decay;
- surface topographical changes;

- mass loss of organic materials under field conditions; and
- respiration and mineralization of organic materials under field and laboratory conditions.

Litter inputs and standing biomass – Trends in the following with changes in peat vegetation, and environmental and edaphic conditions:

- patterns of aboveground litterfall and standing litter dry mass and organic chemistry;
- indices of small and fine root growth and root dry mass and organic chemistry; and
- Peat dry mass and organic chemistry in the top and base of the acrotelm layer.

2.4 SITE DESCRIPTION

2.4.1 Vegetation

Releve' Analysis

Forest composition, structure and abundance were recorded by releve' sampling (Mueller-Dombois and Ellenburg 1974). Two 900 m² (30 x 30 m) study plots were randomly located in each of the five study sites. Species quantities by strata were estimated using the Braun-Blanquet Cover-Abundance Scale (Braun-Blanquet 1932, 1965 cited in Mueller-Dombois and Ellenburg 1974) listed in Appendix 2.1. Species names were identified by field assistants who had knowledge of vernacular names and local forest conditions. Voucher specimens of all plant species were collected, preserved and sent for identification at the National Plant Herbarium at Bogor. Identification to the species level was often not possible, or was of dubious accuracy. In these cases, plants were named to the genus level and different species were numbered. Where genus and family were uncertain, the vernacular name was used. Bianchi (1941), Hildebrand (1949), Anderson (1963, 1972), Departemen Pertanian (1982), and Whitmore and Tantra (1986) provide lists of vernacular and Latin names for tree species found in Sumatran peat forests.

Identification of plant species in Indonesia can be difficult due to the extremely high plant diversity, limited published identification keys, and inadequate herbaria. Fortunately, the focus of the present study was the influence of vegetation structure and quality on litter inputs to peat. In addition, species numbers in peat forests are low compared to the high species diversity found in adjacent lowland forests on mineral soil. Also, Sumatran peat

forests have been adequately surveyed in the past. Nevertheless, the limitations of the tree identification to species level are acknowledged.

Forest Structure

Total (all species) and relative (single species) tree density (stems/area), dominance (basal area) and frequency (species/plot) were estimated quantitatively in the two releve' plots in each study area by measuring all trees with diameter greater than 5 cm at breast height (dbh). The plot information was supplemented with data obtained using plotless distance techniques. The T-Square sampling method (Besag and Gleaves 1973, cited in Krebs 1989) was also used for density measures of both random points-to-trees and trees-to-nearest-neighbor distances. This method was used as it appeared that the spatial patterns of some trees in the study sites were not random. Four point-to-tree and tree-to-nearest-neighbor (T-square) distances were recorded at 10 random points along two 100 m transects randomly located in each site. Tree species, diameter and height were also recorded. Data from the two distance measurements were analyzed separately. A coefficient of aggregation (Hopkins test) was used to determine the type of distribution of trees. The coefficient is determined by dividing the mean value of the sum of the squares of the tree-to-tree distances by the mean value of the sum of the point-to-tree distances according to Hopkins (1954). The coefficient ranges from 0 (uniformity) to 1 (clumped) and is expected to be 0.5 when the spatial pattern is random (Krebs 1989). The distance method is biased by the second tree-to-tree distance measure as the trees are not randomly selected (Pielou 1969). Consequently, the results must be considered preliminary until more thorough surveys are performed.

Preliminary estimates of aboveground stem biomass were calculated by multiplying average tree stem height by basal area by wood densities of the most common trees. A taper factor of 0.7 was used (Brünig 1990). Wood densities were from Martawijaya *et al.* (1986). The stem biomass estimates must be considered preliminary until empirical measurements are taken in these forest stands.

The releve' plot data were classified using Cluster Analysis (CA). Percentage similarity coefficients (Renkonen Index) were used with an average linkage amalgamation as described by Wilkinson (1989). According to Krebs (1989), the percentage similarity measure is little affected by sample size and species diversity, both of which were variable in the Sumatra plots. Following the Cluster Analysis, the plot data were ordinated along hypothetical gradients using Principle Components Analysis (Greig-Smith 1983).

Stem (e.g., straight, buttressed, adventitious roots) and surface root (e.g., stilt roots, knee roots, loop roots, pneumatophores) characteristics of dominant tree species were recorded in each plot (after Kozlowski *et al.* 1991). Characteristics were recorded in the categories: commonly present; seldom present; and not observed.

2.4.2 Environmental Monitoring During the Study Periods

Rainfall data were collected to characterize the spatial and temporal patterns of atmospheric moisture inputs to peat. Meteorological records for the past several decades were obtained for climate stations closest to the study sites (Palembang, Kenten and Plaju in South Sumatra; Bengkalis and Selat Panjang in Riau). Stations were located no further than 60 km from each site.

Peat watertable levels were measured regularly in the five study sites to record daily, seasonal and annual hydrological fluctuations during the study periods. At two randomly located points in each releve' plot, piezometers, consisting of 6 m long x 2 cm diameter perforated aluminum pipes (four 0.5 cm diameter holes every 10 cm), were hand-driven into the peat. The bottom end of each pipe was pinched closed to prevent peat from entering. In the medium depth (3–6 m) peat deposits the pipes were anchored in the underlying clay. Pipes placed in the deep (9–12 m) peat remained suspended in the peat matrix. Subsequent monitoring showed that, relative to the peat surface, the piezometers did not shift due to peat contraction or expansion. During most of each monitoring period, at least 5 m of the 6 m long piezometer tube was embedded in waterlogged peat. Water levels were measured by lowering a thin wooden rod down the pipes. To avoid water displacement and a false reading, the rod was lowered into the pipe twice for each measurement. On the second lowering the rod did not enter the water more than 1 to 2 cm.

Soil temperatures (°C) were measured at each study plot using a 30-cm aluminum-jacketed soil thermometer. Temperatures were recorded for 10 minute periods in the early morning and late afternoon at 2 cm and 25 cm peat depths. A maximum-minimum thermometer was buried in 1 to 2 cm of peat and left between monthly field visits over each study period to record temperature ranges. Measurements were taken during the study periods to characterize daily temperature fluctuations. Continuous monitoring using automated instruments was beyond the scope and budget of the present study.

2.4.3 Peat Edaphic Conditions

Field moisture content was measured in composites of five grab samples from the surface (0-20 cm) and the subsurface (20-30 cm) peat layers in each plot during field visits. Bulked samples were sealed in plastic bags

and refrigerated at 4°C until analysis. The peat was dried at 80°C to constant mass to determine moisture percentage on a dry mass basis (Houba *et al.* 1986, van Reeuwijk 1986).

Bulk density was measured using cores of peat from surface and subsurface layers at each plot. Eight volumetric samples of intact peat were extracted from each layer using open-ended metal coring tubes of 800 cm³ volume (coffee cans). Peat cores were oven-dried at 80°C to constant mass. Dry bulk density was calculated as the oven-dried mass divided by the field volume of each sample and expressed in g cm⁻³ (Black 1965).

Total pore volume (capillary and non capillary space) was determined by dividing the measured peat bulk density by a peat particle density³ of 1.43 g cm⁻³ and subtracting this from 1:

%Total pore volume = 1 - (bulk density/particle density) x 100

Moisture holding capacity (MHC) was measured using four fresh peat cores of known volume extracted from each plot. The open-ended coring tubes filled with peat were saturated with water for 24 hours in the laboratory, gravity drained on mesh screens for 30 minutes, weighed, then dried to constant mass and reweighed. Results were expressed as g max. H₂O g⁻¹ dry soil. Increasing the soaking period to 48 and 72 hours did not significantly affect the results. To measure the rewetting capacity, dry peat cores were soaked in water for 90 days and MHC was remeasured. The 90-day soaking period represented the longest period of heavy rainfall in the study sites.

2.5 AGE DETERMINATION

Peat samples for age determination were taken from the top (0–20 cm) and base (20–40 cm) of the acrotelm peat layer of each study plot. The samples were wet sieved to collect the <0.5 mm peat fraction which comprises the most humified and presumably the oldest organic material in the peat matrix. In addition, fine and small (0.5–2.0 mm) dead intact roots were hand picked from the samples of peat from the subsurface layer. Ages from the bottom of the three peat deposits were not determined as the study focused on organic matter dynamics in the acrotelm layer where peat preservation occurs.

The organic fractions were oven dried (80°C) to constant mass, ground to less than 2 mm and stored in aluminum foil. Prior to analysis the organic samples were pretreated with acid/alkali/acid washes to eliminate carbonates and secondary organic acids. Standard radiocarbon-dating (14C) analyses of the samples was performed

by Beta Analytic Inc. Radiocarbon Dating Services of Miami, Florida. Sample quality was also assessed by Beta using the C13/C12 ratio analyses (Talma and Vogel 1993). Results were expressed either as conventional radiocarbon ages before present (yBP AD 1950), or as percent Modern (post AD 1950) carbon. Both units included \pm 1 sigma standard deviation (68% probability) after applying the C13/C12 corrections.

2.6 MEASURES OF ORGANIC MATTER DECAY

Organic decay processes under different vegetation cover and edaphic conditions were characterized in the study by combining: 1) physical measures of organic decay rates and mineralization at the study sites and 2) chemical measures of decay in the field and under controlled conditions in the laboratory, with 3) a retrospective analysis of the present degree of decay and organic matter quality in the peat profiles of the study areas. The field and analytical methods followed, as much as possible, those of the Tropical Soil Biology and Fertility Programme of the International Union of Biological Sciences (Anderson and Ingram 1989, 1993).

2.6.1 Physical Measures of Organic Matter Decay Rates During the Study Period

Organic Matter Losses

The decay rate quotient for small litter (k_L) was calculated by dividing the annual litterfall input (described below) by the litter layer mass measured in each plot (Duxbury *et al.* 1989). The value of k_L is an approximation of the proportion of the litter layer decomposed in one year and is based on the assumption of simple exponential breakdown of litter in conditions where the amount accumulated on the soil surface oscillates around some steady state value. Thus, k_L is an imperfect indices as litter may decay linearly or double exponentially (Olson 1963). Litter layer residence time in years was calculated as the reciprocal of k_L .

Organic matter losses were estimated using field incubations of several substrates including leaf litter, wood, peat and a standard cotton substrate. The incubations were performed for up to one year in each study area and were used to complement the litter turnover measurements described above. Mixed leaf litter was collected from the surface litter layer each study area, dried at 80°C for 24 hours, placed in standard 25 cm x 25 cm bags of 2 mm nylon mesh, then weighed. The bags were returned to the study plots and eight bags were buried within the surface layer of litter. The bags were left for 90-day periods during two wet and two dry seasons. Because of the high humidity, high rainfall and fluctuating watertable, the leaf litter in the bags usually rewetted within the first

week of each incubation period. After each 90-day incubation bags were removed from the plots, dried, cleaned of root ingrowth and weighed again.

Initial decay rates of wood were measured in each study plot using eight wooden stakes (2 x 2 x 40 cm) of ramin (*Gonystylus bancanus*). The stakes were oven dried to constant weight then inserted vertically so that the bottom of the stake was 40 cm below the peat surface and left. Similar to the dried leaf litter, the stakes rewetted quickly when pushed into the peat. After one year the stakes were carefully removed, oven dried, cut into the respective top (0–20 cm) and base (20–40 cm) sections of the acrotelm peat layer, and then reweighed.

Peat for incubation in mesh bags was collected separately from the top (0–20 cm) and base (20–40 cm) of the acrotelm in PS3 and SE6 study sites. Samples of 500 g of field-moist peat from each of the areas were gently passed through a 2 mm sieve to remove roots and woody pieces. Exactly 70 g field moist portions of the mixtures were sealed in mesh bags (10 cm x 10 cm x 0.5 mm nylon mesh). Additional 70 g portions were oven dried to determine moisture contents. The peat-filled mesh bags were then fumigated with alcohol-free chloroform for 24 hrs to eliminate microbial activity and thus produce similar initial microbial conditions for all incubation bags (after Jenkinson and Powlson 1976). The peat-filled bags were returned to PS3 and SE6 and placed in the peat surface below the litter layer and at 25 cm depth in the peat, according to the origin of the peat in the bags. Following a 90-day incubation period the bags were carefully retrieved. The remaining peat was removed from the mesh bags, oven dried and weighed to determine mass loss. Results of the peat incubations were inconsistent due to peat losses caused by damage to the bags from insects and rodents, or by excessive root ingrowth. Consequently, peat incubations in mesh bags was not performed at the remaining study areas.

A standard decay substrate was placed in the peat at all study plots. Strips of white 100% cotton (0.12 g cm⁻²) were stapled over 40 cm x 50 cm wooden frames and inserted vertically into the peat to a depth of 40 cm below the surface litter layer. The strips were to provide an indication of variation in decay activity between plots at similar soil depths, differences between soil depths at any plot, and seasonal changes in decay.

Analysis of cotton decay was limited to comparisons of the area of cotton disappearance between depths, study plots and wet and dry season incubation periods. After 90-day incubations, the frames were extracted from the peat. If more than 50% of the cotton remained it was carefully removed from the frames and placed in bags. In the laboratory the cotton remains were placed over graph paper and the percentage area of cotton remaining from the

original area in the top (0–20 cm) and base (20–40) was calculated. If less than 50% of the cotton remained the location in the frame and approximate area percentage were recorded visually in the field. Measurements of tensile strength, commonly used in decay studies, were not performed because a high percentage of the cotton on most of the frames disappeared rapidly. The little cotton that remained was insufficient for any type of mechanical manipulation.

Peat Surface Level Changes

Net elevation changes of the peat surface were recorded at the same time as waterlevels were measured in the piezometers. On two sides of each piezometer pipe the distance was measured from the top of the pipe to the ground which was cleaned of litter to the peat surface. Measurements were taken during each field visit over the duration of each study period. Elevation changes in peat reflected the sum of biological decay and physical compaction processes (Driessen and Sudjadi 1984).

2.6.2 Chemical Measures of Organic Matter Decay During the Study Period

To further compare decay rates among and between study areas, peat and other organic materials were incubated under controlled conditions in the laboratory for varying periods of time. Incubations for 30-day periods were used to compare CO₂ respiration of organic materials under varying moisture and temperature regimes (Table 2–2). One year incubations were used to compare rates of CO₂ respiration rates and N mineralization in peat under field temperature and moisture conditions. Substrate induced respiration was also measured over one year in peat amended with saturation amounts of C (glucose) and N (ammonium nitrate).

Moisture and temperature effects on respiration during 30-day incubation periods were determined using five-5 g (dry weight) samples of field fresh leaf litter, fine roots and peat from surface and subsurface layers of each study plot. The samples were placed in 500–cm³ glass canning jars (Kerr wide mouth). A rubber septum was fitted to the airtight lid of each jar. The moisture content of the organic materials was adjusted according to the treatments listed in Table 2–2. The jars were incubated in the dark at either 25°C or 35°C (Table 2–2). Following a 10-day stabilizing period, concentrations of CO₂ in the headspace gas in each jar were estimated at weekly intervals after the last airing of the jars. The gas was sampled by pushing a syringe through the septum in the lid of each jar. Concentrations of CO₂ were measured by infrared gas analysis (Beckman, USA) and converted to estimates of mg

CO₂ produced per gram of each peat layer during the weekly period (Clegg *et al.* as cited in Prescott *et al.* 1994).

The jars were aired for 15 minutes immediately following the weekly gas measurements.

Table 2-2. Summary of treatments for organic matter incubations under laboratory conditions.

No.	Organic matter*	Treatment	Level	Parameter	Measurement frequency (weeks)
		30-day incu	bations		
1	Peat (acrotelm top/base), leaf litter, fine roots	Field temperature and moisture	70% MHC**, 25°C	CO ₂	1–4
2	Peat (acrotelm top/base)	Moisture effects at field temperature	50 and 100% MHC	CO_2	1–4
3	Peat (acrotelm top/base)	Temperature effects at field moisture	25 and 35°C	CO ₂	1–4
		1-year incu	bations		
4	Peat (acrotelm top/base)	Field temperature and moisture	18–25°C, 70% MHC	N_{\min}	1 & 52
5	Peat (acrotelm top/base)	Field temperature and moisture	18–25°C, 70% MHC	CO ₂	1-4, 24-28, 48-52
6	Peat (acrotelm base from PS3/PI12 sites)	Field temp./moist., plus N amendment	17.5 μg N g ⁻¹ dry peat	CO_2	1-8, 24-28, 48-52
7	Peat (acrotelm base from PS3/PI12 sites)	Field temp./moist., plus C amendment	0.05 g C g ⁻¹ dry peat	CO_2	1-8, 24-28, 48-52

^{*}Samples from all sites included unless otherwise indicated. **Moisture holding capacity

Substrate-induced respiration of peat was also measured in glass jars over a 4-week period and remeasured six months and one year later. Three respirometry measurements, basal respiration (*B*), glucose induced respiration rate (*C*) and glucose + mineral N induced respiration rate (*CN*), were measured on replicate samples (5) of peat from the acrotelm base of PS3 and PI12 study sites, which represented the two extremes of the gradient of different peat depths. Following the first CO₂ measurements of incubated 5 g surface and subsurface peat samples, saturation amounts of mineral N (17.5 µg N g⁻¹ dry peat from NH₄NO₃) and C (0.05 g C g⁻¹ dry peat from glucose) were added to separate samples which were then incubated for one year at 25°C. Samples incubated with no amendments were included as controls. Respiration was measured daily for the first two weeks, then followed the measurement schedule listed in Table 2–2. During the 5-month periods between the four respiration measurements in the first and sixth, and sixth and twelfth months, the jars were aired every 30 days. Moisture was maintained at

70% MHC by adding distilled water when required. GasPak Anaerobic Indicators (Becton, Dickenson and Co., MD, USA) were placed in the jars and monitored between airings to confirm that aerobic conditions were maintained. All three rates of peat respiration (B, C and CN) were reported as mg CO₂ g⁻¹ peat d⁻¹. Microbial physiological indices (Bradley and Fyles 1995) were then determined for peat from the two sites as follows:

EDI = energy deficiency index
=
$$[(C - B) \div B] \times 100\%$$

NDI = nutritional deficiency index
= $[(CN - C) \div C] \times 100\%$.

Net N mineralization over one year was also measured in acrotelm peat under controlled temperature and moisture conditions in the laboratory (after Adams *et al.* 1989, Raison *et al.* 1987)(Table 2–2). After adjusting to 70% MHC, five cores (800 cm³) of intact peat from the top and base of the acrotelm layers of each study plot were placed in plastic bags and incubated in the dark at 18–25°C for one year. At the beginning and end of the incubation, replicate 5 g (dry weight) portions of each core were analyzed for concentrations of NH₄-N and NO₃-N in 2 M KCl extracts as described below. A second subsample was oven-dried at 80°C to determine moisture content. Net mineralized N was determined by subtracting extractable N from preincubated peat from extractable N in the incubated peat.

2.6.3 Degree of Peat Decay

Physical Indices

The present degree of decay of peat in the top and base of the acrotelm layer of the study sites was compared using physical indices of bulk density, rubbed fibre and particle size distribution (Boelter 1974, Mathur and Farnham 1985). Bulk density was measured using eight volumetric samples of intact peat, extracted from each layer using 800 cm³ metal coring tubes. The peat cores were oven-dried at 80°C to constant mass. Dry bulk density was calculated as the oven-dried mass divided by the field volume of each sample and expressed in g cm⁻³ (Black 1965).

Eight additional 800 cm³ cores of peat were extracted from each layer to measure rubbed fibre content and particle size fractions. Wet-sieving of peat from the cores was used to separate peat into 0.5–20.0 mm and <0.5 mm

size classes. A known volume of peat was placed in a 0.5 mm sieve and held under a stream of water. The peat fibres were gently hand-rubbed through the sieve until the wash water became clear. The peat remaining in the sieve was then oven-dried to constant mass and recorded. The <0.5 mm fraction was estimated by subtracting the mass of the >0.5 mm fraction from the mean total dry mass. The 0.5 mm sieve was used because fibric material smaller than this size could not be recognized as either wood, roots or leaves. It was also the lower diameter limit for coarse sand which is a size that influences permeability properties (Pritchett 1979). Most of the <0.5 mm fraction was decomposed sufficiently that it could be easily rubbed to pass through the 0.15 mm sieve used in standard fibre analysis procedures (Levesque and Mathur 1979, Sneddon, *et al.* 1971, Boelter 1969) Particle size fractions were expressed as a percentage of the total dry mass per unit soil depth.

The physical indices were combined with the peat edaphic properties described above to classify the peat according to the textural classes defined by Farnham and Finney (1965) and modified by Esterle and Ferm (1994) for wood-based tropical peat (Table 2–3).

Table 2–3. Textural classes of tropical peat used in the study.

Peat textural classes	Colour	Fibres (%)	Fibre description	Matrix	VonPost
Fibric	Yellow to orange-brown	>66	Abundant, mostly long slender roots and rootlets	Fibrous, watery	H1–3
Coarse Hemic	Orange to red- brown	33–66	Medium grained with abundant long slender roots and rootlets	Granular	H4-5
Hemic	Reddish-brown	33–66	Medium grained fragments of wood, roots and rootlets	Compact, granular	H5-6
Fine Hemic	Reddish to dark brown	33–66	Medium to fine grained fragments	Granular to colloidal	H6-8
Sapric	Dark brown to black	<33	Fine granular	Fine granular and colloidal	H810

Chemical Indices

Composite samples of different peat layers and vegetation components were collected for analysis of total N, P and C, and proximate C fractions. Green leaves of the dominant forest tree species were randomly sampled in the study areas. Collections of coarse woody litter, leaf litter, flower and seed litter, live fine roots, dead fine roots, and dead coarse roots were bulked by litter type and a composite sample of each type analyzed for each study plot.

Vegetation and peat samples were oven dried at 80°C for 24 hours, and then ground in a Wiley mill to pass through a 0.5 mm mesh sieve.

Concentrations of N and P were analyzed at the University of British Columbia Forest Ecology Laboratory by micro Kjeldahl digestion according to van Reeuwijk (1986). Approximately 0.1 g of sample were digested in a mixture of potassium sulfate, sulfuric acid and selenium in a block digester. The digest solutions were then analyzed colorimetrically using a Technicon Autoanalyzer II (Method no. 334–74A. Technicon Instrument Corp., Tarrytown, N.Y.). Results of N and P analyses of reference samples of ground plant material were within 5% of the published values (IUFRO no. 84–2 *Eucalyptus intens*).

Ammonium and nitrate N ($N_{mineral}$) were extracted from field moist peat by mixing with 2M KCl (10:1 extract:dry peat) and shaking for 24 hrs. The solutions were filtered through Whatman no. 42 paper then frozen until analysis. The KCl extracts were analyzed for ammonium and nitrate N using a Technicon Autoanalyzer II (Method no. 18–69W and 158–71A, Technicon Instrument Corp., Tarrytown, N.Y.). Mineralizable N was expressed in mass values ($\mu g \, g^{-1} \, dry \, peat$), and combined with peat bulk density to express the values on an area and volume basis (kg ha⁻¹ per sample depth).

Total C and proximate C fractions of peat, leaf and root samples were analyzed at the Oregon State University Forest Science Laboratory. Samples were ground to pass a 0.149 mm (100 mesh) sieve. Total C was determined using a high temperature conduction furnace and thermal conductivity detector (Carlo-Erba NA 1500, series II). The ash content of peat samples was estimated by loss-on-ignition (Houba *et al.* 1986). Peat was ignited for 3 hours at 850°C. Chemical separations into proximate C fractions followed the Pastor Method (Ryan *et al.* 1990) of consecutive extractions using dichloromethane, hot water, sulphuric acid, respectively. Pooled samples of each component were separated into the following proximate C fractions expressed as % ash-free weight: solubles (non-polar compounds such as fatty acids and lipids and polar compounds such as sugars and phenolics), holocellulose (acid soluble cellulose plus hemicellulose), and lignin (acid insoluble aromatic compounds). Water soluble polyphenols were determined by the Folin-Denis procedure using tannic acid as a standard (in Ryan *et al.* 1990).

2.7 ORGANIC MATTER INPUTS FROM VEGETATION

The fine and small size fractions of aboveground litter and roots were selected for study (size classes defined below). It was observed during initial study area selection that these fractions exhibited greater differences between study areas than did large roots and woody litterfall. Few standing snags were observed, other than in patches of tree blow down, and the forest floor in all areas was sparsely covered with woody debris. In addition, neither the time nor financial resources needed for measurement of the large litterfall fractions were available.

2.7.1 Aboveground Forest Litter and Litterfall

The aboveground litter layer was defined as undecomposed leaf material, reproductive organs (flowers, seeds) and small woody debris (<2 cm diameter) above the peat. Woody debris over 2 cm in diameter was not measured as its abundance was observed to be small and unevenly distributed. To measure the standing crop of litter, all recognizable aboveground litter was harvested from four to six randomly-located 25 cm x 25 cm quadrats in each study plot during each litterfall collection period for one year. All litter was removed to the peat surface, or to where a continuous mat of roots was encountered. Woody material >2 cm in diameter was excluded. Harvested mixed litter was placed in cotton bags, oven-dried and weighed. Collections from plots were bulked and stored for analysis of total C, N, P and proximate C fractions (methods in Section 2.6.3).

Fine litterfall (>2 cm diam.) was collected for one year at each study plot in eight wooden-framed litter traps. The 90 cm x 150 cm traps were suspended 30 cm above the forest floor. Nylon mesh (2 mm) was draped loosely over the frames allowing a 5 cm depression. The traps covered approximately 1.3% of each 900 m² study site. There was little wind under the canopy of the peat forests so there was little chance of litter being blown out of the traps. Litter was collected from the traps every 4 to 6 weeks and placed in cotton bags. Large pieces of wood (>2 cm diam.), seldom found in the traps, were discarded. Occasional tree-falls over the traps were recorded. The number of harvests varied among study sites over the one-year collection period due to restricted access to the remote sites in the Padang Island and Sugihan East peat deposits (Table 2–4). After harvests, litterfall collections were dried at 80°C for 24 hours, then separated and weighed by leaves, fine woody material (<2 cm diam.), seeds and flowers, and chaff (indistinguishable litter). The litter fractions of each harvest were then combined and four subsamples were taken for analysis of total C, N, P and proximate C fractions.

Table 2–4. Number of litter trap collection days and number of collections made in this period (in brackets) per season in each study area.

	Collection days and (periods)		
Study site	Wet season	Dry season	
PS3	102 (3)	108 (3)	
SE6	70 (2)	68 (2)	
PI6	102 (3)	103 (3)	
PI9	102 (3)	104 (3)	
PI12	103 (3)	104 (3)	

2.7.2 Belowground Biomass

Root Dry Mass

Small (<10 mm diam.) root biomass was measured in each study plot. Sampling was limited to the small root fraction because previous studies have shown that production and turnover rates were found to be higher in this fraction than in the fraction of larger woody roots (Anderson and Flanagan 1989 and Vogt *et al.* 1991). Although fine and small roots sometimes comprise a small fraction of the total root biomass in an ecosystem, they have been considered a more accurate indicator of root function than large roots (Berish 1982). This is mainly due to their more important role in nutrient and water absorption and in contributing large amounts of organic matter to soil through rapid turnover. Large roots likely play an even less important role in peat forests where elevated watertables with rapid fluctuations inhibit the downward growth of larger, slower growing roots into the peat profile. The turnover of structural support roots is infrequent and usually occurs when plants die (Vogt *et al.* 1991). Discussion of large roots was limited to qualitative observations made during the field period.

Eight volumetric samples of intact peat were taken from each of the study plots using open-ended 800 cm³ metal coring tubes. The tubes were sharpened at one end to minimize peat compression during coring. Without proper care, samples from the soft, low density peat of the deep peat study areas can be easily over-compacted. Cores were extracted from the top (0–20 cm) and base (20–40 cm)of the acrotelm peat layer, below the fresh litter layer at random locations in each plot. Peat cores were taken at least 1 m from large trees to avoid contact with large aboveground and belowground roots (>2 cm diam.) which were not included in the cores. At each sampling point, recognizable litter was brushed away to expose the surface layer of fibric or hemic peat and the corer was gently

pushed into the peat. To avoid compacting or dispersing the peat in the core, a long knife was slipped down the outside of the corer to sever roots as the corer was pushed downwards. The peat-filled coring tubes were sealed at both ends and refrigerated at 4°C until analysis.

In the laboratory, the peat was washed through 2 mm and 0.5 mm stacked sieves. The division between fine and small roots was defined at 2 mm (Vogt *et al.* 1989), while the 0.5 mm mesh was determined to be the minimum size for recognizing and sorting fine and small roots in such large volumes of soil. To avoid fragmenting the roots, washing was performed by partly immersing the sieve screen in standing water rather than using flowing water. Soft aggregates were broken up by hand to expose all roots. The <0.5 mm portion of peat was discarded. Roots from the 0.5–2.0 mm and 2.0–10 mm portions of fibric peat were then separated by hand into live and dead root fractions. Visual criteria to distinguish live from dead roots included color and physical integrity as described by Kurz and Kimmins (1987). A light colored inner bark was present in live roots, while dead roots had dark colored bark. Live roots were firmer and tended to remain intact when handled, while dead roots fell apart easily. Many live roots had an inner strand of white vascular material which tended to be stronger than the outer layers. The root and non-root fractions (>0.5 mm) were dried at 80°C for 24 hours, weighed and stored for determination of total N, P and C fractions. Live and dead root biomass was combined and expressed as kg m⁻² for the top and base of the acrotelm layers. Large roots (>10 mm) were not measured in the study, but were described qualitatively in the field.

Root Production Indices

An index of fine root production was measured for a limited period during the study using peat-filled ingrowth bags (Vogt *et al.* 1989). Standard 5 cm x 5 cm nylon bags of 2 mm mesh were filled with 80 cm³ of root-free peat taken from the same depth on the same plot. Eight bags were carefully placed within the top (0–20 cm) and base (20–40 cm) of the acrotelm layer of each plot for 100 days. The incubation periods were between dry and wet season rainfall extremes when the average water level was 40 cm below the peat surface. The bags were removed from the peat with care being taken to cut roots from the outside of the bags without disturbing those inside. In the laboratory the peat was removed from the bags, the roots were hand separated, dried for 24 hours at 80°C and then weighed. Root dry mass production was expressed as g cm⁻³ 30 d⁻¹ at each 20 cm depth.

2.8 STATISTICAL ANALYSIS

Analysis of variance (ANOVA) techniques were used for focused comparisons of vegetation, peat and environmental variables against fixed and random factors among and within study sites and replicate sample plots (mixed model). I analyzed data as a two-way nested ANOVA, with acrotelm layer and peat deposit depth as main effects (fixed) and subplots nested within study sites (random effect) (Zar 1996, pp. 307–315). The general linear model was

$$y_{ijke} = \mu + A_i + P_{(i)j} + L_k + A \times L_{ik} + P \times L_{(i)jk} + SE_{(ijk)e}$$

where A_i is study site (i = 1-5), $P_{(i)j}$ is plot within study site (j = 1-2) for all i, L_k is acrotelm peat layer (k = 1-2) and $SE_{(ijk)e}$ is random error (e = 1-5) for all i, j, k). All site-level observations were tested both for normality using probability plots, and for variance homogeneity using Bartlett's Test (95% CI). When Bartlett's Tests indicated that raw data violated the assumption of homogeneity of variances, the data were transformed using log transformations. The Tukey test was used for multiple comparison post-hoc tests of means with slight modification for nested ANOVA (Zar 1996, pp. 314). Although three study sites were located on the Padang island peat deposit the assumption of independence among sites was not violated. The Padang island sites were several kilometers apart and located in peat of different thickness. The sites reflected different stages of catenary development in which plant growth is likely to be more dependent on peat characteristics than on the preceding plant communities.

Pearson correlation coefficients were calculated to identify the strength of associations between decay indices and the resource quality attributes of litter and peat. Significant (P < 0.05) correlations were confirmed using Bartlett Chi-square tests. Matrices of Bonferroni probabilities were produced to ensure that performing several tests did not lead to an increased probability of Type I errors (Neter *et al.* 1985). All analyses were performed using SYSTAT (Wilkinson 1989). Results were presented in tables and charts of means and 95% confidence intervals (CI).

FOOTNOTES

¹Outer edge or boundary of peat deposit, typically innundated.

²Outward sloping area near margin of raised peat deposit, between lagg and central expanse.

³Average dry density measurement for Indonesian ombrogenous peats over 2 m in depth with an ash content less than 5% (Driessen 1975).

CHAPTER 3

ANALYSIS OF THE ENVIRONMENTAL, VEGETATION AND EDAPHIC CHARACTERISTICS OF THE STUDY SITES

Age, decay and plant processes of the peat accumulation model (eq. 2) vary among the three deposits of increasing peat depth. Their variability is influenced by the allogenic (geomorphology and climate) and the autogenic (vegetation and peat) factors characteristic of each deposit. The temporal and spatial variation of the environmental, vegetation and edaphic conditions were characterized among and within study sites according to the methods described in Chapter 2. The detailed analysis of site conditions provides important information used to understand how the age, decay and plant processes vary in the accumulation model. The findings were compared with studies of other peat deposits in the region to show that the study sites located on the three peat deposits of increasing depth in East Sumatra generally reflect conditions found across similar gradients in peatlands throughout Southeast Asia.

Readers with less concern about the biophysical setting of the study sites and more interest in organic matter dynamics may proceed directly to Chapter 4 of the study. Both the results and discussion in Chapters 4 and 5, respectively, refer to specific sections of the site characterizations in this chapter.

3.1 COASTAL GEOMORPHOLOGY

The lowland peat deposits of east coast Sumatra occur at, or close to, sea level and are relatively young, having developed during the Holocene about 9000 years (9 ka) ago when sea levels began to rise (Tjia 1990). Coastal accretion was caused by the rapid weathering and erosion of fine-textured sediments from the Barisan Mountain Range located along the western coast of Sumatra (Verstappen 1973). The sediments are classed as unnamed Quaternary Holocene fine grade alluvium and include sands. The extensive deposits provided the location for the accumulation of the vast coastal peatlands (Figure 1–2). The geology of the east coast is described by Verstappen (1973). Detailed geological maps of the Padang Island area of Riau Province have been produced by Cameron *et al.* (1989). Verstappen (1964 and 1973) described the geology and coastal geomorphology underlying the South Sumatra peat deposits around Palembang. Further details of the geomorphology of this region are

provided by DeCoster (1974), Diemont and van Wijngaarden (1975), Chambers and Sobur (1977), Chambers (1979), Oliver (1982) and Scholz (1982).

Sea levels stabilized to near their present levels between 5 and 6 ka ago (Tjia 1990). Bays and sheltered areas began filling in, extending the flood plains seawards at rates of 9–10 m annually (Anderson 1964, Bird and Ongkosongo 1980). Peat deposits began accumulating between 4 and 5 ka ago behind the accreting shorelines and between river levees (Soepraptohardjo and Driessen 1976). Coastal deposits of deep peat throughout Indonesia and Malaysia show basal ages between 3500 and 5000 yBP (Anderson 1961b, Muller 1965, Morley 1981, Diemont and Supardi 1987, Cameron 1987, Supardi *et al.* 1993, Esterle and Ferm 1994). The base of many deposits becomes younger towards the coast. Annual rates of coastal progradation of up to 20 m have been suggested (Chambers and Sobur 1977). Other coastal peatlands, particularly in Sumatra, show more uniform basal ages across much of the deposit (Diemont and Supardi 1987, Supardi *et al.* 1993).

Consensus has been reached by many researchers that peat accumulation is probably not triggered by any single factor, but more likely by a combination of environmental conditions, including stagnant water, excessive rainfall (where ET < P)¹, sediments with low base status, acid conditions resulting from sulphur in marine sediments, and no input of nutrient-rich water and sediments over river levees (Kostermans 1958, Anderson 1961b, Andriesse 1988, Cameron *et al.* 1989).

3.2 CLIMATE

The climate of Sumatra exhibits great variation, mainly in rainfall. Durand-Dastes (1978) identified 12 rainfall regimes, all generally bimodal with two wet and dry periods annually. North-east monsoonal rains fall between November and April, while the south-west monsoon blows relatively drier air across Sumatra from June to October (Oldeman and Frere 1982). The east coast of the island has a wet tropical monsoon climate classed by the Koppen System as "Af". Fontanel and Chantefort (1978) characterized the coast as having a very humid bioclimate with 2000–2500 mm annual rainfall, with no dry season, and mean temperature of the coldest month greater than 20°C. To differentiate the influence of climate and other allogenic factors on Sumatra peat deposits further, the present study considered rainfall variability at different space and time scales.

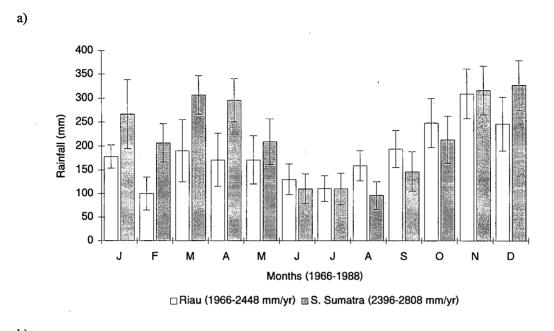
3.2.1 Rainfall

Spatial Variability Between Study Regions

Rainfall patterns differ slightly between the two study regions located along the coastal lowlands of Riau and South Sumatra Provinces (Figures 1–2 and 3–1). This is mainly due to the rain shadow effect of the Malaysian land mass on coastal Riau, which limits the amount of moisture from the north-east monsoon. South Sumatra however, is fully exposed to the monsoonal winds. Combined with the orographic effects of the Barisan Mountain Range of Central Sumatra, the winds bring more rain to this southern region (Republic of Indonesia 1990).

According to the climate classification system developed by Schmidt and Ferguson (1951) for Indonesia, the Padang Island study area has an A-type climate, based on an average of 1.0 dry months (<60 mm rainfall monthly) and 9.6 wet months (>100 mm rainfall monthly) annually. Mean annual rainfall from 1966 to 1988 was 2216 mm with an average of 112 rain days (Figure 3–1). The closest climate station to Padang Island was at Selat Panjang (Figure 2–2), about 50 km away. Another permanent station at Bengkalis was about the same distance away. Average annual rainfall at Bengkalis was higher at 2440 mm annually. The two years of rainfall data recently recorded on Padang Island (presented below) suggest that the rainfall pattern of Selat Panjang was more similar. Rainfall on Padang Island was characterized by two rainfall peaks, one in November and one in April. According to the 20-year record there were no (drier) months with rainfall under 60 mm (Figure 3–1). However, researchers in Sumatra question the use of 60 mm as the lower limit defining a dry month. Oldeman (1977) proposed that due to higher insolation and evapotranspiration rates in Sumatra, dry periods should be defined as occurring when precipitation is less than three times the average monthly temperature (P <3T). Using this definition, dry periods would occur in Sumatra when monthly rainfall is less than 100 mm.

The study sites in South Sumatra to the north-east of Palembang were also classified by Schmidt and Ferguson as having A-type rainfall based on data collected from 1921 to 1940. The sites were located near several permanent climate recording stations; one at Sungsang on the coast and the others at Palembang and Telang Betutu, approximately 90 km inland (Figure 2–1). Mean annual rainfall at the sites falls between 2345 mm (Sungsang) and 2546 mm (Telang Betutu). Moving inland from the coast, mean annual dry months range from 1.0 to 1.3 (60 mm definition) and wet months from 9.3 to 9.4. The confidence interval (P < 0.05) of mean annual rainfall (1966–1988) at Telang Betutu ranged from 2396 to 2808 mm (Figure 3–1).



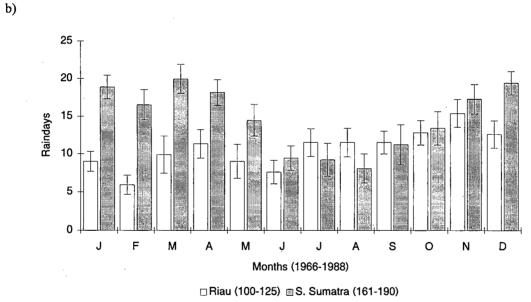


Figure 3–1. Mean monthly (a) rainfall and (b) rain days (with 95% confidence intervals) near Padang Island, Riau Province (Selat Panjang climate station) and Palembang (Telang Betutu climate station).

Rainfall data collected closest to SE6 study site came from a climate station at the Delta Upang Test Farm, located approximately 30 km to the west (Figure 2–1). The station operated from 1975 to 1983 (Ministry of Transmigration 1988). Mean rainfall over 9 years was 2413 mm with 164 rain days. The values lie between those

recorded at the coastal and inland stations mentioned above, and suggest that rainfall at the study sites falls between the coastal and inland rainfall regimes.

Although the study sites in South Sumatra were wetter on average than the study sites in Riau, the difference in mean annual rainfall and rain days for the data analyzed was not significant (P < 0.05) (Figure 3–1). The bimodal rainfall pattern in Riau was more pronounced than in South Sumatra (Figure 3–1a). Average rainfall in both locations, however, does not fall below the monthly dry month limit of 60 mm. A second short dry season (<100 mm rainfall per month) occurs in Riau during January and February, but does not occur as strongly in South Sumatra (Yacono-Janoueix and Perard 1978). The single dry season in South Sumatra that peaks in August was slightly more pronounced than the two-month (June and July) dry season in Riau. In the former, there were often two to three months with less than 100 mm rainfall.

Spatial Variability Among Study Sites

Local annual rainfall patterns can be extremely variable in South Sumatra. In a study on the agroclimatology of coastal South Sumatra, Chambers and Manan (1978) concluded that the spatial distribution of rainfall can often vary more than year to year rainfall differences. Figure 3–2 illustrates such high variability between three rainfall stations on Padang island monitored for one year during the present study. Monthly rainfall within a 40 km radius varied from 9 to 100% of the long-term monthly means. Such high variability illustrates the hazards of extrapolating the results from short-term studies to longer-term hydrological processes.

When rainfall variability was considered over larger areas and longer time periods, spatial variability does not appear as extreme in the study sites (Figure 3–3). The monthly rainfall variability of 55-years of data from stations within a 100 km radius around Palembang ranged from 6 to 23% of the means. The greatest variation occurred during heavy rainfall periods. Ribero and Adis (1984) found similar spatial patterns in the Central Amazon region. Rainfall variability, however, was greater during the dry season than in the wet season. The high dry-season variability was attributed to a combination of local convergences, orographic lifting and diurnal heating.

Alternatively, Chambers and Manan (1978) could not determine any spatial patterns for convective rainfall in coastal South Sumatra based on topography. Rahim (1983) also concluded that there should be no orographic effects in the peat deposits due to topography and that convective rainfall could probably be correlated with local

wind behavior. No subsequent studies comparing frontal, orographic and convective rainfall could be found for the study sites.

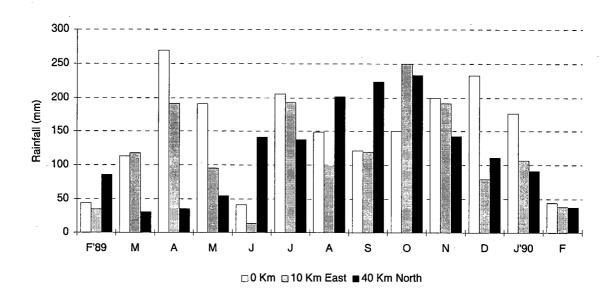


Figure 3–2. Small-scale spatial differences in monthly rainfall in 1990 among three locations within a 40 km radius at Padang Island, Riau.

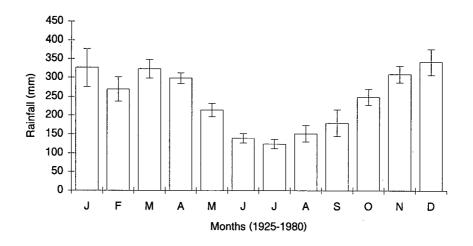


Figure 3–3. Mean monthly rainfall and 95% confidence intervals from eight locations within a 100 km radius around Palembang, South Sumatra. Calculated from 55 years of data (after Government of Indonesia 1984).

Temporal Variability

Rainfall patterns on the east coast of Sumatra vary over increasing time scales from intra-annual daily and monthly rainfall variability, to inter-annual dry period frequencies, and to longer-term climatic changes. The two study regions on the east coast of Sumatra were classified by both Koppen (*ibid.*) and Schmidt and Ferguson (*ibid.*) as humid and ever-wet. However, because of the various ways in which rainfall is generated, a high proportion falls in short, intense storms which may be separated by relatively dry periods. Both the frequency of rainfall events and the mean daily intensity were recognized as important characteristics of climate for hydrological studies related to forestry and agriculture (Jackson 1986).

The intensity and duration of rainfall in Sumatra has only been analyzed to a limited extent because of a lack of accurate and continuous records. Halcrow and Fox Consultants (Government of Indonesia 1984) analyzed the available 3.5 years of hourly rainfall recorded at Palembang (Telang Betutu). They estimated from the limited data that up to 60% of annual precipitation falls at a moderate intensity of greater than 25 mm hr⁻¹, and that up to 15% falls at a higher rate of over 100 mm hr⁻¹. They also suggest that in the dry months of July and August, the proportion of high intensity rain can reach 70 to 75% of total monthly rainfall. At the same time, high intensity rainfall is common in other tropical regions. Brünig (1971) estimated that in Sarawak three quarters of annual precipitation falls at moderate to heavy intensities (greater than 25 mm hr⁻¹) as convective rainfall. In forested catchments on peninsular Malaysia, Rahim (1983) measured maximum rates of 114 mm hr⁻¹.

With local open pan evaporation rates as high as 5.3 mm d⁻¹ (Chambers and Manan 1978, Government of Indonesia 1984) a greater proportion of the moderate to high intensity rainfall should infiltrate the surface layers of peat compared to lower intensity precipitation, much of which is intercepted in the forest canopy. Another factor enhancing infiltration of higher intensity rainfall is the characteristically flat topography of the ombrogenous peat deposits in Sumatra. In the moderate to deep peat deposits there were few open streams, suggesting both high infiltration and low rates of surface water runoff.

Temporal Variability of Days to Months

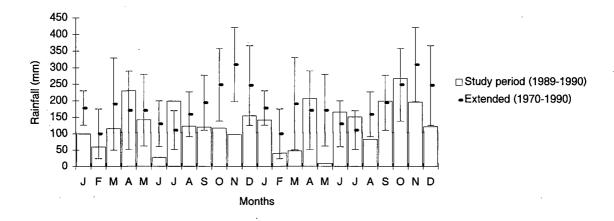
When the time scale of moisture inputs was extended over months, the pattern of rainfall intensity appears to shift. In Sumatra, the percentage of rainfall in excess of 50 mm d⁻¹ was low with the fewest days occurring in July

and the most in December. Chambers and Manan (1978) calculated that the amount of rain per rain day was significantly less in the dry season than in the wet season. At the Sungsang climate station (Figure 2–1) the dry season wet-day average was 11–13 mm d⁻¹, while the wet season average was 17–20 mm d⁻¹. Moreover, during the dry season total monthly rainfall can occasionally fall in one day, and 50% in one day was not uncommon.

Occasional dry periods were also common in the study regions. Chambers and Manan (1978) performed an analysis of dry-period frequency on Palembang data and found that during the dry months, from June to September, the percentage occurrence of no rainfall over seven days ranged from 17 to 26%. Again, Brünig (1971) noted that in the humid tropics, months with less than 100 mm of rainfall can occur in almost any season. In an analysis of successive days without rain, he calculated that in Sarawak, 30-day dry periods, with less than 60 mm rainfall, occur on average once a year, even though the long-term average was above 60 mm month⁻¹. Looking at higher rainfall periods of up to 100 mm month⁻¹, he found that these periods could occur three to four times a year in areas receiving up to 3000 mm annually. Considering that open pan evaporation rates along the east coast of Sumatra range from 120 to 150 mm month⁻¹ (Chambers and Manan 1978, RePPProT 1990), and that evapotranspiration rates in peat forest (40 m tall, 5 layers) can reach as high as 170 mm month⁻¹ (from Government of Indonesia 1984, and Brünig 1971), moisture deficits develop for at least part of the year. The occurrence of a moisture deficit in peat deposits would depend on the effect of the previous month's rainfall on peat water table levels. The importance of the water table leads this discussion to a consideration of longer climatic time scales, i.e., wet and dry periods extending over months up to years.

Temporal Variability of Months to Years

At Padang Island, 10 of the 24 months of the study period had rainfall below the standard deviation range of the 20-year record, while only one month exceeded the upper range (Figure 3–4a). Of the 24 months, 54% fell within the upper and lower ranges. Rainfall in November 1989 and May 1990 exceeded the lowest monthly totals recorded between 1970 and 1988.



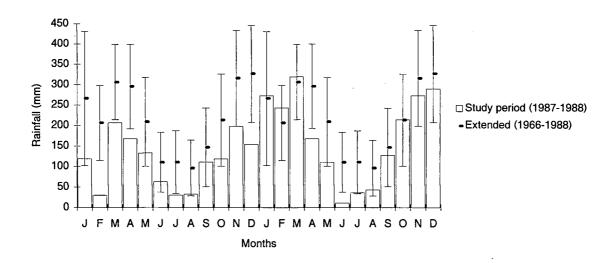


Figure 3–4. Comparison of monthly rainfall at the Padang Island (top) and South Sumatra (bottom) study regions during the study periods against average (± 95% CI) monthly totals of long-term rainfall records.

The study period coincided with an El Nino Southern Oscillation (ENSO) event which took place in 1990 and 1991, resulting in elevated sea surface temperature in the western equatorial Pacific ocean. As the higher temperature water moved eastwards, there was a corresponding shift of the region of tropical storm genesis, and precipitation in Indonesia declined (Rasmusson and Arkin 1984). Quinn *et al.* (1978) found that Indonesian droughts between 1830 and 1953 corresponded well with the El Nino events. Moreover, it is now recognized that ENSO is the most dominant element of the inter-annual variability of global climate. During the study period, the

ENSO event had its strongest effect on Sumatra rainfall during the last half of 1990 and all of 1991 (the monthly progress of the ENSO event is described in NOAA 1987–1992).

Monthly rainfall during the study period in South Sumatra was also highly variable. Similar to Padang Island rainfall, it was below average (Figure 3–4b). This was attributed to the ENSO event which occurred in 1986 and 1987 (NOAA 1987–1992). Both Barnett *et al.* (1988) and Ramanathan and Collins (1991) described this ENSO event in detail, with rainfall in all months of 1987 below average. Beginning in January 1988, after the ENSO event, precipitation began falling within the long-term ranges. In seven of the 24 months of the study period, the rainfall exceeded the lower range of the 22-year average. Again, during the ENSO period in 1987, rainfall in February, June and December exceeded the 20-year lower range.

The dry period frequency analysis illustrated in Figure 3–5 was calculated for South Sumatra using 55 years of rainfall data (from Government of Indonesia 1984). The low rainfall periods in the South Sumatra study sites in July 1987 and 1988 were wetter than the 1 in 10 year occurrence of a 92-day (26 + 34 + 32) rainless period predicted in the frequency analysis. Extended dry periods have been recorded elsewhere in the region by Hanson and Koesoebiono (1979). Woods (1987) noted that at Sandakan, Sabah on the Island of Borneo, there have been 7 periods in 56 years when total rainfall over three consecutive months was less than 100 mm. These observations show that although rainfall levels were low during the study periods, they did not fall outside the extremes of the recent historical rainfall patterns in the regions.

A comparison of the study period rainfall with the longer-term records suggests that the 20-year records (Figure 3–4a, b) do not reflect the low rainfall during ENSO events. According to analyses by Quinn *et al.* (1978) and Ghil and Vautard (1991), ENSO events occur at a frequency of 3 to 7 years. Along the east coast of Sumatra the years 1972, 1977 and 1982–83 were notable for drought conditions associated with ENSO events. Annual rainfall in 1987 averaged 63% below the 65-year average and was lower than both the 1972 and 1982–1983 totals (Table 3–1). However, the cumulated rainfall during the driest months in 1987 ranged from 28 to 88% of the 65-year mean monthly rainfall totaled over the same months. In recent years in Sumatra, the most intense drought occurred in 1982 when the total rainfall during the driest months of July, August and September was only 4 to 9% of the 65-year mean monthly rainfall totaled over the same months. Such dry period extremes have been recorded in other tropical forest regions of Southeast Asia. For example, in Sabah, Woods (1987) calculated that rainfall during the driest months of the 1982 ENSO event was 36 to 44% of the long-term mean monthly rainfall for the same months.

Again, Leighton and Wirawan (1985) confirmed that repeated droughts occur in East Kalimantan. They matched 9 of the 10 droughts over the past 44 years to ENSO events.

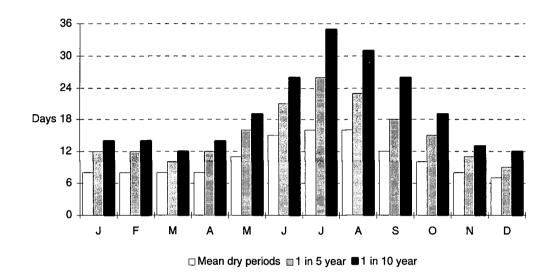


Figure 3–5. Long-term dry period frequency analysis based on 55 years of data from 8 stations in South Sumatra. Days listed on the Y-axis are dry days with mean rainfall less than 0.15 mm d⁻¹ (after Government of Indonesia 1984). The analysis shows that a 1 in 10 year dry period can last as long as 92 days.

In summary, both study periods in the two Sumatra regions were drier than average, but wet months did occur and most of the monthly rainfall was not outside the recorded limits. The above discussion highlights that when considering moisture inputs to peat, total annual precipitation may be less important than the distribution of rainfall throughout the year. High rainfall does not ensure that high peat moisture levels will occur in all seasons, as weekly to seasonal rainfall can influence evapotranspiration from soil and vegetation. Both Chambers and Manan (1978) and Laumonier (1980) have suggested that although a dry season in the peat deposits of South Sumatra was not clearly defined by the current classification systems, potential evapotranspiration may exceed rainfall at least four months annually, usually from June to September. Anderson (1983) also noted moisture deficit conditions in the normally humid peat deposits of Sarawak. Finally, Nieuwolt (1964) estimated that despite high annual rainfall, moisture deficits occur twice a year in Peninsular Malaysia and sometimes last up to six consecutive months. It is evident from this discussion that rainfall patterns vary on annual and inter-annual time scales in the peat regions of

Southeast Asia. Whether this level of variability has occurred throughout the genesis and development of the Sumatra peatlands is considered below.

Table 3–1. Mean monthly rainfall and percentage of long-term averages for the 1972, 1982 and 1987 El Nino droughts compared to the 65-year rainfall averages in Palembang, South Sumatra (from Telang Betutu).

	1920–85	Mear	monthly rain	fall (mm) and	percentage of	65-yr average	
Months	Mean	1972	%	1982	%	1987	%
J	284	378	133	109	38	119	42
F	242	147	61	185	76	30	12
M	292	. 205	70	299	102	207	71
Α	278	310	111	375	135	168	60
M	207	61	30	340	164	133	64
J .	120	69	58	263	220	62	52
J	105	17	16	6	6	30	28
A	102	8	8	9	9	32	31
S	126	10	8	5	4	111	88
O	193	2	1	80	42	118	61
N	282	184	65	148	53	198	70
D	321	452	141	219	68	154	48
Totals	2549	1843	70	2038	92	1361	63

Temporal Variability of Interglacial Climate Change

To understand the effects of short-term and medium-term rainfall variability in tropical peat deposits, it is necessary to consider the patterns of climate fluctuations beyond the two year study periods. Numerous researchers have hypothesized about the climatic conditions prevailing during the initial period of peat accumulation. Both Morley (1982) and Morley and Flenley (1987) have suggested that the kinds of historical events leading to the initiation of coastal peat deposits in Southeast Asia are allogenic changes of three main types: sea-level changes; temperature changes; and changes in rainfall quantity and seasonality.

After the last glacial maximum, 18 000 years before present (18 ka), sea-levels in Southeast Asia rose rapidly and reached just above their present levels near 6 ka (Williams 1985). Tjia and Fuji (1989) estimated that at 6 ka, sea-levels in the Malacca Strait transgressed to 5 m above current levels. They then dropped step-wise over 1

ka intervals. During one of the regression periods in the late Holocene (1.2 ka), sea levels probably dropped below current levels and have since risen. Sea-level decline must have been a dominant factor in the deposit of the vast alluvial plain along the entire east coast of Sumatra 5 ka before present (Verstappen 1973), with peat initiation soon after. According to the radiocarbon dating of Diemont and Supardi (1987a), peat began accumulating along the east coast of Sumatra at about 4.8 ka. Peat also began accumulating on the Island of Borneo around the same period.

Morley (1981) noted that the base of the peat domes in Southern Kalimantan and Sarawak have been dated to the mid Holocene at 5 to 6 ka.

The peat-clay boundary is currently found between high water level and mean water level in South Sumatra (Ministry of Public Works 1984). Silvius *et al.* (1984) studied peat deposits in the Berbak Reserve in Jambi Province, Sumatra. They mention the possible occurrence of coastal uplifting prior to peat initiation to explain the presence of higher than present sea-levels. Tjia and Fuji (1989) claim however, that isostatic crustal movements in the Sunda Shelf region can be ignored within 10 ka periods. No references could be found that cite evidence of recent volcanic or tectonic activity in the coastal region. Regardless of past sea-level changes, most peat deposits are protected from tidal inundation by levees of sediment and mangrove forest. However, there were areas along the coast where the recent sea level rise has caused considerable changes to peat deposits. Cliffs up to 3 m in height of exposed and eroding peat were found along the western coastlines of Padang and Tebing Tinggi Islands.

Temperatures were also lower during the last glacial maximum with sea-surface temperatures being 2 to 3°C below present temperatures (Whitten *et al.* 1984). From about 12 to 5 ka, temperatures increased in Sumatra. As a result of the increase, the glaciers in the Gunung Leuser mountains melted between 14 and 7.6 ka (Morley and Flenley 1987). It is not known whether temperatures for Sumatra for the past 5000 years have been estimated. Temperatures were likely 1 to 3°C higher than present, similar to New Guinea (Crowley and North 1991), tropical Australia (Williams 1985 and Walker *et al.* 1984) and tropical South Asia (Dickinson and Virji 1987). Higher temperatures were also thought to have occurred in northern peat deposits during this period. Payette (1988) hypothesized that in Eastern Canada temperatures and air humidity were higher between 5.1 and 3.2 ka, and that these conditions were necessary for the initiation of peat accumulation. During the late Holocene around 3.5 ka, the climate became cooler and drier (Crowley and North 1991). Remaining consistent with this temperature pattern, Solomon and Tharp (1985) estimated that carbon storage increased to a maximum level 9.5 to 4.5 ka ago and has since declined to an intermediate amount by present day.

During the early Holocene 11 to 7 ka ago, rainfall was higher and the wet season was longer in Southeast Asia (Williams 1985). Higher rainfall has also been suggested to have occurred at this time in sub-Saharan tropical Africa (Sieffermann *et al.* 1988), tropical South America (Dickinson and Virji 1987), sub-tropical Queensland (Walker et al. 1984) and the Tibetan Plateau (Gasse *et al.* 1991). Higher rainfall rates would have increased outflows from rivers and perhaps have produced the sediment plain upon which the Sumatra peatlands developed. Morley (1981) suggests that ombrogenous peat development in central Kalimantan may have been initiated by a change to less seasonal rainfall during the mid Holocene. Increased rainfall was the main reason Morley used to explain the progression from a 1 m topogenous peat at 4 ka, to the present 7 m thick ombrogenous peat deposit in the Sebangau River area near Palangkaraya.

Sieffermann *et al.* (1988) studied peat deposit development in Kalimantan. Their findings suggest that following the hotter and more humid period during the mid-Holocene there has been a strong decrease in rainfall over the past 5.5 ka. They claim that increased seasonality is responsible for the current process of peat regression occurring in deposits in Kalimantan located on ancient river benches (high peats). Drying during this period has been noted elsewhere. Williams (1985) stated that much of Australia became drier with more erratic summer rainfall after 4.5 ka. Morley (1982) found charcoal at the bottom of peat deposits in upland Sumatra which he attributed to widespread vegetation burning during drier periods just prior to peat accumulation.

Of the three environmental factors discussed above, long-term temperatures changes are the most uncertain and difficult to predict. The influence of temperature changes on evapotranspiration from peat forests may exert a stronger influence on the water balance and subsequent peat accumulation than do changes in rainfall. A climate without a pronounced dry season and high rainfall was considered by Kostermans (1958) as being necessary for the large-scale peat development that occurred on the east coast of Sumatra. Payette (1988) described the spatio-temporal development of a peat deposit in eastern Canada in such a way that the influence of climate and plant succession was effectively separated. His study demonstrated the importance of processes such as water table fluctuations, organic matter dynamics and forest succession within the slower processes of climatic changes. Payette (*ibid.*) and Starkel *et al.* (1991) proposed that hydrological balances in temperate peat deposits have changed since their initial development. Their studies suggested that high temperatures and associated high rainfall initiated peat development thousands of years ago. Since then temperatures and rainfall have declined, but the lower evapotranspiration rates associated with the temperature drop have helped to maintain the peat deposits. Whether

this sequence of events has occurred in the coastal peat deposits of Sumatra cannot be assessed until longer-term climate patterns are reviewed.

Temporal Variability of Interdecadal Climate Change

Climatic changes over tens to hundreds of years are even less certain than the changes that occur during interglacial periods. Climatic data compiled by Berlage (1949) from 1879 to 1941 for outside Java is the longest continuous record available for Sumatra. Unfortunately, more recent records are less complete. In a review of recent Indonesian climatic records, Fontanel and Chantefort (1978) found that few climate stations have continuous series of observations for more than 30 years. Many stations have 10 years of data or less. In one of the few studies of long-term climatic change in Indonesia, Chambers and Manan (1978) compiled all available rainfall data between 1915 and 1975 from 12 stations in and near the South Sumatra peat deposits. They could detect no trend towards wetter or drier conditions and emphasized that the extreme year to year variability complicated the analysis (*CV* = 20%). Laumonier (1980) analyzed Sumatra climate as part of a vegetation classification study. He could not find any evidence that there has been a change in climate since large portions of South Sumatra were deforested at the turn of the century.

On a global scale, Bach and Jain (1991) estimated that the mean global long-term natural temperature change between glacial and interglacial periods is in the order of approximately 0.01° C 100 a^{-1} . They showed that this rate has been enhanced since the beginning of the industrial revolution rising to 0.6° C 100 a^{-1} . Similarly, Ghil and Vautard (1991) have analyzed global surface temperatures for the past 135 years. The results of their analysis showed a warming trend with a small number of oscillatory modes separated from the noise. The temperature trend was flat until 1910 with an increase of 0.4° C since then. The increase is in relative agreement with the Bach and Jain data. Crowley and North (1991) also suggested that the last 50 years may have been the warmest period in the last 10 000 years.

Two distinctive oscillations within the increasing temperature pattern were noted by Ghil and Vautard (1991), each ranging from 1.0 to 1.5°C. One oscillation is interdecadal and attributed to solar variability and ocean warming during ENSO events. The other is bidecadal, but remains poorly understood. The authors found that seasonal distribution of rainfall at Adelaide, Cape Town and Santiago oscillated on a 23-year cycle. This oscillation

is thought to be associated with changes in deep water ocean circulation outside the tropics (Weaver *et al.* 1991, Charles and Fairbanks 1992).

3.2.2 Rainfall Patterns and Peat Depth

The review of rainfall patterns above suggests that the rainfall regimes of the study sites in South Sumatra and Riau were similar. It is evident that at present, the deeper accumulations of peat in East Sumatra are not associated with higher rainfall. In comparing peat deposits of these two regions, Polak (1933) observed that the depths of peat domes are not more than 7 m in South Sumatra, whereas in Jambi and Riau Provinces they can reach up to 15 m, with no large difference in rainfall. Others have observed similar conditions elsewhere. In a North Selangor peat deposit in Malaysia, Low and Balamurugan (1989) measured maximum peat depth at 5 m. This peat area receives 2000 mm of rainfall annually, about 400 mm less rainfall than recorded at the South Sumatra peat deposits which have a maximum depth of about 6 m. Conversely, Sieffermann *et al.* (1988) estimated that the high peat deposits around Palankaraya in Kalimantan have been in a state of decomposition for the last 2500 years. Annual rainfall in this area is 2800 mm which is higher than both the medium peat and deep peat study sites in Sumatra. The relationship between peat depth and rainfall cannot be fully understood without knowing the duration of peat accumulation in the deposits to be compared. Peat ages in the study sites are discussed in Chapter Four.

3.3 VEGETATION ANALYSIS

To assess the similarities and differences in vegetation between the sites located on peat deposits of increasing depth, several features were characterized including: composition, vertical structure, spatial distribution and stand history.

3.3.1 Vegetation Composition

The forest types distinguished during initial field visits to the sites were confirmed by Cluster Analysis (CA) of the relevé plot data (Figure 3–6). The CA grouped the ten plots into four clusters of study sites of decreasing similarity in the order: PI12 > PI9 > PS3 > SE6 and PI6. The tall and low pole forest types were less similar to each other compared to the two mixed forest types on 6 m and the chablis forest type on 3 m of peat. This was largely due to the heavy dominance of *Calophyllum* spp. in PI9.

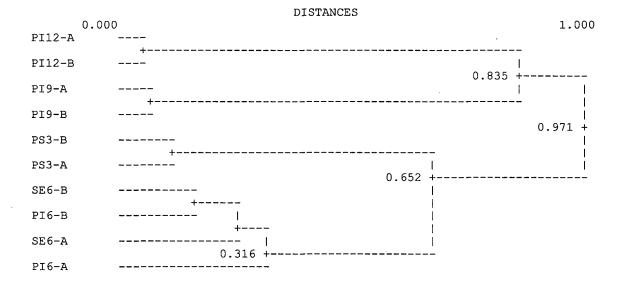


Figure 3–6. Hierarchical tree diagram of increasing amalgamation distances. The Cluster Analysis results were based on species composition and abundance data from the 10 study plots (PI-Padang Island, PS-Padang Sugihan, SE-Sugihan East). Shortest horizontal distances indicate most similar plots.

Differentiating plants in the plots of each forest type and character plants of the study area are listed in Table 3–2. Photographic plates of site features are included at the end of Chapter 3. In order of decreasing abundance, *Garcinia* sp. followed by *Shorea teysmannia*, *Shorea leprosula*, *Diospyros* sp., *Palaquium rostratum* and *Campnosperma auriculatum* were found in all plots of all forest types. *Eugenia* sp. was most abundant in each of the forest types. *Cyrtostachys lakka*, *Thorocostachyum bancanus* and *Timonius* spp. were also common. Most of these plants were restricted to primary forest and were not found in nearby degraded mixed forest, possibly because of the drier soil conditions resulting from peat drainage.

Table 3–2. Summary table showing differential and character plants in the five forest types. The figures are percent constancy/mean cover-abundance class.

Study area	3 m deposit	6 m deposit		12 m deposit	
Site	PS3	SE6	PI6	PI9	PI12
Forest type	Chablis	Mixed	Mixed	Tall pole	Low pole
1. Differential plants	•				
Macaranga triloba	100/1				
Sageraea lucida	100/0.5	50/0.5			
Licuala spinosa	100/4	100/1	100/0.5		
Koompassia malaccensis	100/2	100/2	100/1		
Dyera costulata		100/1	100/2		
Euphoria malaiensis		100/0.5	100/0.5		
Bruguirea sp. 1		100/0.5	100/0.5		
Freycinetia javanica		100/0.5	100/0.5		
Freycinetia sumatrana		100/0.5	100/0.5		
Ganua motleyana		100/0.5	100/1		
Cratoxylon arborescens		100/0.5	100/1		
Syzyium anticepticum		100/0.5	100/1	100/2	
Canarium sp. 1				100/0.5	
Xanthophyllum heteropleureum				100/0.5	
Calophyllum costulatum			100/0.5	100/4	100/1
Calophyllum ferrugineum			100/1	100/3	100/1
Tristania obovata		,		100/0.5	100/3
Calophyllum sundaicum	•			100/0.5	100/3
Nepenthes reinwardtiana				100/0.5	100/1
Pandanus artocarpus		100/0.1	100/0.5	100/1	100/2
Shorea leprosula	50/0.1	50/0.1	100/0.1	100/0.5	100/2
2. Character plants					
Thoracostachyum bancanus		100/4	100/3	100/1	100/0.5
Garcinia rostrata	100/1	100/0.5	100/1	100/3	100/2
Diospyros maritima	100/0.5	100/2	100/2	100/0.5	100/0.5
Palaquium rostratum	100/1	100/0.5	100/0.5	100/0.5	100/0.5
Campnosperma auriculatum	100/0.5	100/0.5	100/1	100/0.5	100/0.5
Cyrtostachys lakka	50/0.1	100/0.1	100/0.1	100/0.5	100/0.5
Eugenia sp. 1		100/1	100/2	100/2	100/3
Shorea teysmannia	100/1	100/1	100/2	100/0.1	50/0.1

Cover-abundance classes are defined in Appendix 2.1. Complete plant names are listed in Appendix 2.2.

In order of decreasing abundance Eugenia spp., Calophyllum costulatum, Calophyllum ferrugineum, Pandanus artocarpus, Tristania obovata, Calophyllum sundaicum, Shorea spp., Stemonurus spp., Pandanus sp. were common in the tall and low pole forest types. These forest types have not been described in detail in other published studies of peat forests in Sumatra and Kalimantan.

Anderson (1976b) surveyed peat forests at Telok Kiambang near the Indragiri River, and at Muara Tolam near the Kampar River in Riau Province. He listed many of the species mentioned above, but did not describe the association of *Eugenia, Calophyllum, Pandanus* and *Tristania* found on Padang Island. He noted that there were extensive Padang/Pole forests near the Siak Kecil River in Riau. However, the vegetation of this area is not well documented. Stevens (1980) noted that *Calophyllum costulatum, C. ferrugineum* and *C. sundaicum* grow together in peat forests in South Jahore, Malaysia.

PS3-Chablis Forest

Much of PS3 study site was chablis forest (Laumonier 1980) characterized by an open canopy likely due to the selective logging in the mid 1970's. Emergent trees included *Koompassia malaccensis, Palaquium* spp., *Xylopia* spp., *Campnosperma coriaceum* and *Ficus retusa* (Plate 3–1). The main canopy was occupied by *Macaranga triloba* and *M. tanarius* which appeared following canopy openings by logging. Cover in the subcanopy varied from 60 to 100% and was dominated by *Licuala spinosa* with occasional *Salacca conferta* and *S. edulis*. Shrubs were mostly absent and herb cover was sparse with large areas of bare forest floor under the heavy *Licuala* subcanopy. Where sunlight reached the ground, ferns *Asplenium longissimum*, *A. nidus*, *Nephrolepis biserrata* and *N. hirsutula* were abundant.

According to the inventories taken prior to selective logging in the mid-1970's, PS3 was originally similar to SE6 forest type (Dept. of Agriculture 1970, 1971a, 1971b). Selective logging removed many trees including *Koompassia, Dyera, Gonystylus* and *Shorea*. Following drainage of the area in the early 1980's, the *Pandanus, Thoracostachyum and Freycinetia* spp. have disappeared, while it is likely that *Macaranga, Nephrolepis* and *Stenochlaena* spp. have increased in abundance under the drier secondary conditions. Whitmore (1969) described the dominant role of *Macaranga* in secondary forests in Malaya.

The main canopy of SE6 was more open than in PS3, allowing direct sunlight to the forest floor. The canopy was dominated by Diospyros maritima, Koompassia malaccensis, Dyera costulata, Gonystylus bancanus, Campnosperma auriculatum, C. coriaceum, Shorea leprosula and S. teysmannia. A sparse subcanopy contained Diospyros maritima, D. siamang, Eugenia spp., Koompassia malaccensis, Licuala spinosa, Pandanus artocarpus and Pandanus spp. Herb cover was mostly continuous in the stand with sunlight reaching through the high canopy to the forest floor. Herbs included Thoracostachyum bancanus, with Freycinetia spp. and Alocasia longiloba common. Maranthes spp. and Litsea spp. were common low shrubs.PI6-Mixed Forest

The main canopy of PI6 was similar in composition to SE6 with relatively abundant tree species including: Tetramerista glabra, Gonystylus bancanus, Shorea leprosula and S. teysmannia, Campnosperma auriculatum, C. coriaceum, Koompassia malaccensis, Cratoxylon sp. and Dyera costulata (Table 3–2). A sparse subcanopy contained Diospyros maritima, Tetramerista glabra, Eugenia spp., Koompassia malaccensis, Licuala spinosa, Pandanus artocarpus and Pandanus spp. Herb cover was mostly continuous in the study plots with sunlight reaching through the high canopy to the forest floor. Herbs included Thoracostachyum bancanus, with Freycinetia spp. and Alocasia longiloba also common.

PI9-Tall Pole Forest

Located along the outer edge of the deep peat area, the PI9 was characterized by an abundance of Calophyllum costulatum, C. ferrugineum and C. sundaicum trees. Other abundant trees included Garcinia parviflora, G. rostrata and Eugenia spp. The subcanopy was sparse and mainly occupied by Pandanus artocarpus, Canarium spp. and kayu degemo (v). The shrub layer was heavy, providing up to 70% cover and was dominated by Dillenia spp. Garcinia spp. and Eugenia spp. suckers (ramets) and saplings, and the shrub Syzygium anticepticum. The forest floor was sparsely covered (approximately 30%) with mainly Pandanus spp., Thoracostachyum bancanus and Nepenthes spp. Average leaf area on the canopy trees appeared to decrease from PI9 to PI12. It is not known whether the difference was due to changes in species composition, or to physiological changes in species common to both stands.

The main canopy trees of PI9 were dominated by *Calophyllum* spp. which occupied 70 to 80% of the total basal area. This degree of dominance seldom occurs in tropical forests and was likely to represent a wave of stand

regeneration following some significant past disturbance. The heavy dominance of *Calophyllum* spp. in PI9 produced a sharp structural and composition change compared with PI6 mixed peat forest located on the outer edge of the rand of the Padang Island peat deposit (Plate 3–2).

PI12-Low Pole Forest

Eugenia spp. and Tristania obovata were the dominant trees in the canopy layers, with lesser numbers of Calophyllum sundaicum, Pandanus artocarpus, Shorea teysmannia, S. smithiana and Garcinia spp. present. The low shrub (B2) layer was extremely sparse and contained mainly Pandanus spp., Calophyllum sundaicum, Ilex cymosa, Garcinia parviflora and Timonius flavescens. The herb layer was also sparse with Nepenthes spp., bakong api² and Thoracostachyum bancanus, providing 10% cover over the bare forest floor.

3.3.2 Ordination of Forest Types

PCA ordination was used to transform the plot data to dimensions that reveal relationships between plots (Ludwig and Reynolds 1988). The gradients of each axis illustrated in Figure 3–7 were related to differences in species composition and abundance. The first three PCA axes accounted for 72% of the total variation in the species-plots matrix. The ordination agreed with the initial classification of the plot data using Cluster Analysis (Figure 3–6). Axis 1 contained the largest dissimilarity between plots and accounted for 33% of the variation in species composition and abundance between study plots. The PS3 forest type (plots I and J) was the least similar grouping of plots because of the dense shrub layer and diverse, but highly uneven canopy layer (due to selective logging). The second axis accounted for 22% of the total variation. It grouped the Padang Island plots A, B, C and D together, indicating the relative similarity of plots on deep peat compared to the mixed forest stands on 6 m peat (E, F, G and H). The third axis accounted for 17% of the variation with the greatest dissimilarity between plots in the tall (PI9) and low (PI12) pole forest types in the deep peat deposit on Padang Island. Less *Calophyllum* spp. and reduced shrub and herb layers in the low pole forest study plots accounted for the difference. Similar to the Cluster Analysis, the PCA results did not reveal differences in species composition and abundance among the mixed forest types on 6 m of peat in the Sugihan East and Padang Island peat deposits.

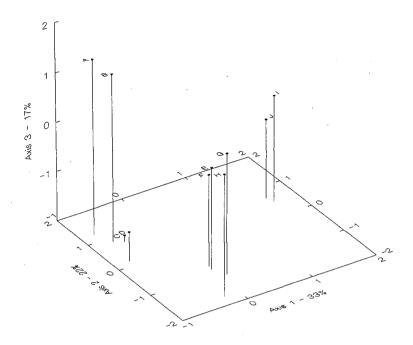


Figure 3–7. Principal components ordination of the ten peat forest plots based on species composition and abundance. Three components or axes explain 72% of the total variation. $\underline{A+B}$ = low pole forest (PI12); $\underline{C+D}$ = tall pole forest (PI9); $\underline{E+F}$ = mixed forest (PI6); $\underline{G+H}$ = mixed forest (SE6); $\underline{I+J}$ = chablis forest (PS3).

3.3.3 Aboveground Forest Structure and Stand History

PS3-Chablis Forest

With tree diameters (dbh) ranging from 10 to over 80 cm (mean of 25 cm), PS3 chablis forest represented the most heterogeneous forest type overlying medium depth peat. Tree density (1036 to 1131 trees ha⁻¹) was lower in PS3 than in SE6 forest type, likely due to previous logging. The selective logging had resulted in a multi-cohort forest stand in which a new age cohort had developed in the subcanopy (Figure 3–8).

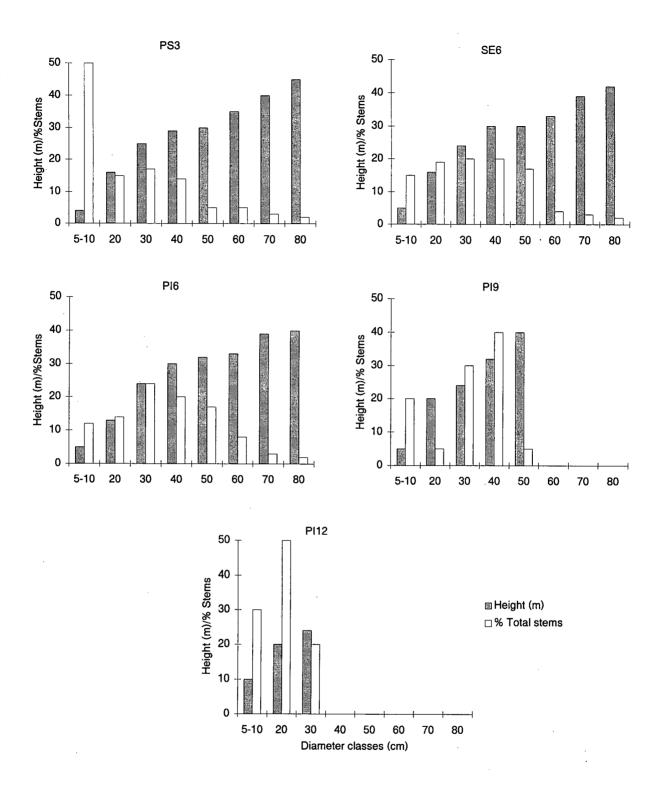


Figure 3–8. Distributions of height and stem classes according to tree diameter (>5 cm dbh) illustrate the structural differences among forest types in the five study sites in East Sumatra.

Previous logging also affected the horizontal distribution of trees in the PS3 forest type. The dense subcanopy of *Licuala* dominated the distribution pattern, creating a random, rather than clumped distribution as was seen in the other study sites. Point-to-tree and tree-to-tree distance measures did not vary as widely as in the other forest types (Table 3–3). This pattern was attributed to tree regeneration by seedlings rather than by root suckers, as was common in the deep peat forest types. In the pole forest study sites, both *Pandanus* and *Calophyllum* regenerated vegetatively in clumps, but these species were not present in PS3 which was selectively harvested in the 1970's. Muktar (1986) also performed forest surveys in the Padang-Sugihan peat deposit forest. His basal area measurement was slightly lower (45.2 m² ha⁻¹) than that of the present study (51.7–56.4 m² ha⁻¹) for reasons not understood and indices of variability about the mean basal area were not provided.

SE6-Mixed Forest

The 25 m main canopy of SE6 forest type in Sugihan East, South Sumatra was similar in cover percentage and height to PI6 forest type over medium depth peat on Padang Island discussed below, but contained numerous emergent trees extending 10 to 20 m above the main canopy. The subcanopy reached 15 m and consisted of pole trees, perhaps suppressed by limited sunlight. Forest cover was moderate, ranging from 40 to 60% (Table 3–2 and 3–3). The subcanopy had 25% cover, while shrubs and herbs provided 98% cover which was the heaviest of all study sites.

With tree diameters ranging from 10 to 50 cm, the SE6 plots represented typical mixed forest overlying medium depth peat in Sumatra. Species composition of this forest type has been recorded in Sumatra by Anderson (1976b), Laumonier (1980), Silvius *et al.* (1984) and RePPProT (1988). Forest inventories of peat tree species have been performed by the Institute Pertanian Bogor, the Ministry of Agriculture and Departemen Pertanian³. The inventories focused, however, on commercial species (a small and variable number of the total species) and do not include structural analysis of the forest stands.

Tree density was highest in SE6 (742–2134 trees ha⁻¹). The lower value was derived from measures of tree-to-tree distances while the higher one represents random point-to-tree distances (Table 3–3). The variability in measurement distances indicates that tree distribution was clumped. *Gonystylus bancanus* forms the most obvious groups. Combining data from the two distance measures together gives a stand density of 1207 to 1316 trees ha⁻¹.

Table 3-3. Summary of spatial and structural forest characteristics of the five study sites in East Sumatra.

	Study area and site							
	3 m deposit	6 m deposit		12 m deposit	t			
Characteristics	PS3 chablis	SE6 mixed	PI6 mixed	PI9 low pole	PI12 low pole			
Vertical distribution:					•			
A canopy height (m)	25 ± 10	25 ± 5	27 ± 5	32 ± 5	. 11 ± 4			
A canopy cover (%)	20 ± 2	50 ± 10	40 ± 10	50 ± 20	40 ± 5			
B canopy height (m)	4 ± 1	15 ± 1	18 ± 2	10 ± 4	2 ± 1			
B canopy cover (%)	70 ± 1	20 ± 5	20 ± 5	20 ± 10	10 ± 2			
Shrub height (m)	2 ± 1	2 ± 2	2 ± 1	3 ± 1	1 ± 1			
Shrub cover (%)	20 ± 10	98 ± 2	75 ± 8	60 ± 20	5 ± 2			
Mean tree diameter (cm)	25 ± 25	24 ± 19	23 ± 22	13 ± 9	10 ± 5			
Peat depth (m)	2-3	4–6	5-6	8–9	11–12			
Basal area range (m² ha ⁻¹)	52–56	53-58	51–57	7 –11	4–5			
Wood density range (g cm ⁻³)	0.45-0.65	0.45-0.65	0.48-0.76	0.54-0.77	0.54-0.85			
Tree stem biomass (Mg ha ⁻¹)	395–623	407–641	384–593	85–177	13–24			
Spatial distribution:								
- Mean distance (cm)§ (tree-to-tree / point-to-tree)	130 / 144	104 / 158	138 / 167	143 / 189	162 / 269			
- Hopkins index of pattern	0.52	0.60	0.56	0.57	0.62			
- Distribution type	random	clumped	random	random	clumped			
Stand density (trees ha ⁻¹) (95% CI)	1036–1131	1207–1316	1105–1238	712–1034	473–597			

Note: Standard deviations (± 1 SD) are indicated. Where not significantly different (P < 0.05), plot results are combined within forest types (n = 20–24 trees >5 cm dbh). §Distance measures (numbers separated by slash marks) are separate averages of tree-to-tree and point-to-tree distances. The averages are presented separately to compare the results of the two survey methods. A Hopkins index value of 0.60 indicates clumped tree distribution.

The SE6 plots contained the highest basal area (53–58 m² ha¹) and tree stem biomass (407–641 Mg ha¹) of all study sites. The aboveground biomass was comparable to the biomass of lowland mixed forest. A review of studies in Sumatra showed that measurements of standing volume range from 134 to 200 m³ ha¹ and total aboveground biomass can reach 500 Mg ha¹ (RePPProT 1988). Similarly, in East Kalimantan, Yamakura *et al.* (1986) measured aboveground biomass of 509 Mg ha¹ of which leaf, stem and branch biomass measured 6.5, 420,

and 80 Mg ha⁻¹, respectively. The only other reliable estimate of tree phytomass in peat deposits was from Brünig (1990). Measurements in a *Shorea albida* stand at Batang Lupar, Sarawak showed a basal area of 38 m² ha⁻¹. The tall *Shorea* in Sarawak contains 1150 Mg ha⁻¹ of biomass—double the amount of biomass in the SE6 plots.

According to Brünig, the biomass was high, but not unusual in Sarawak.

An analysis of diameter class and height distributions of PS3 and SE6 forest types illustrates the structural differences among the different peat deposits (Figure 3–8). The height-diameter distribution shows the larger number of trees in the 20 to 30 m canopy layer in SE6. In contrast, PS3 contained a large number of small diameter (5–10 cm) secondary trees in the shrub layer. This may be partly due to the effects of canopy opening during selective logging and improved soil condition following artificial drainage.

Vegetation in the SE6 plots was comparable to lowland mixed forest on mineral soil, with slight differences. Few tree species are entirely restricted to the peat deposits, but some are seldom found in other habitats, including *Cyrtostachys lakka*, *Palaquium ridleyi*, *Ganua motlyana* and *Pandanus artocarpus*. When found outside the deposits, many of the peat species are restricted to nutrient poor soils. These include the heavily leached redyellow Podzols on mainland Sumatra and the Kerangas forests on heath over sands found on Bangka Island (Whitten *et al.* 1984).

PI6-Mixed Forest

The 27 m main canopy of PI6 on the outer edge of the rand of the Padang Island peat deposit was similar in cover percentage and height to SE6 in South Sumatra, but contained fewer emergent trees above the main canopy. The subcanopy reached 18 m and consisted of pole trees. Forest cover was moderate, ranging from 30 to 50% (Table 3–2 and 3–3). The sub canopy had 25% cover, while shrubs and herbs provided about 75% cover. Similar to SE6, the plots in PI6 represented typical mixed forest overlying medium depth peat in Sumatra. Tree density was high (742–2134 trees ha⁻¹) with a clumped distribution (Table 3–3). *Gonystylus bancanus* formed the most obvious groups. Combining the data from the two distance measures together gave a stand density of 1105–1238 trees ha⁻¹. The basal area (51–57 m² ha⁻¹) and tree stem biomass (384–593 Mg ha⁻¹) of PI6 study plots were similar to the PE6 plot measurements. Comparison of the distribution of height and diameter classes of trees in PI6 and SE6 forest types illustrated the structural similarities between the two peat deposits (Figure 3–8).

PI9-Tall Pole Forest

The canopy of the PI9 plots on Padang Island was more uniform in height than in PI12 low pole forest. The main canopy layer was at 32 m tall with a subcanopy layer reaching 10 m (Plate 3–3). Forest cover was moderate with the main canopy providing from 30 to 70% cover (Table 3–2). Shrubs and herbs in this stand provided up to 80% cover. Direct sunlight reached 10 to 20% of the forest floor. With a mean tree height and diameter of 32 m and 12.6 cm, respectively, the stand represented the tallest pole forest on Padang Island peat. Stand density in PI9 (712–1034 trees ha⁻¹) was the highest of the pole forest types. The variability in these measurements indicated that tree distribution was more random than clumped (Table 3–3). *Pandanus artocarpus* still formed occasional clumps of trees. The second survey of trees >10 cm dbh showed that the distribution of larger trees was more random than clumped, and stand densities (458–509 trees ha⁻¹) were considerably less variable (Table 3–4).

Table 3–4. Comparison of the tree distribution characteristics in each study site using a 5 cm and 10 cm minimum diameter limit during the surveys.

		Study area and site					
	DBH	3 m deposit	6 m deposit		12 m deposi	t	
Characteristics	limit	PS3 chablis	SE6 mixed	PI6 mixed	PI9 tall pole	PI12 low pole	
Spatial distribution:		_			-		
- Mean distance (cm)*	>5	130 / 144	104 / 158	104 / 158	143 / 189	162 / 269	
(tree-tree / point-tree)*	>10	135 / 168	92 / 157	92 / 157	209 / 234	315 / 340	
- Hopkins index of	>5	0.52	0.60	0.60	0.57	0.62	
pattern	>10	0.55	0.63	0.63	0.53	0.52	
- Distribution type	>5	random	clumped	clumped	random	clumped	
	>10	random	clumped	clumped	random	random	
Stand density:							
(trees ha ⁻¹ 95% CI)	>5	1036–1131	1207-1316	1105–1238	712–1034	473–597	
	>10	742-867	805–949	769–883	458-509	198–220	

Note: Where not significantly different (P < 0.05), plot results are combined within forest types (n = 20-24 trees). *Distance measures (numbers separated by slash marks) are separate averages of tree-to-tree and point-to-tree distances. The averages are presented separately to compare the results of the two survey methods. A Hopkins index value of ≥ 0.60 indicates clumped tree distribution.

As discussed above, the dominance of a single tree species seldom occurs in tropical forests (Connel and Lowman 1989, Richards 1952). The tall *Calophyllum* stand appeared to be a single cohort, possibly a wave of stand regeneration following some significant past disturbance to the peatland (Whitmore 1984a). The regeneration may be the result of either large-scale wind throw caused by a severe storm (Anderson 1964a, Brünig 1973), or due to a natural change in peat drainage brought about by the erosion of the peat-bordered coastline as described above in Section 3.1. Analysis of aerial photographs and satellite images combined with ground checks revealed a clearly visible boundary between PI6 mixed peat forest and PI9 tall pole forest of *Calophyllum* spp (Plate 3–2). The boundary between mixed and pole forest types followed the minimum peat depth contours of approximately 6 to 9 m. Moreover, the peat depth contours appeared to follow drainage patterns of streams and rivers flowing from the inland peat areas to the coast.

Alternatively, the forest in PI9 may have represented a single cohort stand that had developed after a major disturbance. Patches of wind thrown trees up to 2000 m² in area were common and easily detected on aerial photographs and satellite images of the forest type. Whitmore (1991) described Malaysian records of three to four wind storms in the past century that destroyed swathes of forest several kilometers in length and width. Despite the possibility, there was little evidence suggesting that larger patches of wind thrown forest occurred in the recent past. The large amounts of woody debris found in older wind throw patches were not found on the forest floor of the study sites and in the top and base of the acrotelm peat layer of the intact pole forest stands (described in Appendix 2.3).

The age range within the cohort of *Calophyllum* trees may be narrow or as wide as a few decades depending on how long trees continued invading after a disturbance event (Oliver and Larson 1990). As shown in the analysis of height-diameter class distribution (Figure 3–8), the PI9 stand had not reached the stage of understory reinitiation. Although *Calophyllum* spp. seedlings were locally abundant in the sites, older saplings were rare. The single cohort *Calophyllum* stand may also have regenerated following commercial forest clearing. Sewandono (1938) described logging activities on Padang Island at the turn of the century. However, no evidence could be found of past logging in PI9 or other pole forests during the field study (see Appendix 1.4). It was likely that, due to poor access and small tree size in the central expanse of the peat deposit, logging occurred mainly in the mixed peat forest stands near the coast.

Regardless of its disturbance history, the single cohort *Calophyllum* stand in PI9 did not possess the characteristics of a stable forest ecosystem. The apparent lack of regeneration of *Calophyllum* spp. was interpreted as an indication of a future change in the species composition. Many of the understory saplings in PI9 also occurred as canopy trees in PI12. Lack of regeneration of a particular tree species has been noted in other lowland forests in Southeast Asia (Poore 1978). In Sarawak, Primack and Hall (1992) monitored three forest types over 20 years and found that 38 to 47% of the tree species were not represented among the saplings. They concluded that some forests were undergoing successional changes as they recovered from a past catastrophic disturbance.

PI12-Low Pole Forest

The main canopy of PI12 on Padang Island was uniform and averaged 11 m in height (Plate 3–4). Forest cover was the lowest of all forest types with the canopy providing approximately 50% cover and shrubs and herbs 5% cover (Table 3–3). As a result, direct sunlight reached a large portion of the forest floor. The absence of ground cover under high light conditions suggested that edaphic factors were more important in controlling vegetation in this site. A noticeable feature of this forest type was that the leaves of most tree species were smaller (4–10 cm in length, 2–4 cm in width) and more heavily cutinized than those in PI9. Brünig (1971, 1990) noted similar xeromorphic⁴ features of leaves in the Sarawak peat deposits and Kerangas forest over heath.

With a mean tree diameter of 10 cm dbh and an average height of 11 m, PI12 low pole forest represented the most stunted vegetation on Padang Island peat and overlay the thickest accumulations of peat. Low aboveground productivity in PI12 was apparent when the tree height-diameter distribution was compared to that of PI9 (Figure 3–8). Comparison of the distribution classes shows that although tree canopy height decreased from the tall to low pole forest, average stem diameters did not decline significantly (Table 3–3). Brünig (1990) emphasized the danger of using height-diameter relations as an indicator of average life or residence time of trees and aboveground turnover rates of the biomass of the pole forest stands in peat deposits. He proposed that reduction in stand height is more likely to be an indicator of lower growth rates and general ecosystem dynamics in the central zone of peat deposits than in the perimeter zone. Observations in PI12 study plots indicated that aboveground turnover of biomass was low. There was little coarse woody debris on the forest floor and wind throw patches were uncommon (Appendix 2.3). Tree density (473–597 trees ha⁻¹) and basal area (3.8–4.9 m² ha⁻¹) were both low in PI12 study plots, which also suggested lower productivity in this forest type. The aboveground biomass of stem wood (13–24 Mg ha⁻¹) was significantly lower than in PI9 study plots (85–177 Mg ha⁻¹). However, the presence of a thick root

mat in PI12 suggested that the lower aboveground biomass in the pole forests may not solely reflect a decline in total tree biomass, but may be attributed to a shift in shoot/root distribution (Plate 3–5). Measurements of belowground biomass are presented in Chapter 4.

The largest difference in distance measurements (tree-to-tree: 162 cm and point-to-tree: 269 cm) occurred in the PI12 low pole forest (Table 3–3). The large difference confirmed the clumped distribution pattern of trees, particularly of smaller diameter size classes. The use of either distance method alone provided an inaccurate measurement of tree density in the forest. A survey of the literature shows that this type of combined analysis has not been commonly performed in tropical forest studies (see Hall 1991). *Pandanus artocarpus* and *Calophyllum sundaicum* form the most obvious clumps of trees in PI12. With a dense network of adventitious stilt roots, the base of pandan trees formed 40 to 60 cm high and 2 to 3 m diameter tree mounds in the peat. The mounds typically supported 4 to 6 mature trees and were separated by a thick and continuous mat of small and fine roots over the surface layer of peat.

Pole forests of similar structure have been described in other peat deposits in Sumatra and Southeast Asia. Anderson (1976b) surveyed three pole (Padang) forests on mainland Riau and two forests in Kalimantan. The height, basal area and tree densities were similar to PI12 and PI9 on Padang Island. Morley (1981) surveyed a pole forest in a peat deposit in central Kalimantan and recorded high abundance of five species of *Calophyllum* (28% of all tree species). However, Anderson (1983) pointed out that vegetation structure is not well correlated with peat depth. Soepadmo (1987) in Johore, Malaysia, and Silvius *et al.* (1984) and Lee (1979) in Sarawak each surveyed peat forests over deep peat (>8 m). The range of values from the published studies for tree density (1455–1505 trees ha⁻¹), height (19.9–47.8 m) and basal area (28.7–47.8 m² ha⁻¹) were significantly higher than for those on Padang Island.

The catenas of forest types among the three peat deposits of the present study and across Padang Island followed the general vegetation patterns described by Anderson (1961a and 1983) for other peat forests in Southeast Asia. The vegetation changes with increasing peat depth include: a reduction in tree species, a decrease in tree height, a decrease in basal area, an increase in tree stem density, and an increase in surface root biomass from mixed forest to low pole forest. The pole forest on Padang Island was also comparable to Kerangas forest on heath.

Kerangas forests were surveyed in Sarawak by Newbery *et al.* (1986), and in East Kalimantan by Riswan (1981) and Riswan and Kartawinata (1991). The basal areas, stem densities, clumping patterns and species numbers

mentioned in these studies were comparable to those in the pole forests over deep peat on Padang Island. Plants common to deep peat and Kerangas ecosystems include: *Tristania obovata, Calophyllum* spp., *Eugenia* spp., *Tetramerista glabra* and *Nepenthes* spp (Brünig 1974).

3.3.4 Ground-Level Forest Structure

Tree species having straight butts with no adventitious roots occurred in all forest types and peat depths (Table 3–5). Trees with buttresses were more common in medium depth peat than deep peat, while no buttressed trees were found in PI12 over the deepest peat. A similar pattern between sites was also observed for stilt roots.

Table 3–5. Comparison of butt and root characteristics of the dominant tree species found in the five study sites in East Sumatra.

·	Study area and site							
	3 m deposit	6 m deposit	12 m deposit					
Characteristics	PS3	SE6	PI6	PI9	19 PI12			
Tree base:								
- straight butt	+++	+++	+++	+++	+++			
- buttresses	+++	+++	+++	+	0			
Roots:								
- stilt roots	+++	++-+	+++	+++	+			
- loop roots	0	+	+	+++	+++			
- root mounds	+++	+++	+++	+++	+			
- fine root mats*	0	+ .	+	+	+++			
- coarse root mats**	0	+	+	+++	+++			

Note: +++commonly present; +seldom present; 0 not observed. *surface roots with average diameter of <2 mm. **surface roots with average diameter between 2–10 mm.

These observations did not support the thesis that the primary function of stilt roots and flying buttresses is to provide structural stability to trees. Deep peat provides a soft and unstable growing medium for large trees. The presence of surface mats of fine and coarse roots suggested that trees in deep peat acquire their physical stability by producing lateral surface roots (discussed further in Chapter 4). Moreover, observations of wind throw patches in the study sites revealed few instances of uprooted trees in deep peat. Stem breakage in deep peat was commonly observed, suggesting that rooting instability was not the primary factor leading to wind throw. Conversely, in the

wind throw patches in PS3 on medium peat, uprooted trees were more commonly observed than was stem breakage.

Also, the medium depth peat areas did not contain mats of fine and coarse roots over the peat surface.

3.4 EDAPHIC PROPERTIES

Several peat properties were measured in samples taken from the study plots including: bulk density, capillary and non-capillary pore space, water holding capacity and rewetting capacity (Table 3–6). The properties provide the basis for classifying peat from the study sites according to the USDA Soil Taxonomy System, which has been commonly used for Indonesian peatlands.

Table 3–6. Summary of physical and hydrological conditions in the top and base of acrotelm peat layers in the study sites.

			•		
			Study area and sit	e	
Depth	3 m deposit	6 m deposit		12 m deposit	
(cm)	PS3	SE6	PI6	P19	PI12
		1. Bulk der	nsity, mean g cm ⁻³	(± 95% CI)	
0–20	0.19 (0.03)	0.15 (0.03)	0.14 (0.02)	0.12 (0.01)	0.10 (0.03)
20–40	0.14 (0.01)	0.15 (0.03)	0.15 (0.03)	0.12 (0.02)	0.10 (0.02)
		2. Pore spa	ice range* (% of to	otal peat volume)	
0-20	78.6–82.6	82.3-87.9	83.4-88.2	84.7–91.6	84.4–95.1
20–40	83.6–88.1	82.3–87.9	82.1–88.7	86.9–91.9	83.6–88.6
		3. Maximu	m water holding c	apacity, mean % (± 95% CI)
0-20	464 (27)	626 (143)	641 (52)	695 (65)	665 (107)
20–40	543 (38)	689 (44)	702 (74)	767 (74)	823 (85)
			ge of original WF 0-day rewetting pe		ove) after drying
0–20	64	73	75	77	80
20-40	62	72	68	81	80

^{*}Based on a particle density of 1.43 g cm⁻³.

Peat bulk densities in the study plots ranged from a minimum of 0.07 g cm⁻³ in the top (0–20 cm) of the acrotelm peat layer of PI12, to a maximum of 0.22 g cm⁻³ in the base (20–40 cm) of the acrotelm peat layer in SE6

(Table 3–6). The findings were in general agreement with those of Driessen and Rochimah (1976). Their surveys of Indonesian peats showed that fibric, relatively undecomposed peat in pole forests had bulk densities from 0.08 to 0.11 g m⁻³, while more decomposed sapric peats in mixed forest contained higher bulk densities, ranging from 0.14 to 0.23 g cm⁻³. In the waterlogged catotelm peat layer below approximately 50 cm, peat bulk densities were often extremely low, ranging from 0.05 to 0.07 g cm⁻³. The lowest bulk density found in the literature was 0.04 g cm⁻³ in the waterlogged layer of a peat deposit in Jambi, Sumatra (Cameron 1987). In contrast, Silvius *et al.* (1984) found relatively high bulk densities of 0.16 g cm⁻³ in the waterlogged zone in 9 m deep peat of another peat deposit in Jambi.

Total pore space in the top and base of the acrotelm peat layer ranged from 79 to 95% (Table 3–6). The highest total pore space was found in the top of the acrotelm in PI12 low pole forest. The results were similar to the percentages and patterns determined by Driessen *et al.* (1976). They calculated a particle density of 1.43 g cm⁻³ (range of 1.29–1.67 g cm⁻³) after analysis of many types of Indonesian peats. However, the factors leading to the range were not stated. Boelter (1974) measured total pore space in peats of different texture and determined that fibric peats contain up to 90% pore space by volume, while sapric peats contained around 80% total pore space. These classes apply well to the peats in the study sites which ranged in texture from fibric in deep peat to hemic in medium peat (classes defined in Table 2–4). Probably of more importance than total pore space in peat is the distribution and connectedness of pore spaces (Pritchett 1979). In deep fibric peats on Padang Island (PI9 and PI 12) much of the peat matter consisted of roots of different sizes and degrees of decomposition. In viewing soil pits and trenches in the two study sites, it was observed that under forest vegetation there was a strong vertical pattern of root growth into the peat. The masses of dead and often hollow root sheaths formed a visible structure of vertically connected pore spaces. The vertically-oriented matrix of medium-sized roots was not present in the mesic and sapric surface layers of PS3, SE6 and PI6 sites on medium depth peat.

Maximum water holding capacity (WHC) was greatest in the fibric to hemic textured deep peats on Padang Island (Table 3–6). The lowest WHC was measured in the sapric, well humified surface peat layer in PS3 chablis forest. These differences were in agreement with other studies of tropical peat. Andriesse (1988) found that maximum WHC of tropical peats decreased with increasing humification: Fibric - 1057%, mesic - 374%, sapric - 289%. He also found, however, that while fibric peats lose most of their water at low suction, more water is held at higher suctions in peats with higher degrees of decomposition. Analyses performed by Driessen and Rochimah

(1976) and Institute Pertanian Bogor (1976d) revealed that the moisture content of hemic peats and sapric peats at standard field capacity (pf of 2.5 or 0.033 MPa) ranges between 244 and 567% and 85 and 150%, respectively. The Institute Pertanian Bogor study measured moisture contents of 37 to 56% in hemic peats at the standard permanent wilting point of pf 4.2 or 1.5 MPa (Kramer 1983, Pritchett 1979).

In a review of tropical peat properties, Andriesse (1988) commented that little is known about the availability of water held at different tensions, but that the quantity of water available to plants in peat appears to be less than in mineral soils. Driessen and Rochimah (1976) also noted that the pf curves of lowland peats were remarkably flat. The difference between moisture contents at field capacity and the actual permanent wilting point may be much less in peat than in mineral soil. This phenomenon is important in the deep peat study sites where, during a dry period in 1991, the moisture content of the top (0–20 cm) of the acrotelm peat layer dropped to 160% and was associated with considerable mortality of fine roots.

The WHC was lowest in peat samples from SE3 (Table 3–6) and was attributed mainly to the sapric texture of the peat. However, peat exposure, under the open canopy, to direct sunlight may have also influenced WHC. Upon drying, a reduction in WHC occurred in peat samples from all sites, ranging from 62 to 81% of the original WHC values (Table 3–6). The greatest reduction in WHC occurred in the sapric-textured peat from PS3, SE6 and PI6, while the smallest reduction from the original WHC value occurred in the fibric-textured peat from the pole forest sites. Researchers studying other peat deposits have noted the loss of WHC, usually due to disturbance and increased exposure. Brady (unpublished data) measured low MHC of 200 to 393% in peat cleared for agriculture in South Sumatra. Similarly, Andriesse (1988) referred to a study in which peat MHC was measured in an area cleared and cultivated for agriculture in West Kalimantan. The peat was sapric in texture and had a low MHC of 275 to 322%.

Soil Classification

The organic soils of the raised peat deposits in Sumatra were classified as Histosols according to the U.S. Department of Agriculture Soil Taxonomy System (Soil Survey Staff 1975). The deep peat overlying marine clays and sands contains at least 18% or more organic carbon by weight and more than 50% of the upper 80 cm consists of organic materials. Fibric peats commonly have a bulk density of <0.1 g cm⁻³ and a moisture content of 850 to >3000%, while for Hemic peat these values range from 0.1 to 0.2 g cm⁻³ and 450 to 850%, respectively (Soil

Survey Staff 1975). The Soil Taxonomy System has been used in the extensive surveys for the transmigration settlement programs in the Sumatra and Kalimantan peatlands (Institute Pertanian Bogor 1976d)⁵.

3.5 PEAT HYDROLOGY AND MICROCLIMATE IN THE STUDY SITES

The climate, vegetation and peat edaphic properties described above have a combined effect on the hydrology and microclimate of the study sites. Spatial and temporal fluctuations of peat water levels, moisture and temperature were characterized between and within sites to the extent possible during the field study period.

3.5.1 Peat Water Levels

Comparison of Water Level Fluctuations Between Raised Peat Deposits

Water table levels monitored during the study periods exhibited similar patterns of wide fluctuations in response to seasonal wet and dry periods. Although not significantly different among sites, the monitoring results showed a pattern of declining average water table level with increasing peat depth, with the lowest average water table depth of -49 cm below the peat surface occurring in PI12 sites (Table 3–7). The pattern of water table decline was evident among the three peat deposits of increasing peat depth, and also across the depth gradient of study sites on Padang Island. The largest amplitude of water level movement during the study periods occurred in PS3 study plots (208 cm), while the smallest was in PI12 study plots (114 cm). Anderson (1961a) observed the opposite pattern in the peat forests of Sarawak. He noted that the smallest variations in water table movement (10–11 cm) occurred near the perimeter, while larger fluctuations of up to 18 cm occurred towards the centre of peat deposits. However, systematic measurements over time at permanently anchored piezometers were not provided in Anderson's report.

The general pattern of deeper peat water levels towards the centre of the peat deposits containing the study sites was also reflected in the attributes of forest trees in the different forest types associated with increasing peat depth. Trees with aerial roots such as buttress, knee or stilt roots were more commonly found in the medium depth study sites (PS3, SE6, PI6) than in the deep peat forests, and in PI9 than in PI12 sites (see Table 3–5). Kostermans (1958) and Corner (same publication) noted a similar occurrence in Sarawak and Kalimantan medium and deep peat forests. They observed that the stilt roots on trees often reach the height of flood water levels, and suggested that the

trees have adapted these root forms to withstand the higher water levels and flooding in medium peat. Stilt roots were not common in PI9 and PI12 study plots.

Table 3–7. Water table level fluctuations (cm) recorded at the five sites in East Sumatra during the field study.

	Study areas and sites							
	3 m deposits	6 m deposits		12 m deposits				
Parameters	PS3	SE6	PI6	PI9	PI12			
Average (± 95% CI)	-35 (9)	-38 (7)	-37 (9)	-39 (7)	-49 (6)			
Wet season max.	28	35	20	5	0			
Dry season min.	-180	-170	-110	-105	-85			
Monitoring period (mo.)	25	20	36	36	36			

Only once during the 36-month monitoring period in PI12 study plots did the water table rise above the top of the acrotelm surface. This occurred in April 1991 when monthly rainfall exceeded 350 mm for two consecutive months (Figure 3–9). Analysis of the 100 years of rainfall data collected in Sumatra, indicated that this level of high and continuous rainfall occurs every 4 to 6 years (Section 3.2.1). The monitoring results suggested that surface flooding may be less common in deeper peat compared to shallow peat. Surface flooding was also thought to be uncommon in the pole forests over deep peat in Kalimantan (Kostermans 1958) and Sarawak (Anderson 1961a).

The generally lower water levels in the centre of the deep peat deposit probably resulted from the larger mass of fibric material in the top of the acrotelm peat layer compared to the mesic and sapric peat that was found in the top of the acrotelm layer of the medium-depth peat deposits (Table 3–6). The fibric peat layer allows rainwater to dissipate laterally more rapidly, particularly during localized convective rain storms. In medium depth peat, where the hydraulic conductivity (K) of peat in the top of the acrotelm layer was lower (K <100 m d⁻¹), lateral subsurface movement of water would be slower, allowing surface flooding to occur. Other researchers have made similar observations. Anderson (1961a) attributed the absence of flooding in Sarawak peat domes to the increased hydraulic conductivity of acrotelm peat near the centre of the deposit. Driessen (1977) and Tie and Kueh (1979) also contended that higher lateral permeability of surface peat towards the dome centre of a deposit resulted in

flooding near the margins and dryness at the centre. Despite these observations, this explanation remains untested until the peat surface and water table level profiles across a peat deposit have been carefully surveyed.

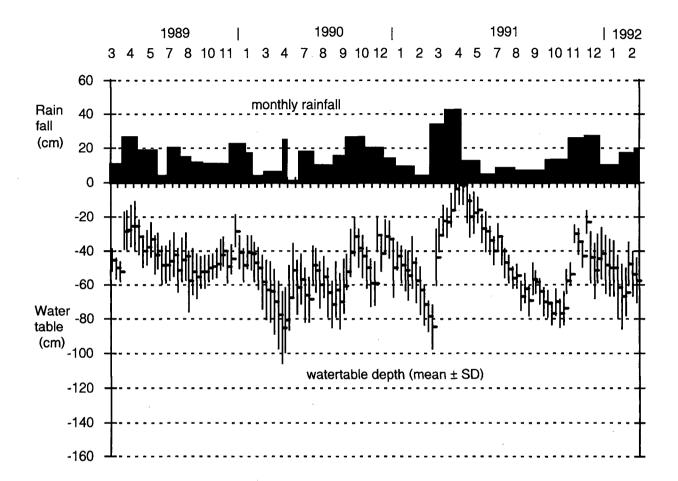


Figure 3–9. Water table levels rose above the peat surface in PI12 once during the 36-month monitoring period. Upper and lower water table ranges were based on mean \pm SD of 8-weekly piezometer measurements within a 5 ha area.

Flooding in PS3 and SE6 sites was usually continuous from mid-September to mid-March (Table 3–7). Wet season flooding has been recorded in other forested peat deposits in South Sumatra (Department of Agriculture 1970, 1971a, 1971b; IPB 1976c; Laumonier 1980). IPB (1976d) reported that before the Sugihan West peat forest was cleared and drained for transmigration settlements, much of the area was flooded with 10 to 40 cm of water during wet seasons. Flooding also occurs in medium depth peat deposits located in other regions of South East Asia.

Anderson (1961a) observed in Sarawak and Brunei deposits that water levels were close to the surface and during the wet season they rose above the peat surface. Seasonal flooding was also noted in the peat forests in Central Kalimantan (R.G. Sieffermann, personal communication).

Water Level Fluctuations and Rainfall

The water table monitoring results demonstrated the close relationship between rainfall and water levels in peat. The most rapid drop in water level measured during the study period occurred in PI9 study site in April 1990 at the beginning of the 1990–91 El Nino Southern Oscillation event. The water table dropped 65 cm over three months during which total rainfall was less than 40 mm. The relationship between daily rainfall and water table levels in deep peat over a 34-day period is illustrated in Figure 3–10. The graph shows a 20 mm rainfall on day-30, resulting in a 10 cm rise in the water table within 24 hours. A similar rapid rise in water level was observed during the onset of the 1988 wet season flooding in SE6 study site in medium depth peat. During three weeks of rainy weather in October, the water level in SE6 rose 15 cm above the peat surface with no decline recorded between rainfall events.

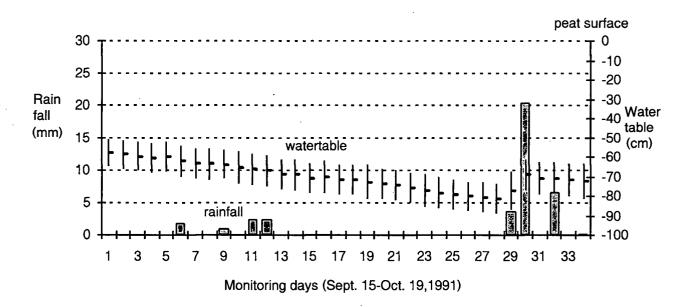


Figure 3–10. Range of daily water table movement (mean and SD, n=8) and rainfall on Padang Island deep peat over a 34-day period in 1991.

Monitoring results showed that water levels also varied within study sites. At a smaller scale of observation (10–10000 m²: 4–7 days), water fluctuations in the piezometers in PI12 were affected by factors other than local rainfall. Water table increases of up to 3 mm per 1 mm of rainfall occurred with measured rainfall rates of 10 to 50 mm over 4 to 7 days. The largest rise in water level recorded during the study period was 400 mm over 7 days, during which rainfall totaled 138 mm (Figure 3–11). At other times during the monitoring period, with similar rainfall rates, no water level increases were recorded. Further, on occasion, daily water levels rose up to 75 mm during 4 to 7-day periods with no effective rainfall⁶. The maximum total rise recorded over a 7-day rainless period was 75 mm (Figure 3–11). The analysis includes a conservative estimate of daily evaporation at 0.1 mm d⁻¹.

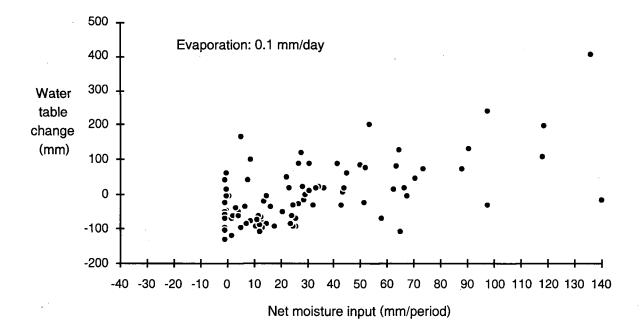


Figure 3–11. Effect of net moisture input from rainfall (mm/period) on water table fluctuation, assuming a conservative evaporation rate of 0.1 mm d⁻¹. Water levels were measured in 10 piezometers for 94 periods (4–7 days/period) from 1989 to 1991 near the Padang Island PI9 deep peat study site.

The analysis in Figure 3–11 shows that, in addition to periods of rapid water level rise during rainfall, there were periods when the effects on water levels of other input sources equaled or exceeded the effects of maximum weekly rainfall inputs of up to 138 mm. The source of moisture that causes the rises was most likely from lateral

interflow within the acrotelm layer of the peat profile. Sofjan (1990) measured the effect of interflow on water levels at Padang Island. He used parallel transects (2 km) of evenly spaced (50 m) piezometers which had been leveled to compare elevation. Monthly water level rises and drops of up to 200 mm occurred independent of locally-measured rainfall patterns.

Oscillating water levels may be attributed to localized convective rainfall. Short intense storms covering areas as small as 10 ha create saturated water-mounds in peat of up to 200 mm above the surrounding water table level (I. Sofjan, personal communication). Without further rainfall, the water mounds dissipated over periods of 4 to 7 days, likely through evapotranspiration and interflow. These processes have not been measured directly in Sumatran peat and their relative influence cannot be separated.

During periods of low rainfall when water levels dropped, the daily decline in peat water levels ranged from 2 to 11 mm (Figure 3–12). The maximum daily decline of 11 mm occurred even when weekly rainfall reached approximately 30 mm, indicating that rainfall below 30 mm per 4–7 days may not have affected water table levels. Portions of rainfall were intercepted by vegetation cover, remained in the unsaturated peat above the water table, and were lost through evapotranspiration and lateral interflow.

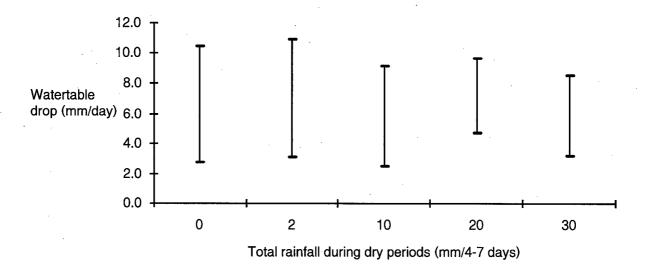


Figure 3–12. Rates of daily water table drop (95% CI) during dry periods of up to 30 mm rainfall. Rainfall data were not corrected for evaporation losses. Level changes were measured in 10 piezometers every 4–7 days during dry periods (<30 mm rainfall) from 1989–91 at the PI9 study site on Padang Island.

3.5.2 Water Levels and Peat Moisture Fluctuations

Within the study periods the average moisture content of peat in the top of the acrotelm layer (373%) in all study sites was lower than in the bottom (581%), but variability was high (Table 3–8). Among the sites, the widest range of moisture content was measured in the bottom of the acrotelm layer of PI12. The lowest moisture content was recorded during the 1991 dry season/El Nino period. This demonstrated that the fibric-textured acrotelm layer of the deep and undrained peat deposits experiences moisture fluctuations as severe as the fluctuations in medium depth peats, both under forest cover and in areas cleared and drained for agriculture. For comparison, the moisture content of the top of the acrotelm layer of peat in the Sugihan West agricultural area ranged from 29 to 970%⁷ while the base of the acrotelm ranged from 322 to 1600% moisture content.

Table 3–8. Peat moisture in the top and base of the acrotelm layer of peat in the five study sites.

	Study area and site								
Depth	3 m deposit	6 m deposit							
(cm)	PS3	SE6	PI6	PI9	PI12				
		1. Peat moistu	re content, mean	% (± 95% CI)					
0-20	318 (162)	564 (300)	455 (180)	398 (64)	295 (49)				
2040	371 (172)	667 (208)	632 (189)	635 (107)	483 (323)				
	2.	Peat moisture and	water level correl	ation coefficients	(r)				
0–20	0.44	0.56	0.51	0.63	NS				
20-40	0.46	NS	0.53	0.70	0.53				
•	2 :	Dank marinkum and		1-4:					
		Peat moisture and	•		. ,				
0–20	0.34	0.68	0.76	0.91	0.49				
20-40	0.40	0.72	0.66	0.59	0.88				

There was no particular pattern of significant or non-significant correlations between water levels and peat moisture contents in the top and bottom of acrotelm peat layers, and again in medium depth and deep peat study sites (Table 3–8). Correlations between peat moisture and rainfall also showed no discernible pattern. The weak relationship between water level and peat moisture in the top of acrotelm peat reflected the high variability among

sites of water retention in the peat matrix. This variability was attributed to differential seepage or interflow rates due to texture differences and to differences in evapotranspiration losses. These processes appeared to have less effect on the bottom of the acrotelm peat layer, as suggested by the generally stronger correlations between subsurface peat moisture with water levels and with rainfall. It was also likely that the peat moisture sampling regime was insufficient in length and intensity to accurately measure both the rapid changes following rainfall events and the more gradual moisture changes occurring within seasons (*i.e.*, early, mid and late dry season). Coulter (1950) measured moisture contents in Malaysian peats. He reported surface and subsurface levels of 146 and 730%, respectively, which were within the range of the Sumatra peats. However, seasonal variability was not described.

3.5.3 Temperature Fluctuations in the Study Sites

Average daily air temperatures in the study sites were between 27 and 28°C, with a maximum temperature range of about 10°C. Minimum and maximum 30-day mean air temperatures were similar in the sites and between seasons (Table 3–9). The highest mid-day maximum temperatures were recorded in PI12 study plots. They were 36.0°C at 50 cm above the forest floor and 33°C in the 0–3 cm layer of surface peat. The higher temperatures can be attributed to the lower and thinner tree canopy and the sparser shrub and herb layers in this study site, compared to the other areas (see Section 3.3.1). Temperatures varies the least (27.0–29.0°C) in the subsurface (25 cm) peat layer. Air and peat temperatures in the study plots were similar to the mean monthly air temperatures measured by Low and Balmurgan (1989) under the canopy of peat forest in Malaysia.

In both forest tree-fall gaps (approx. 250 m²) and cleared peat areas near the study plots, air temperatures just above the forest floor reached as high as 42°C during 30-day monitoring periods. Night-time minima were similar to those under intact canopy. The maximum daily temperature fluctuations in the gaps were as high as 20°C, an increase of approximately 10°C in the daily range compared with the forest. Uhl *et al.* (1981) measured even greater surface soil temperatures (53°C) in a burned tropical forest floor. The maximum surface peat temperatures found in the literature were recorded in stockpiled peat in Kalimantan (Ministry of Mines and Energy 1987). There, peat temperatures rose from 55 to 60°C at air temperatures of 32 to 37°C. Bouman and Driessen (1985) refer to peat temperatures as high as 70°C, but do not provide details.

Table 3–9. Comparison of air temperatures at 50 cm aboveground, and in the top (0–3 cm) and base (25 cm) of acrotelm peat layers in the study sites. Peat temperatures were measured in the forested study plots during wet and dry seasons. Temperature ranges in large forest canopy openings (250 m²) and in the Sugihan West reference area are provided.

		30-day air and peat temperature ranges (min °C-max °C)								
	Forested study sites						Open peat areas			
Height or						Forest gap	Sugihan West			
depth (cm)	PS3	SE6	PI6	PI9	PI12	near SE6	cleared peat			
		Wet season (November-May)								
+50 air	22.0-34.0	22.0-34.0	22.5-34.0	22.0-34.5	22.0-36.0	23.0-42.0	23.0–37.0			
0-3 peat	27.5–28.0	27.5–28.0	27.5–28.0	27.5–29.0	27.0-32.0	28.0-37.0	30.0-42.5			
-25 peat	27.0–28.0	27.5–28.0	26.5–28.0	27.0–28.5	27.0–29.0	28.0–29.5	28.0-30.0			
	Dry season (June-October)									
+50 air	21.5–34.5	22.0-34.5	21.0-34.5	20.0-35.0	20.0–36.5	23.0-40.0	20.0-42.0			
0-3 peat	27.0-28.0	27.5–28.0	27.0-28.5	27.5–29.0	27.0-33.0	25.0-34.0	25.0-40.0			
-25 peat	27.0-28.5	27.5–28.0	26.5–28.5	27.0-28.5	27.0-29.0	28.0-29.5	28.0-31.0			

Note: range based on 30-day continuous measurements in each season.

In addition to the larger absolute temperature changes measured in PI12 sites compared with those in the more heavily canopied mixed forest study sites, temperatures fluctuated more rapidly. Daytime surface peat temperatures in the mixed forest stands increased steadily over the day with no detectable hourly fluctuations. In PI12 sites, peat temperature fluctuations of up to 5°C in 20 minutes were measured. The rapid fluctuations were associated with periods of alternating sunshine and cloud cover and had the greatest impact on the forest floor under the sparse canopy cover of the PI12 low pole forest. The extreme temperature variations in exposed peat are due to high heat capacity and low thermal conductivity (Soepraptohardjo and Driessen 1976).

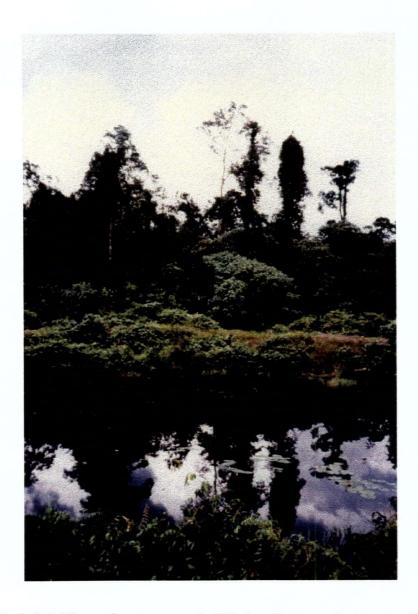


Plate 3–1. Typical chablis peat forest type near the SE3 site with *Gonystylus bancanus*, *Koompassia malaccensis* and *Dyera costulata* as emergents over a subcanopy of primary and secondary species including *Macaranga*, *Litsea* and *Ficus* spp and *Licuala spinosa*. The drainage canal in the foreground provided access to the central plateau of the peat deposit.



Plate 3–2. Distinctive boundary between the PI6 mixed forest (bottom) and PI9 tall pole forest (top) on Padang Island. The even canopy of the pole forest was dominated by three *Calophylum* spp.



Plate 3–3. Typical profile of PI9 tall pole forest on 9 m of peat showing abundance of *Calophyllum* spp. This degree of dominance seldom occurs in tropical forests and likely represents a wave of stand regeneration following disturbance. The recently excavated canal in the foreground shows the high water table characteristic of the peat deposit.



Plate 3—4. Typical profile of PI12 low pole forest on 12 m of peat. The forest canopy, dominated by *Tristania obovata*, Calophyllum sundaicum and *Pandanus artocarpus*, dropped from 32 m in the PI9 tall pole forest to 11 m in PI12.



Plate 3–5. Exposed acrotelm layer of peat profile in the PI12 low pole forest on Padang Island. The photo shows the abundance of vertically-oriented roots near the water table which was 50 cm below the peat surface.

FOOTNOTES

¹ET - evapotranspiration, P - precipitation

²(v) identifies the vernacular names of plants which could not be identified at the Bogor Herbarium.

³Reports are listed in the Bibliography by institution names.

⁴Low soil fertility and droughty conditions are known to induce thick leaf cuticles, a decrease in leaf size and tree height, and what is known as a xeromorpohic form (Kramer and Kozlowski 1979).

⁵There are several other peat classification systems which have been proposed. One relevant to this study, but not yet fully developed, is a classification by Kivinen (1980). He proposed to classify peats using much of the Soil Taxonomy criteria, with the addition of botanical and trophic status.

⁶Assuming that at least 20 mm of rain are intercepted by the forest canopy per period (Bruijnzeel 1990).

⁷Based on wet mass percent.

CHAPTER 4

RESULTS OF ORGANIC COMPONENT STUDIES

The analysis in Chapter Three demonstrated that allogenic factors such as coastal geomorphology and climate did not vary substantially among the sites located on the three peat deposits in Sumatra. The sites do, however, contain important differences in vegetation, hydrology and edaphic conditions which are associated with increasing depth of the peat deposits. As discussed in Chapter One, changes in vegetation, hydrology and edaphic conditions with increasing peat depth are greater in tropical peat deposits than in raised *Sphagnum* peat bogs in temperate zones. Because of the different conditions in tropical peatlands, their effects on the three components of the peat model—peat age, organic matter fixation and organic matter decay—are evaluated below.

4.1 AGE CHARACTERISTICS OF ACROTELM PEAT

Radiocarbon dating of organic matter was used to determine whether age accounts for the variable accumulation of peat in the three Sumatra peat deposits (Figure 1–3). The results in Table 1–4 show that the top (0–20 cm) of the acrotelm peat layers of the sites contain greater than 100% Modern C (*pMC*), compared to the internationally accepted radiocarbon dating reference value, ¹ and are younger than 1950. The exact ages of the young peat samples could not be determined, but because of their activity range (100–122 *pMC*), they were likely to be younger than 1963 when the atmospheric ¹⁴C content reached a maximum of 190 *pMC* due to nuclear bomb detonation (Beta Analytic, personal communication, October 1996, Minz Stuiver, personal communication, December 1996). For this study, it was assumed that samples containing >100% *pMC* were aged at 45 years from 1995, the date of sampling and ¹⁴C analysis.

The young ages of the surface peat layers suggested that, on a decadal scale, the surface layers of the peat deposits have not subsided. If the surfaces had degraded, peat in the top of the acrotelm layer would be older, reflecting a reversal of peat accumulation and leading to net degradation of the raised peat deposit. Although the acrotelm layers in the sites did not appear to be degrading, the age results alone could not be used to determine whether the surfaces of the peat deposits were in steady state or aggrading.

Peat in the base of the acrotelm layer decreased in age across the gradient of increasing peat depth (Table 4–1). The matrix of fine (<0.5 diam.) peat particles was of younger age in the deeper PI12 site (122 yBP), than that in PS3 (660 yBP). The base and top of the acrotelm layer in PI12 were of similar age. The thick layer of modern

peat in PI12 suggested that the acrotelm in deeper peat deposits receives higher rates of organic additions than that in medium depth deposits. Peat in the base of the acrotelm in PI12 was about six times younger than in the same layer in PS3.

When small roots removed from the peat matrix of the acrotelm base were aged, a similar age pattern occurred with the youngest roots found in the thickest peat deposits (Table 4–1). In all sites however, the small root fraction was younger than the peat matrix. The smallest age difference between peat and roots occurred in PI12. The ages are not likely to be significantly different given the declining accuracy of radiocarbon dating methods with the young samples (Stuiver *et al.* 1993). The difference in age between the fine peat and dead root material was greatest both in magnitude and proportion in SE6 on medium depth peat.

Table 4–1. Comparison of radiocarbon ages of fine peat (0.5 mm) and intact, but dead, small roots sampled in the sites. Ages are mean (\pm 1 SD) conventional radiocarbon years before present, n = 2. Samples containing greater than 100% modern C (post AD 1950) are italicized.

		Study area a	and site	
Organic fraction	3 m deposit	6 m deposit	12 m dep	osit
and (size in mm)	PS3	SE6	PI6	PI12
		Top of acrotelm	(10-20 cm)	
Peat age (< 0.5) δ^{13} C (‰)	120 (0.7) pMC -25.0	112 (1.0) pMC -31.1*	113 (1.1) pMC -25.0	118 (0.7) pMC -25.0
Roots (0.5–2.0)	NS	NS	NS	NS
		Base of acrotelm	(30-40 cm)	
Peat age (< 0.5) δ^{13} C (‰)	660 (80) -25.0	580 (60) -25.0	377 (40) -25.0	122 (1.0) pMC -25.0
Fine peat as % of total mass	90.4	87.5	84.4	54.0
Root age (0.5–2.0) δ^{13} C (‰)	NS	330 (60) -25.0	265 (40) -25.0	100 (0.8) pMC -31.0*
Roots as % of total mass**	NS	2.7–12.6	3.4–15.6	20.0–46.0

Notes: pMC = % modern C. *Sample isotopic fractionation (δ^{13} C) are estimates based on values typical of material type. Unmarked δ^{13} C values are calculated (Stuiver *et al.* 1993). NS-not sampled due to modern C or insufficient sample quantities of dead intact roots. **Range is intact roots alone to all roots and chaff. Ages were not determined for the PI9 site. Laboratory code numbers for organic samples include Beta-75559–75567 and Beta-88579–88580.

The small age difference between peat and intact roots indicated that in the deep peat sites, the preserved peat at the base of the acrotelm received appreciable quantities of fresh organic matter from roots. The younger age of the roots shows that roots were also added to the preserved peat in the acrotelm base of the thin peat sites, but in lesser amounts and to a shallower depth. The important effect of root additions to subsurface peat was demonstrated by the significantly higher proportion of intact root mass as a percentage of total organic mass in PI12 (up to 46%), compared to that in SE6 (up to 12%) on thinner peat (Table 4–1).

The young ages of the organic components in the acrotelm layers of the sites suggested that the surfaces of the three peat deposits in Sumatra were either in steady state or aggrading. The results did not suggest that peat surfaces had degraded below the 1950 levels. In addition, the larger mass of younger, intact roots in PI12 indicated that roots may be increasingly important for peat accumulation in the acrotelm layer of the deeper deposits. The role of roots in organic matter fixation and decay processes is further discussed below.

4.2 COMPONENTS OF ACROTELM PEAT

The vegetation analysis in Chapter Three revealed significant differences in forest composition and structure among the sites. The temperate peat accumulation model (eq. 2) assumes that at all depths of peat accumulation, plants of similar composition and structure are preserved as peat in a similar pattern. Following the study framework (Figure 1–3), the results below show how vegetation composition and structure affect organic matter additions from plants.

4.2.1 Peat Mass and Composition

The total mass of peat in the top and base of the acrotelm layer decreased significantly with increasing depth of peat deposit ($F_{4,5} = 10.28$, P = 0.013)(Table 4–2). The decreasing mass was due to lower bulk densities in the acrotelm layer of the thicker peat deposits. Bulk density ranged from a maximum of 0.21 g cm⁻³ in PS3 to a minimum of 0.08 g cm⁻³ in PI12. The bulk density and mass in the top and base of the acrotelm were similar in all sites except in PS3, which had significantly greater bulk density and mass in the top of the acrotelm. The changes in bulk density are attributed below to changes in the chemistry and form of organic additions to the acrotelm layer which occur with increasing peat depth, and to decay processes.

Table 4–2. Mass and concentration of resource quality attributes in peat samples from the top and base of acrotelm layers of the five peat forest sites in East Sumatra. Data are means (\pm 95% CI), n = 10.

•		Study area and site				
·	Depth	3 m deposit	6 m deposit		12 m deposit	
Peat variable	(cm)	PS3	SE6	PI6	PI9	PI12
Total dry mass			·			
(kg m ⁻²)	0–20	38.25 <i>a</i> (5.01)	29.01ab (5.33)	26.84 <i>ab</i> (3.42)	23.01 <i>b</i> (2.43)	20.35b (5.29)
	20–40	27.82ab (2.92)	30.63 <i>ab</i> (5.10)	29.17ab (5.33)	24.05 <i>b</i> (4.28)	19.38 <i>b</i> (2.98)
Total C						
(kg m ⁻²) (mg g ⁻¹)	0–20	21.30 557.0 <i>ac</i> (7.1)	16.31 549.0 <i>a</i> (6.0)	16.75 561.3ac (5.3)	13.45	11.48
(mgg).	20.40				560.2ac (6.3)	564.1 <i>ac</i> (7.9)
	20–40	15.77 566.9 <i>ac</i> (6.3)	17.49 582.6ab (3.6)	17.79 593.7d (6.9)	14.16 588.9 <i>bd</i> (6.7)	12.00 591.0 <i>d</i> (7.4)
Γotal N		(0.0)	(515)		2001304 (01.7)	031.00 (7.1)
(kg m ⁻²)	0-20	0.75	0.54	0.55	0.43	0.29
(mg g ⁻¹)		18.7a(0.5)	18.3ab (0.7)	18.5ab (0.6)	17.9 <i>b</i> (0.7)	14.2d(0.9)
	20-40	0.49	0.55	0.53	0.40	0.27
		17.6 <i>b</i> (0.4)	18.2 <i>ab</i> (0.3)	$17.8bc\ (0.6)$	16.7c(1.1)	13.3e (0.9)
N mineral						
(mg N 100 g ⁻¹ a ⁻¹)	0–20	34.7 <i>ab</i> (3.0)	52.4 <i>a</i> (1.7)	52.3 <i>a</i> (2.1)	44.3 <i>a</i> (4.2)	55.2a (3.2)
	20–40	13.5 <i>b</i> (3.3)	8.7 <i>b</i> (4.1)	15.2 <i>b</i> (4.0)	12.0 <i>b</i> (1.9)	17.3 <i>b</i> (0.4)
Fotal P						
$(\log m^{-2})$	0–20	0.0283	0.0214	0.0200	0.0118	0.0079
(mg g ⁻¹)		0.74 <i>a</i> (0.03)	0.72a(0.05)	0.67a (0.04)	0.49c(0.05)	0.39c(0.03)
	20–40	0.015 0.54 <i>b</i> (0.03)	0.020 0.67 <i>ab</i> (0.06)	0.017 0.58ab (0.05)	0.009 0.39 <i>c</i> (0.07)	0.005 0.27 <i>c</i> (0.04)
**		0.540 (0.05)	0.0740 (0.00)	0.38ab (0.03)	0.390 (0.07)	0.276 (0.04)
oH (1:2.5 H₂O)	0–20	3.95 <i>a</i> (0.21)	4.47 <i>a</i> (0.26)	4.19 <i>a</i> (0.19)	3.96a (0.16)	3.79a (0.10)
(1.2.3 1120)	20–40	3.57a (0.11)	, ,	4.21 <i>a</i> (0.29)	, ,	, ,
		3.57a (0.11)	4.16 <i>a</i> (0.28)	4.214 (0.29)	3.99a (0.10)	4.01 <i>a</i> (0.12)
Proximate C fractio	ns:					
Solubles*	0.20	4.22	2.24	2.20	2.27	2.07
(kg m ⁻²) (mg g ⁻¹)	0–20	4.33 113.2 <i>a</i> (4.1)	3.34 112.4 <i>a</i> (4.5)	3.39 113.8 <i>a</i> (4.0)	3.37 140.2 <i>c</i> (3.6)	2.87 141.1 <i>cd</i> (3.4)
(20–40	2.94	3.20	3.30	3.55	3.02
	20-40	104.6 <i>b</i> (2.8)	107.6 <i>ab</i> (2.1)	110.7 <i>ab</i> (3.3)	146.9 <i>cd</i> (3.4)	148.5d(4.3)
Holocellulose**		` ,	` ,		. ()	()
kg m ⁻²)	0–20	7.81	4.94	4.49	2.09	0.40
$(mg g^{-1})$		203.6a (12.1)	165.2ab (12.6)	150.5ab (14.6)	87.0 <i>c</i> (9.4)	19.5d (4.1)
	20–40	3.65	2.04	2.20	1.41	2.11
On the state of th		131.1 <i>b</i> (8.3)	67.8 <i>c</i> (6.2)	71.6ce (10.4)	58.6 <i>c</i> (8.2)	101.7 <i>c</i> (11.2)
Continued						

Table 4-2. Continued.

		Study area and site				
	Depth	3 m deposit	6 m deposit		12 m deposit	. = 1984
Peat variable	(cm)	PS3	SE6	PI6	PI9	PI12
Lignin*** (kg m ⁻²) (mg g ⁻¹)	0–20	26.13 683.3 <i>a</i> (13.3)	21.46 722.3ad (16.0)	22.02 707.0 <i>b</i> (19.2)	18.57 773.4 <i>c</i> (13.6)	17.10 839.4 <i>d</i> (21.1)
•	20-40	21.26 764.3 <i>b</i> (9.1)	24.80 825.6 <i>c</i> (14.8)	24.51 807.5d (20.3)	19.11 794.5 <i>c</i> (14.1)	15.21 749.4 <i>bc</i> (25.0)
Polyphenol**** (kg m ⁻²) (mg g ⁻¹)	0–20	0.36 9.4 <i>a</i> (0.5)	0.28 9.5 <i>a</i> (0.4)	0.31 10.4 <i>a</i> (0.5)	0.25 10.3 <i>a</i> (0.4)	0.20 9.9 <i>a</i> (0.4)
	20–40	0.27 9.8 <i>a</i> (0.5)	0.30 10.1 <i>a</i> (0.6)	0.31 10.3 <i>a</i> (0.6)	0.23 9.5 <i>a</i> (0.5)	0.22 10.7 <i>a</i> (1.5)
Chemical quality in	ndices:					
C:N	0–20	29.8	30.0	30.3	31.3	39.7
	20-40	32.2	32.0	33.3	35.3	44.4
Lignin:N	0–20	36.5	39.5	39.8	43.2	59.1
	20-40	43.4	45.4	45.4	47.5	56.3
LCI	0–20	0.77	0.81	0.83	0.90	0.98
	20–40	0.85	0.92	0.92	0.93	0.88

Notes: Means for different parameters within a row (depths combined) followed by the same letter are not significantly different at P = 0.05 (using Tukey HSD test). ANOVA results in Appendix 3.1. *Extracted with dichloromethane and hot water, **Sulphuric acid soluble, ***Sulphuric acid insoluble. ****Tannic acid equivalents. LCI = Lignin:lignocellulose index.

Concentrations of total C in peat varied across the gradient of different peat depths, increasing significantly from top to base of the acrotelm layer ($F_{1,5} = 100.60$, P < 0.001) (Table 4–2). The second main source of variation was among sites ($F_{4,5} = 17.30$, P < 0.001). The highest concentrations of total C (up to 591 mg g⁻¹ oven dry peat) were found in the base of the acrotelm layer of the Padang Island sites on medium and deep peat. These sites contained the youngest surface peat with the lowest bulk density of all sites. Concentrations of acrotelm N and P decreased significantly across the gradient of increasing peat depth. The largest decline in N occurred between PI9 and PI12, and in P between PI6 and PI9. Both N and P concentrations significantly decreased from the top to the base of the acrotelm layers in most sites (Table 4–2). The small, but significant site × layer interaction in N concentration was probably due to the relatively high N concentration in SE6. The largest difference in P between the acrotelm top and base layers was in PS3 which contained a lower P concentration in the acrotelm base than

found in SE6. This probably resulted from the higher degree of decay due to artificial drainage in PS3. Between plot variability of P among study sites was small, but significant, and reflected the higher spatial variability of P than N concentrations (Appendix 3.1).

Mineral N (N_{min}) in acrotelm peat following the one-year incubations was also highly variable between plots and among sites, but showed no pattern across the gradient of increasing peat depth. The top of the acrotelm peat layers contained significantly higher N_{min} than in the base across all sites ($M_{top} = 47.7$; $M_{base} = 13.3$, $F_{1,5} = 148.42$, P < 0.001) except in PS3. The pH of peat slurries was generally low, ranging from 3.58 to 4.47. There was a small, but significant difference among sites, but a pattern along the peat depth gradient was not discernible.

In contrast to the N and P patterns above, concentrations of the soluble and lignin proximate C fractions in the top of the acrotelm increased significantly with increasing peat deposit depth. The increase in lignin, which ranged from 683 mg g⁻¹ in PS3 peat, to a maximum of 840 mg g⁻¹ in PI12 peat, was proportionally greater than the increase in the soluble C fraction (Table 4–2). The significant site × layer interaction in the nested factorial analysis resulted from increasing soluble C and decreasing lignin fractions in the base of acrotelm peat in the PI9 and PI12 deep peat sites and was due to changing aboveground litter and belowground root inputs (discussed below).

Concentrations of the soluble C fraction and polyphenols did not differ between the top and base of the acrotelm. Lignin concentrations, however, generally increased with depth in the acrotelm layer, except in PI12 where lignin was greater in the top of the acrotelm peat layer, and was the highest among all sites.

The ratios of C:N, lignin:N and lignin:lignocellulose (LCI) listed in Table 4–2 are commonly used as resource quality indices. Studies in other forests have shown that as the indices increase, organic matter becomes increasingly resistant to microbial attack (Melillo *et al.* 1989). The three indices increased across the gradient of increasing peat depth and the range of each index across the site gradient was greater than for those of N, lignin and soluble C concentrations alone. Among the indices, the lignin:N ratio in the top of the acrotelm varied the most (162%) across the peat depth gradient, while the LCI index in the base of the acrotelm layer varied the least (103%).

The general pattern of declining organic matter mass and resource quality with increasing peat deposit depth was attributed to changes in vegetation along the gradient of increasing peat depth. The vegetation classification in Chapter3.3 revealed that of all sites, PI9 and PI12 were most different from each other in composition and structure. Vegetation changes were also associated with changes in the physical composition of peat (Figure 4–1).

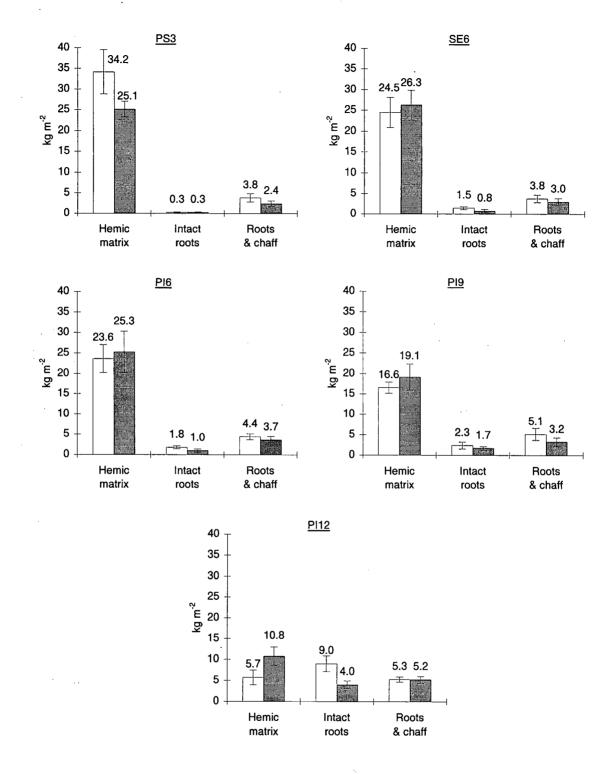


Figure 4–1. Distribution of organic components in peat from the top (open bars) and base (shaded bars) of acrotelm layers in the five peat forest sites in East Sumatra. Data are means \pm 95% CI (n = 10). Components are: 1) matrix of hemic peat (< 0.5 mm); 2) intact live and dead roots (0.5–2.0 mm); and 3) mostly dead root fragments and chaff (0.5–10 mm). ANOVA results in Appendix 3.2.

Of the three organic components distinguished in the particle fraction analyses, the hemic peat fraction (<0.5 mm) represented the highest percentage of organic mass in all sites. Despite high variability between sample plots with sites, there was a large and significant decline in the proportion of hemic peat mass in the acrotelm layer across the site gradient of increasing peat depth ($F_{4,5} = 1390.52$, P = 0.002). The decline was associated with a small, but significant site × layer interaction which resulted from the highly decomposed acrotelm in the PS3. The proportion of hemic material to the total peat mass declined in the top of the acrotelm layer from 89% in PS3, to 28% in PI12 on deep peat. The proportional decline of hemic peat and increase in mass of small and fine roots, and chaff, reduced peat bulk density across the depth gradient (Figure 4–1).

The proportion of live and dead intact roots, and fragments of dead roots in the top of the acrotelm also exhibited high between plot variability, but increased significantly from 8% of the total organic dry mass in PS3, to 52% in PI12 peat. The results also showed an increased proportion of aboveground litter fragments in the top and base of the acrotelm layers of the deep peat sites. Litter fragments represented about 50% of the root fragments and chaff component (Figure 4–1). The significant changes in the organic chemistry and physical composition of peat across the site gradient required that plant inputs of aboveground litter and roots be characterized separately.

4.2.2 Aboveground Litter

The litter layer included all recognizable leaf material, reproductive organs and small woody debris (<2 cm in diameter) above the peat and root mat, where the latter was present. In contrast to the pattern of litterfall, litter layer mass increased significantly across the gradient of increasing peat depth ($F_{4,5} = 4530.89$, P < 0.001)(Table 4–3). The litter layer in PI12 on deep peat contained almost twice the mass (4.81 kg m^{-2}) in PI9 (2.88 kg m^{-2}) and in the chablis and mixed forest sites (PS3, SE6 and PI6) on medium depth peat ($1.34-1.52 \text{ kg m}^{-2}$).

Total C concentrations of litter layers were similar in all sites except in PS3 which was lower, probably resulting from the large number of fast-growing species present in the site after logging and drainage.

Concentrations of N and P generally declined with increasing peat depth, but varied significantly between plots and among sites (Table 4–3). Total N concentrations in litter layers were significantly lower than those in acrotelm peat, while P concentrations in the litter layers and peat layer were comparable (Table 4–2). Mineralized N in incubated leaf litter varied significantly between plots, but not among sites. This probably reflected stronger effects of micro site variation in moisture and temperature within sites, compared to vegetation differences among sites.

Table 4–3. Mass and resource quality attributes of samples from 0.25 m² portions of litter layers at the five peat forest sites in East Sumatra. Data are means (\pm 95% CI), n = 8.

			Study area and site		
_	3 m deposit	6 m deposit		12 m deposit	
Litter variable	PS3	SE6	PI6	PI9	PI12
Litter dry mass (kg m ⁻²)	1.34 <i>a</i> (0.24)	0.73 <i>b</i> (0.09)	1.52a (0.27)	2.88 <i>c</i> (0.43)	4.81 <i>d</i> (0.56)
Total C (kg m ⁻²) (mg g ⁻¹)	0.69 516.5 <i>a</i> (14.4)	0.39 538.0 <i>b</i> (1.00)	0.81 536.0 <i>b</i> (8.6)	1.56 542.4 <i>b</i> (8.4)	2.64 548.6 <i>b</i> (8.0)
Total N (kg m ⁻²) (mg g ⁻¹)	0.019 14.1 <i>a</i> (0.7)	0.007 10.0 <i>b</i> (0.6)	0.017 11.1 <i>b</i> (0.7)	0.014 9.0 <i>b</i> (0.8)	0.038 8.0 <i>b</i> (0.8)
N mineralized (mg 100 g ⁻¹ a ⁻¹)	33.2a (5.7)	48.8 <i>a</i> (6.4)	56.5a (5.7)	67.5 <i>ba</i> (4.0)	53.7a (4.2)
Total P (kg m ⁻²) (mg g ⁻¹)	0.0011 0.81 <i>a</i> (0.04)	0.0004 0.57 <i>b</i> (0.04)	0.0009 0.61 <i>b</i> (0.05)	0.0017 0.59 <i>b</i> (0.05)	0.0017 0.40 <i>c</i> (0.04)
Solubles* (kg m ⁻²) (mg g ⁻¹)	0.46 343.1 <i>a</i> (5.1)	0.22 303.86 <i>b</i> (9.1)	0.27 180.3 <i>c</i> (10.2)	0.50 173.9 <i>c</i> (4.5)	0.87 181.0 <i>c</i> (4.9)
Holocellulose** (kg m ⁻²) (mg g ⁻¹)	0.30 221.0 <i>a</i> (25.1)	0.07 93.1 <i>b</i> (9.0)	0.31 206.6 <i>a</i> (24.1)	0.63 216.8 <i>a</i> (16.5)	0.99 204.3 <i>a</i> (18.2)
Lignin*** (kg m ⁻²) (mg g ⁻¹)	0.58 438.8 <i>a</i> (14.0)	0.44 603.3 <i>b</i> (15.4)	0.93 613.3 <i>b</i> (12.3)	1.75 607.4 <i>b</i> (14.4)	2.95 613.5 <i>b</i> (15.7)
Polyphenol**** (kg m ⁻²) (mg g ⁻¹)	0.02 12.2 <i>a</i> (2.0)	0.01 10.4 <i>a</i> (0.4)	0.01 10.3 <i>a</i> (0.3)	0.03 10.0 <i>a</i> (0.3)	0.05 11.0 <i>a</i> (0.6)
C:N ,	36.5	53.7	47.9	60.1	68.6
Lignin:N	30.8	60.3	55.3	67.5	76.7
LCI	0.66	0.87	0.75	0.74	0.75

Note: Means for different parameters within a row followed by the same letter are not significantly different at P = 0.05 (using Tukey HSD test). *Extracted with dichloromethane and hot water, **Sulphuric acid soluble, ****Sulphuric acid insoluble. ****Tannic acid equivalents. ANOVA results in Appendix 3.3.

Concentrations of soluble and lignin proximate C fractions showed opposing patterns across the peat depth gradient. While the soluble C fraction concentrations increased in acrotelm peat, as discussed above, solubles in the litter layer declined significantly across the site gradient ($F_{4,5} = 326.38$, P < 0.001). Similar to acrotelm peat (Table 4–2), although lower (ca. 30%) in concentration, the lignin fraction in litter increased significantly in concentration

and total dry mass across the peat depth gradient (Table 4–3). The litter layer in PS3 contained a much lower concentration of lignin than in the other sites, probably because of the fast-growing species that have colonized the drained and logged forest.

Also similar to the acrotelm peat layer, ratios of C:N and lignin:N in litter increased across the peat depth gradient, while the lignocellulose index showed no pattern. The range of index values across the site gradient was greater than for values of N, lignin and solubles concentrations alone. Among the indices, lignin:N varied most (149%) across the gradient, while C:N varied least (88%).

Differences in litter layer mass and chemistry were attributed mainly to changes in plant composition, but also to drought conditions which affected all sites in 1987 and 1991. The greater litter layer mass in PS3 was likely due to changes in forest composition as the peat dried following excavation of drainage canals in 1980–81, while the improved resource quality of the litter layer was due to changes in litterfall components (drought effect on litter components discussed below) and in plant species. Pioneer tree species such as *Macaranga* spp., *Campnosperma* spp. and *Licuala spinosa* had colonized PS3, mainly in open spaces created by selective logging. The litter collections did not distinguish between primary and secondary tree litterfall, but the PS3 collections contained numerous large thin leaves characteristic of fast growing species.

Litterfall

Annual rates of fine litterfall were considerably higher in the PS3 (1.19 kg m⁻² a⁻¹) on medium depth peat than in all other sites on deeper peat. Litterfall mass in the remaining sites generally decreased from SE6 to PI12 (0.51 kg m⁻² a⁻¹) (Table 4–4). The PS3 also exhibited the widest range of 30-day litterfall mass (0.086–0.16 kg m⁻² a⁻¹) among the sites during the two-year study period. The variable litterfall rates in PS3 were associated with a greater proportion of small wood, seeds and flowers (Figure 4–2). Higher proportions of seed and flower in litterfall were also observed, but not quantified in PI9 and PI12 pole forests during the 1991 drought which followed the sampling period (see Chapter 3). The decreasing litterfall mass was significantly correlated (r = 0.61, n = 15, P = 0.015) with declining basal area of trees across the gradient of increasing peat depth. The higher litterfall rate in PS3 was attributed to the effects of earlier logging and the peat drainage activities described above.

Table 4–4. Comparison of dry mass and resource quality attributes of mixed litterfall from sixteen 1.35 m² litter traps on each of the five peat forest sites in East Sumatra (Litterfall consists of leaves, small wood <1 cm diam., seeds and flowers, and chaff). Data are means (± 95% CI) of combined litterfall from eight collection periods.

			Study area and site		
	3 m deposit	6 m deposit		12 m deposit	
Litter variable	PS3	SE6	PI6	PI9	PI12
Litterfall: Estimated [#] (kg m ⁻² a ⁻¹)	1.19	0.73	0.69	0.55	0.51
Collected (g m ⁻² 30 d ⁻¹)	97.78 (19.72)	59.98 (7.39)	56.70 (9.04)	45.19 (16.43)	41.91 (13.15)
Total C (kg m ⁻² a ⁻¹) (mg g ⁻¹)	0.61 515.2 <i>a</i> (42.5)	0.39 537.0 <i>a</i> (14.6)	0.37 532.6 <i>a</i> (21.8)	0.30 541.3 <i>a</i> (16.4)	0.28 549.1 <i>a</i> (24.4)
Total N $(kg m^{-2} a^{-1})$ $(mg g^{-1})$	0.024 19.8 <i>a</i> (0.9)	0.013 18.0 <i>b</i> (1.1)	0.010 14.7 <i>c</i> (0.7)	0.006 11.3 <i>d</i> (0.4)	0.005 10.6 <i>d</i> (0.6)
Total P (kg m ⁻² a ⁻¹) (mg g ⁻¹)	0.0016 1.35 <i>a</i> (0.07)	0.0009 1.19 <i>b</i> (0.05)	0.0004 0.91 <i>c</i> (0.05)	0.0004 0.81 <i>c</i> (0.06)	0.0003 0.63 <i>d</i> (0.04)
Solubles* (kg m ⁻² a ⁻¹) (mg g ⁻¹)	0.41 343.2 <i>a</i> (5.4)	0.22 304.5 <i>b</i> (9.9)	0.12 180.0 <i>c</i> (10.7)	0.09 174.1 <i>c</i> (5.7)	0.09 181.2 <i>c</i> (5.5)
Holocellulose** (kg m ⁻² a ⁻¹) (mg g ⁻¹)	0,26 222.6 <i>a</i> (16.1)	0.07 93.4 <i>b</i> (5.4)	0.14 206.0 <i>a</i> (31.9)	0.12 218.1 <i>a</i> (19.7)	0.10 205.7 <i>a</i> (9.1)
Lignin*** (kg m ⁻² a ⁻¹) (mg g ⁻¹)	0.52 435.0 <i>a</i> (69.6)	0.44 603.1 <i>b</i> (30.1)	0.42 614.5 <i>b</i> (75.0)	0.33 608.4 <i>b</i> (47.6)	0.31 614.7 <i>b</i> (17.0)
Polyphenol**** (kg m ⁻² a ⁻¹) (mg g ⁻¹)	0.01 12.2 <i>a</i> (2.0)	0.01 10.4 <i>a</i> (0.4)	0.01 10.3 <i>a</i> (0.3)	0.01 10.0 <i>a</i> (0.3)	0.01 11.0 <i>a</i> (0.6)
C:N	26.0	29.8	47.9	47.9	51.8
Lignin:N	22.0	33.5	55.3	53.8	57.9
LCI	0.66	0.87	0.75	0.74	0.75

Notes: *Annual litterfall estimates based on sum of eight 4-week collections for each trap extrapolated to one year. Means for different parameters within a row followed by the same letter are not significantly different at P = 0.05 (using Tukey HSD test). *Extracted with dichloromethane and hot water, **Sulphuric acid soluble, ***Sulphuric acid insoluble. ***Tannic acid equivalents. ANOVA results in Appendix 3.4.

The resource quality attributes of litterfall varied across the gradient of peat depth in patterns similar to those discussed above for the top and base of the acrotelm peat layer. Carbon concentrations in litterfall were similar in all sites, while concentrations of N and P generally declined across the gradient of increasing peat depth (Table 4–4).

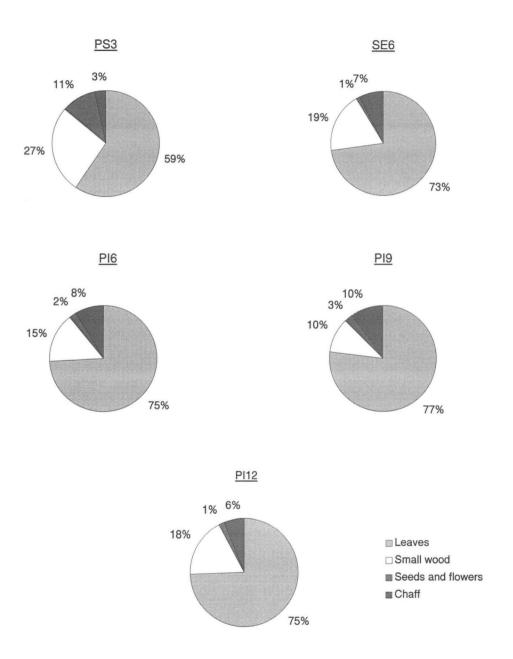


Figure 4–2. Comparison of percentage distribution of small litterfall fractions in the five peat forest sites in East Sumatra.

Total N concentrations in litterfall were similar to those in the underlying peat at the top of the acrotelm in the medium depth sites, but of lower concentrations than the acrotelm peat in the deep peat sites (Table 4–2). Litterfall P concentrations were higher than in the acrotelm peat layers of all sites and were significantly correlated (r = 0.91, n = 15, P < 0.01). Similar to the litter layer, concentrations of soluble and lignin proximate C fractions in litterfall showed opposing patterns across the gradient of increasing peat depth. Polyphenol concentrations did not vary significantly among sites. In contrast, lignin in litterfall increased in concentration and decreased in total dry mass, in a similar pattern to acrotelm peat across the gradient of increasing peat depth (Table 4–4). The soluble C fraction was negatively correlated with increasing concentrations of the same fraction in acrotelm peat (r = -0.71, n = 15, P = 0.05). This suggested that the soluble C fraction was mainly from root inputs, rather than from aboveground litterfall.

Similar to the pattern found in the litter layer, the ratios of litterfall C:N and lignin:N increased across the peat depth gradient, while the lignocellulose index showed no pattern because of the large difference between PS3 and SE6. The range of each index across the site gradient was greater than for those of N, lignin and soluble C concentrations alone. Similar to the litter layer, the lignin:N ratio varied the most (163%) across the gradient of different peat depths.

Large litterfall (>2 cm diam.) was not measured quantitatively during the present study due to access and time constraints in the remote forested sites. Patterns of large litterfall were recorded qualitatively and are presented in Appendix 2.3.

The litterfall results demonstrated the important relationship between the organic chemistry of fine litterfall and acrotelm peat across the gradient of increasing peat depth. However, the litterfall analysis could not explain the increasing concentration of the soluble C fraction in acrotelm peat. The contribution of organic inputs from roots is described below.

4.2.3 Root Biomass in Acrotelm Peat

Similar to aboveground litter, the mass and organic chemistry of small roots (0.5–2.0 mm) in peat varied among the sites. The quantity of intact roots increased across the site gradient of increasing peat depth. The PI12 site on the deepest peat contained almost four times the amount of root mass of PI9, and over 30 times the amount of roots measured in PS3 acrotelm peat (Table 4–5). Root mass declined from the top to the bottom of the acrotelm only in PI12 on the deepest peat deposit. The small, but significant site × layer interaction in the nested plot analysis

 $(F_{4,5} = 9.02, P + 0.017)$ probably from the differences in roots in the top and base of acrotelm peat which were small in PS3 and large in PI12.

Table 4–5. Comparison of oven dry mass and resource quality attributes of small roots (< 10 mm diam. live and intact dead) in acrotelm peat samples from the five peat forest sites in East Sumatra. Data are means (\pm 95% CI) of root mass and chemical concentrations, n = 10.

				Study area and si	te	
	Depth	3 m deposit	6 m deposit	<u> </u>	12 m deposit	
Root variable	(cm)	PS3	SE6	PI6	PI9	PI12
Root dry mass (kg m ⁻²)	0–20	0.28a (0.07)	1.45bc (0.19)	1.79c (0.17)	2.34 <i>d</i> (0.31)	9.00e (1.80)
	20-40	0.26a(0.07)	0.75ab (0.17)	1.02 <i>b</i> (0.19)	1.71 <i>cb</i> (0.20)	3.99f(0.45)
Total C (kg m ⁻²) (mg g ⁻¹)	0–40	0.28 519.0 <i>a</i> (13.7)	1.20 547.7 <i>a</i> (12.8)	1.54 550.1 <i>a</i> (20.3)	2.27 560.9 <i>a</i> (17.4)	7.11 547.8 <i>a</i> (21.8)
Total N (kg m ⁻²) (mg g ⁻¹)	0–40	0.007 13.1 <i>a</i> (0.7)	0.029 13.0 <i>a</i> (0.8)	0.035 12.5 <i>a</i> (0.8)	0.047 11.6 <i>ab</i> (0.6)	0.131 10.1 <i>b</i> (0.9)
Total P (kg m ⁻²) (mg g ⁻¹)	0–40	0.0004 0.80 <i>a</i> (0.04)	0.0013 0.61 <i>b</i> (0.04)	0.0017 0.60 <i>a</i> (0.06)	0.0025 0.61 <i>a</i> (0.06)	0.0041 0.32 <i>b</i> (0.06)
Soluble* (kg m ⁻²) (mg g ⁻¹)	0–40	0.07 131.7 <i>a</i> (12.6)	0.41 188.6 <i>b</i> (5.8)	0.56 200.1 <i>bc</i> (6.8)	0.97 239.7 <i>c</i> (18.0)	4.08 313.8 <i>d</i> (14.9)
Holocellulose** (kg m ⁻²) (mg g ⁻¹)	0-40	0.10 195.9 <i>a</i> (12.1)	0.35 161.8 <i>a</i> (7.3)	0.47 169.2 <i>a</i> (8.9)	0.53 131.0 <i>a</i> (11.4)	1.76 135.7 <i>a</i> (7.9)
Lignin*** (kg m ⁻²) (mg g ⁻¹)	0–40	0.36 673.3 <i>a</i> (35.5)	1.43 648.1 <i>ab</i> (30.4)	1.77 630.6 <i>ab</i> (55.6)	2.55 628.1 <i>ab</i> (28.6)	7.14 546.9 <i>b</i> (27.2)
Polyphenol**** (kg m ⁻²) (mg g ⁻¹)	0–40	0.01 11.5 <i>a</i> (1.0)	0.02 9.8 <i>a</i> (0.8)	0.03 9.6 <i>b</i> (0.7)	0.04 9.6 <i>b</i> (0.7)	0.12 9.6 <i>b</i> (0.6)
C:N	0-40	39.6	42.0	44.0	48.3	54.3
Lignin:N	0–40	51.2	49.9	50.5	54.2	54.5
LCI	0–40	0.77	0.80	0.79	0.83	0.80

Notes: Means for different parameters within a row followed by the same letter are not significantly different at P = 0.05 (using Tukey HSD test). ANOVA results in Appendix 3.5. *Extracted with dichloromethane and hot water, **Sulphuric acid soluble, ***Sulphuric acid insoluble. ****Tannic acid equivalents.

A continuous mat of small roots was found in the top of the acrotelm peat layer in the sites on the deepest peat. The mats were approximately 30 cm thick in PI12, and about 2–5 cm thick in PI9. Roots were present in the acrotelm of PI6 and SE6, but in smaller quantities and discontinuous patches. Surface peat of PS3 contained the lowest root mass and no root mat was present. The acrotelm layer of PS3 consisted of sapric-textured peat with a dense network of deep (50–75 cm) vertical cracks and crevices. The absence of regular inundation in PS3 during wet periods suggested that sapric peat and the low mass of dead intact roots were related to accelerated peat decay due to drainage and to forest degradation from previous selective logging.

Concentrations of total C, N, P, and soluble and insoluble proximate C fractions were measured in small roots combined from the top and bottom of the acrotelm layer. The C concentration of roots in was highly variable, but no trend occurred with increasing peat deposit depth (Table 4–5). The C concentration in roots was generally lower than that of fine peat. Total root N and P decreased significantly across the gradient of increasing depth, with P in roots of PI12 over 50% lower than the average of all other sites combined.

Concentrations of soluble and lignin C fractions in small roots showed opposite patterns with increasing peat depth (Table 4–5). Solubles in root mass increased across the gradient ($F_{4,5} = 455.59$, P < 0.001), while lignin concentrations decreased ($F_{4,5} = 5.10$, P = 0.052). The average soluble C content in roots (215 mg g⁻¹) was higher than that in the surrounding peat matrix (124 mg g⁻¹). In contrast, the average lignin concentration in roots (626 mg g⁻¹) was lower than that in the surrounding peat matrix (766 mg g⁻¹) in all sites. Because of the higher root biomass in the deep peat areas, the dry mass of the soluble and lignin C fractions of these roots in the acrotelm layer increased 41 and 18 times, respectively, between PS3 and PI12 sites (Table 4–5). The ratio of C:N in roots was the only chemical index that changed across the gradient of increasing peat depth, but was of similar magnitude to the change in N concentration across the gradient.

Root Mass in the Catotelm Layer

Small root mass was not measured in the catotelm layers (below 40 cm) of all the sites. Where root samples could be obtained, visual inspection showed that the waterlogged peat sometimes contained large amounts of dead, but intact small roots. High root mass was confirmed by a quantitative particle analysis of catotelm peat in the PS3 which contained the lowest mass of intact roots in the acrotelm of all sites. Here, peat samples were taken from 1 m above the underlying clay surface. The dry peat mass from this depth contained 19 to 23% intact small roots, or an estimated 3.76 to 4.62 kg m⁻² per 20 cm of peat. The remaining dry mass consisted of hemic (<0.5 mm)

peat. There was little large intact woody material in the basal peat samples. The root mass in PS3 catotelm peat was significantly greater than that in the acrotelm layer (0.26 kg m⁻²), and was comparable to the root mass measured in the PI12 acrotelm layer (3.99–9.00 kg m⁻²).

The PS3 catotelm peat was sieved to measure relative size fractions and to identify the constituents. The 0.5 to 2 mm fraction peat consisted almost entirely of small roots and root pieces. The material was identified as either intact small roots approximately 0.5 to 2 mm in diameter and 2 to 10 mm long, or papery thin strips or flakes of root epidermis of approximately 2 to 6 mm². Based on comparisons with live specimens common in the peat swamps, the latter material appeared to originate from roots sheaths of *Pandanus*, palms such as *Licuala spinosa* and *Cyrtostachys lakka*, or other plants with roots not containing secondary thickening of epidermal tissue. The intact fine roots appeared to have grown into the matrix of older peat and roots. None was living, but most were firm and elastic in structure when compressed. The larger size fraction (>2 mm diameter) of the PS3 catotelm peat sample also contained many roots. The intact woody pieces appeared to be from pneumatophore roots and contained large amounts of aerenchyma tissue. Based on a comparison of external morphology with live plant specimens, the roots were thought to be from *Cratoxylon arborescens*, a tree common to very wet areas of peat forests. However, this could not be verified.

The origin of the fine, well-humified fraction (<0.5 mm) of peat was not identified in the study. A portion of this organic material likely originated from the spongy cortex aerenchyma that filled the mass of the now hollow sheaths of small roots from the species mentioned above (Shearer and Moore *In press*). In living roots of 0.5 to 0.75 mm diameter, the thick, well-lysed cortex layer occupied 80 to 85% of the cross-section area, while the inner endodermis and stele accounted for the remaining area.

Upon close examination of the washed roots, many of the larger diameter roots contained smaller roots that have grown in through the outer sheath of the larger root. This indicated that preserved peat in the acrotelm and upper catotelm layers receives continued inputs of fresh small roots. A pattern of younger roots in a matrix of older and more humified peat was confirmed for all sites by the radiocarbon dating results presented in Section 4.1.

The higher mass of small roots in the PS3 catotelm layer indicated that both root preservation and production were considerably greater during earlier stages of peat accumulation at this site. Decay rates in the present acrotelm layer must be relatively higher with less preservation of the fine and small roots that enter the catotelm layer.

Direct measurement of small root production and mortality in peat was beyond the scope of the present study. Instead, several indices of root additions to acrotelm peat were combined to show the important contribution of roots additions, particularly in the deepest peat deposits. Both total root mass and the proportional mass of roots in acrotelm peat increased significantly across the gradient of increasing peat depth (Table 4–6). The proportional mass of roots in acrotelm peat increased from as low as 1% in PS3 to over 70% in P12 peat.

Table 4–6. Indices of small root (<10 mm) dynamics in the top and base of acrotelm peat. Root ingrowth data are means (± 95% CI) of root mass from 20 mesh bags buried in five peat forest sites in East Sumatra.

			Study area and site			
	Depth	3 m deposit	6 m deposit		12 m deposit	
Root variable	(cm)	PS3	SE6	PI6	PI9	PI12
Dry root mass	0.00	0.00 (0.05)	1 457 (0 10)	1.50 (0.15)		0.00 (4.00)
(kg m ⁻²)	0–20	0.28a(0.07)	1.45bc(0.19)	1.79c(0.17)	2.34cd(0.31)	9.00e (1.80)
	20–40	0.26a(0.07)	0.75ab (0.17)	1.02 <i>b</i> (0.19)	1.71bc (0.20)	3.99d(0.45)
Range of root mass in peat (%)	0–20	1–11	5–17	6–21	10–31	45–71
mass in peat (70)	0-20	1-11	J-17	0-21	10–31	45-71
	20–40	1–10	3–12	3–16	7–20	20–46
Ratio live:dead					v ^r	
small root mass	0–20	0.52	0.23	0.19	0.15	0.11
	20–40	0.73	0.31	0.27	0.04	0.05
Root ingrowth:						
Estimated*	0–20	0.03	0.03	0.03	0.12	1.02
$(kg m^{-2} a^{-1})$	20–40	0.02	0.01	0.02	0.09	0.57
Measured						
$(g m^{-2} 30 d^{-1})$	0–20	2.25a(0.38)	2.35a(0.39)	2.78a(0.47)	9.58d(0.99)	83.71 <i>f</i> (4.70)
	20-40	1.37b (0.34)	1.19b (0.28)	1.74bc (0.26)	6.04e (0.75)	46.64g (2.97)

Note: Small roots are 0.5-10.0 mm diameter. Root ingrowth not measured in top of acrotelm. *Root ingrowth estimates are based on the sum of two 100-day mesh bag incubations in each plot extrapolated to one year. Means for different parameters within a row (depths combined) followed by the same letter are not significantly different at P = 0.05 (using Tukey HSD test). ANOVA results are in Appendix 3.6a and b.

A comparison of live root mass also showed important differences among sites. The trend of increasing root mass across the peat depth gradient was associated with a decrease in the ratio of live:dead small roots in the acrotelm layer. As a result, the range of total live root mass across the gradient of sites (0.14 to 0.99 kg m⁻²) was considerably less than the range of dead root mass (0.14 to 8.01 kg m⁻²) across the same gradient (Table 4–6). The

larger proportion of dead roots found in the deeper peat sites suggested either faster rates of root growth and mortality (turnover), or slower decay of dead roots than in the medium depth sites.

Results of the root ingrowth bag study confirmed that additions of small roots to the acrotelm layer were greatest in sites on the deep peat deposit. From PS3 to PI12, root ingrowth rates increased up to 32 times ($F_{4,5}$ = 3158.74, P <0.001) (Table 4–6). The trend of increasing root ingrowth and peat depth was opposite to the pattern for aboveground litterfall. The PS3 on medium depth peat had the highest litterfall (1.31 kg m⁻² a⁻¹) and lowest acrotelm root ingrowth (0.05 kg m⁻² a⁻¹) estimates during the study period. An opposite trend occurred in PI12, where mean root ingrowth (1.59 kg m⁻² a⁻¹) was significantly higher than mean litterfall (0.51 kg m⁻² a⁻¹) during the same period. Root ingrowth also varied with depth. Rates also declined significantly from the top to the base of the acrotelm layers ($F_{1.5}$ = 330.72, P <0.001), with the greatest difference between layers in PI12.

Mesh bag ingrowth rates of small roots did not vary significantly between incubation periods (Appendix 3.6b). Field observations during wet and dry periods revealed that roots were exposed to frequent drying and wetting due to water table fluctuations, particularly in PI12 where the peat was fibric-textured. The PI12 peat dried rapidly during rainless periods when the water table dropped (peat moisture ranges are discussed in Chapter 3). The observations suggested that the high variability in root ingrowth measurements may reflect the effect of rapid moisture fluctuations on patterns of small root production.

The importance of belowground organic inputs to peat was revealed when the estimates of litterfall (Table 4–4) and root ingrowth (Table 4–6) were combined. Mainly because of roots, annual inputs of fine and small plant matter to peat were highest in PI12 (2.10 kg m⁻²) on deep peat and lowest in PI6 (0.74 kg m⁻²) on medium depth peat. Annual inputs to PS3 were moderate (1.24 kg m⁻²) and mainly from aboveground litterfall.

The measurements of live and dead small root mass discussed above were corroborated with field observations from soil pits excavated in peat. Root mortality in the acrotelm peat appeared to be sensitive to seasonal fluctuations in soil moisture. High root mortality was observed directly by the large mass of dead intact roots in peat. High mortality rates were demonstrated indirectly by observations of numerous scars on small roots where root branches had died back in response to flooding or drought-related moisture stress. New roots branches were observed to resprout above the scars.

At the base of the acrotelm layer and top of the catotelm, root production and mortality were partially controlled by monthly to seasonal water level fluctuations. Roots of *Pandanus artocarpus*, *Cyrtostachys lakka*,

Calophyllum spp. and Cratoxylon arborescens were observed to form a dense, vertically-oriented matrix of small roots. Mortality of these roots appeared to be partially controlled by seasonal rises in the water table which were of sufficient duration to kill the roots (Kozlowski 1982). Small roots, when pulled from the peat surface, were over 3 m in length. The roots had scars every 10 to 15 cm and new rootlets sprouting 0.5 to 2 cm above the scars. The bottom ends of the roots extracted from below the water table were usually dead, with the cortex and stele discolored and no longer firm. Live roots of a larger diameter (>0.5 cm), however, were found growing to depths of up to 3 m below the water table.

4.2.4 Summary of Litter Balance

The results of the organic component study show that the acrotelm layer in PS3 on the medium depth peat deposit contained the highest dry mass for this layer of all study sites. Over 90% of the organic mass in the PS3 acrotelm consisted of hemic (<0.5 mm) peat. Across the gradient of increasing peat depth there was a trend of decreasing total organic mass in the acrotelm layer (Figure 4–3). This decline was due to significant reductions in bulk density. However, as discussed in Chapter 3, the depth of the acrotelm layer increased across the gradient and was deepest in PI12 over the deepest peat. The trend of declining dry mass was associated with increasing proportions of organic components other than hemic peat. The small root fraction showed the largest increase across the gradient of increasing peat depth, while the proportion of hemic peat declined. In PI12, the proportion of hemic peat was less than one third of that in PS3 (Figure 4–3).

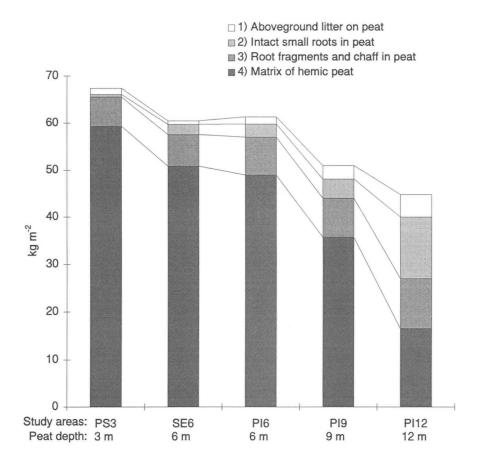


Figure 4–3. Variation in mean aboveground litter layer and organic components in the acrotelm peat layer (to 40 cm) across the gradient of peat depths. Size range of organic components: 1) small litter (<10 mm); 2) intact live and dead small roots (0.5–2.0 mm); 3) small and large root fragments and chaff (0.5–10 mm); and 4) matrix of hemic peat (< 0.5 mm).

The changes in organic mass across the gradient of increasing peat depth were also reflected in the chemistry of the organic components. The C, N, P and lignin contents of the acrotelm layers changed in proportions similar to that of total dry mass (Figure 4–4). Across the gradient of increasing peat depth, total C content of all components of the acrotelm layer (peat base, peat top, small roots and litter) decreased the least, while the total P content of all components decreased the most. The mass of the soluble C fraction increased by up to 70% across the gradient of peat depth. The importance of changes in the physical and chemical composition of litter and peat on decay processes is presented below.

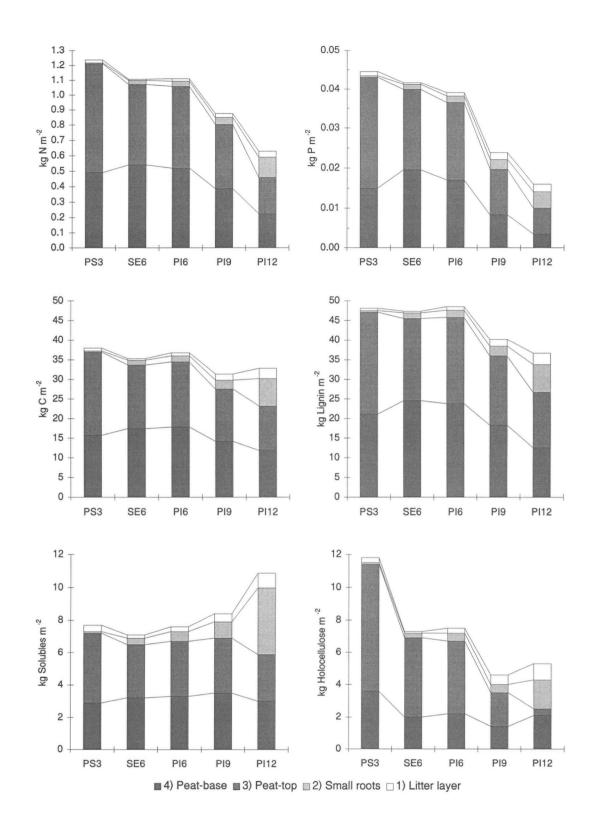


Figure 4–4. Comparison among sites of total N, P, C and proximate C fractions of lignin, solubles and holocellulose in: 1) the litter layer overlying peat, 2) small roots separated from acrotelm peat, 3) peat from the top (0–20 cm) of the acrotelm layer and 4) peat from the base (20–40 cm) of the acrotelm layer.

4.3 ORGANIC MATTER DECAY IN THE STUDY SITES

Following the study framework (Figure 1–3), various direct and indirect measures of organic matter decay were used to determine whether increased peat accumulation in the study sites could be attributed to differences in decay of aboveground litter and peat in the acrotelm layer.

4.3.1 Decay of Aboveground Leaf and Wood Litter: Peat Depth and Moisture Effects

The early and later stages of decay were measured for site-specific and common aboveground plant litters to determine if decay rates differed among the sites and the controlling factors involved.

Early Stages of Litter Decay

Mass losses of intact litter varied along the gradient of increasing peat depth and between wet and dry periods (Figure 4–5). The highly significant site × period interaction in the nested factorial analysis ($F_{4,5}$ = 948.10, P <0.001) probably resulted from the extreme decay patterns of litter in SE6 in which the peat surface was flooded during wet periods (low decay) and remained moist during dry periods (high decay). The highest dry-period litter losses occurred in SE6, perhaps because the sapric-textured peat held moisture longer than both the drained peat in PS3 and the fibric-textured deep peat in PI9 and PI12. In contrast, the highest wet-period losses occurred in PS3 where, due to the construction of drainage canals in the area in the early 1980's, the water table did not rise above the peat surface during wet periods. Plant litter in PS3 remained moist, but unsaturated. The peat surface in PI9 and PI12 did not flood during wet periods, but desiccated during dry periods (see Section 3.5.2). During extended dry periods of more than several weeks in the latter sites, the surface litter rapidly desiccated and became brittle. The lowest mass losses over 90 days occurred in the Padang Island sites (Figure 4–5). Here, litter loss rates declined with increasing peat depth, but not significantly (P <0.05). Lack of inundation and litter desiccation in the fibric-textured deep peat areas may explain why litter losses were higher in the wet season.

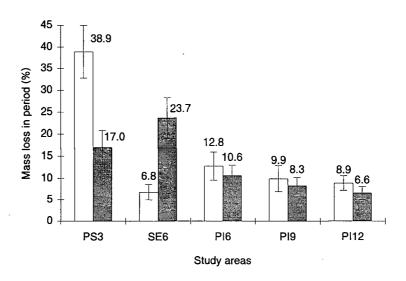


Figure 4–5. Comparison among sites of mass losses of mixed leaf litter placed in mesh bags during wet (open bars) and dry (shaded bars) 90-day periods during the field study. Data are mean percentage \pm 95% CI of litter mass loss, n = 10. ANOVA results in Appendix 3.7.

The patterns of initial litter decay measured in the field were supported by the results of litter incubations in the laboratory (Table 4–7). Litter decay rates, as represented by aerobic respiration of CO_2 from samples in glass jars, declined between saturated and unsaturated moisture conditions and with increasing peat depth. The site × moisture interaction ($F_{4,5} = 60.26$, P < 0.001) resulted from the stronger effect of moisture on decay of acrotelm peat from the medium depth sites (PS3 and SE6) compared with surface samples from the PI9 and PI12 deep peat sites.

Table 4–7. Mean (\pm 95% CI) respiration (mg CO₂ g⁻¹ 30 d⁻¹) of mixed leaves from litter layers incubated for 30-days under saturated and unsaturated moisture conditions, n = 10.

		Study area and site						
Saturation (%)	3 m deposit	6 m deposit	12 m deposit					
	PS3	SE6	PI6	PI9	PI12			
100	10.38a (1.78)	8.72 <i>a</i> (1.83)	6.03df (0.43)	6.94 <i>d</i> (0.66)	5.45f (0.54)			
50	26.82 <i>b</i> (3.73)	20.47 <i>c</i> (0.64)	14.57e (1.25)	13.74e (1.28)	8.58 <i>a</i> (0.84)			

Means followed by the same letter are not significantly different at P = 0.05 (using Tukey HSD test). ANOVA results in Appendix 3.8.

The greater effect of moisture on decay in the laboratory incubations than in field incubations was likely due to the high rainfall variability and water table fluctuations in the sites (Section 3.5). Conversely, the weaker

effect of site differences in the laboratory incubations was attributed to the smaller relative differences in respiration between PS3 and the other sites, compared with the differences in mass losses between the same areas. The smaller relative difference in respiration may be due to the constant moisture content of the laboratory incubations. The high rainfall variability, but lack of inundation during wet periods in PS3, led to rapid wetting and drying cycles in the surface litter which promoted more rapid decay compared to the other sites.

Early Stages of Wood Decay

Gonystylus bancanus, the standard wood used in the field incubation, was a commonly found tree in the three peat deposit sites. With a moderately dense bolewood (0.63 g cm⁻³ Martawijaya *et al.* 1986), it was used to represent average forest wood quality among the sites. Wood decay over one year on the peat surface varied up to 50% among sites, with the slowest decay in PI12 on deep peat (Figure 4–6). The trend of wood decay across the site gradient was similar to that of leaf decay, but rates were 3–4 times lower. Wood of other trees in the sites was observed to decay more rapidly. In PS3 pioneer species had colonized forest gaps created by selective logging in the 1970's. Species included the palm *Licuala spinosa* and several fast growing species of *Macaranga* trees. When felled during the field study, the aboveground parts of these trees decompose completely within two years.

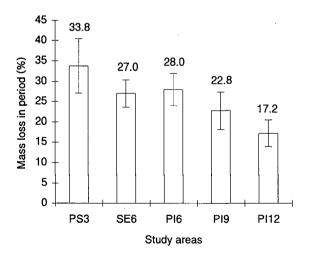


Figure 4–6. Comparison among sites of mass loss of standard wooden pegs (*Gonystylus bancanus*) placed in the top of the acrotelm peat layer for one year during the field study. Data are mean percentages \pm 1 SD of wood mass loss, n = 20.

Later Stages of Litter Decay

Decay quotients (k_L) , calculated from litter layer mass and annual litterfall, declined significantly across the site gradient of increasing peat deposit depth. The larger crop of litter mass on the forest floor of PI12 and PI9, compared with that in the medium peat sites, was due to slower rates of decay, rather than higher litterfall (Table 4–8). If steady state conditions over time are assumed, the litter layer residence times increased substantially, from one year in PS3 on medium depth peat, to 9 years in PI12 on deep peat.

The large differences in litterfall and litter layer mass among sites reduced, but not eliminated the uncertainty of using the single year of litterfall collections to calculate litter residence times. The annual collections during the study (some in different years) did not account for between-year variation in litterfall which may have been affected by climatic events such as the extended dry periods associated with the El Nino Southern Oscillation (Section 3.2 and 3.5).

Table 4–8. Comparison of decay characteristics from litterfall, litter layer and litter loss measurements from the five peat forest sites in East Sumatra.

	Study area and site						
_	3 m deposit	6 m deposit		12 m deposit			
Litter variable	PS3	SE6	PI6	PI9	PI12		
Litter dry mass (kg m ⁻²)	1.34	0.73	1.52	2.88	4.81		
Litterfall dry mass (kg m ⁻² a ⁻¹)	1.19	0.73	0.69	0.55	0.51		
Decay quotient (k_L) :							
Mass	0.89	1.00	0.45	0.19	0.11		
N	1.26	1.86	0.59	0.43	0.13		
P	1.45	2.25	0.44	0.23	0.18		
Mean residence time in litter layer (years)	1.13	1.00	2.20	5.24	9.43		
Mean residence time in litter bags (years)*	1.01	1.08	2.12	2.73	3.26		

^{*}Litter decay estimates based on sum of two 90-day litter bag losses extrapolated to one year.

A comparison of the estimated residence time of litter in mesh bags and the entire litter layer suggested that long-term litter decay patterns varied across the gradient of increasing peat depth (Table 4–8). In the PS3, SE6 and PI6 chablis and mixed forest sites over medium depth peat, the residence times of fresh intact litter (1.0–2.2 years) and of the entire litter layer (1.0–2.1 years) were similar, suggesting a near-linear pattern of decay. In contrast, the estimated residence time of the entire litter layer in the PI9 and PI12 deep peat sites were up to three times longer than that of fresh litter (based on initial mass losses from mesh bags). The longer residence times of litter on deep peat suggested a negative exponential decay pattern in which the rate of loss is proportional to the amount of litter remaining. Litter buried below the surface in PI12 remained moist and did not appear to desiccate. The declining rates of decay over time suggested that the mesh bags did not create an artifact and that other factors were more important than desiccation in controlling litter decay in the deep peat areas.

4.3.2 Decay of Acrotelm Peat: Peat Depth and Moisture Effects

Saturated peat decays slowly (10⁻⁴-10⁻⁷ a), so mass losses of peat were not measured directly during the study. Instead, several indices of decay were measured under field (cotton strips) and laboratory (respiration and N mineralization of organic samples) conditions.

Field Measures of Decay in Peat

The standard cotton strips placed in acrotelm peat disappeared rapidly under most vegetation and hydrological conditions in the sites (Figure 4–7). Decay was most variable in PS3 where, due to drainage and logging activities, moisture fluctuations were greatest. Reduced decay during flooding was most evident in SE6. Cotton losses here were consistently lower during wet periods when the water table was up to 1 m above the peat surface for several months. This finding was consistent with litter losses from mesh bags during wet periods in SE6.

Mean dry period losses of cotton were higher than wet period losses in all sites, except in PI12. This site contained the lowest mean water table level, the most fibric-textured peat and the largest root mat compared to the other areas. These factors promoted the driest peat (<160% moisture content) measured in all the sites (Section 3.5.2). The peat may have been sufficiently dry to inhibit cotton decay, particularly where desiccation and shrinkage created air spaces between cotton strips and the surrounding peat matrix. The results suggested that readily decomposable material such as cotton decayed rapidly in all sites under moderately wet and dry conditions, but decay was inhibited under extended periods of saturation in SE6 and desiccation in PI12.

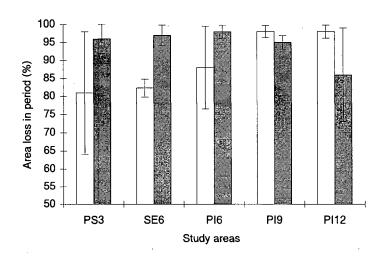


Figure 4–7. Comparison of loss of cotton strips placed in acrotelm peat layers for 90-day wet (open bars) and dry (shaded bars) incubation periods during the field study. Data are means and min. and max. values.

Peat Respiration Under Controlled Moisture and Temperature Conditions

Although the acrotelm peat layers were reasonably similar in age (<660 years BP), CO₂ respiration from the different sites varied considerably (Table 4–9), increasing from the base to the top of the acrotelm layer ($M_{\text{base}} = 0.57$; $M_{\text{top}} = 1.24$) and across the gradient of increasing peat depth ($M_{\text{PS3}} = 0.85$; $M_{\text{PII2}} = 1.15$). The site × layer interaction in the nested factorial analysis ($F_{4,5} = 30.08$, P < 0.001) probably resulted from the relatively higher respiration rates in peat samples from the top of the acrotelm layer of PI12 on the deepest peat. The stronger effect of acrotelm layer depth than differences among sites, was due to higher rates in peat from PS3, compared to the adjacent sites (SE6 and PI6) on the peat depth gradient.

The high respiration rates of PS3 peat were not related to measured differences in peat resource quality attributes between PS3 and the SE6 and PI6 sites (Table 4–2). They were, however, related to the improved resource quality (>N and P, lignin) of the litterfall and litter layer samples from PS3, compared to that of SE6 and PI6 (Tables 4–3 and 4–4). The higher litter quality of PS3 samples was attributed to previous logging and drainage activities in the Padang-Sugihan peat deposit which has resulted in drier conditions, increased numbers of pioneer plant species, and possible inundation of mineral-laden waters from the nearby Padang and Sugihan Rivers (Figure 2–1).

During the incubation periods peat respiration was not affected by different moisture levels. Although respiration was slightly higher in unsaturated (50%) peat, there were no significant differences in rates among the sites when peat samples were water saturated (Table 4–9). Respiration from peat drier than 50% saturation was not measured. Field measurements showed that the moisture content of peat under forest cover seldom fell below 50% of the saturation level (Chapter 3).

Table 4–9. Mean (\pm 95% CI) respiration (mg CO₂ g⁻¹ 30 d⁻¹) of peat samples from the top and base of the acrotelm layers in the sites incubated in saturated and unsaturated moisture conditions, n = 10.

	Study area and site							
Saturation	3 m deposit	6 m deposit		12 m deposit				
(%)	PS3	SE6	PI6	PI9	PI12			
			Top (0-20 cm)					
100	1.00a (0.22)	0.71ab (0.08)	0.91ab (0.05)	1.34c (0.06)	1.48cd (0.09)			
50	0.99a (0.19)	1.00 <i>a</i> (0.07)	1.08a (0.05)	1.58 <i>d</i> (0.10)	1.74 <i>d</i> (0.16)			
			Base (20-40 cm)					
100	0.75a(0.05)	0.29b (0.03)	0.41bc (0.03)	0.67d (0.09)	0.69de (0.12)			
50	0.77a (0.03)	0.30 <i>b</i> (0.02)	0.50c(0.03)	0.56c(0.08)	0.71e (0.11)			

Notes: Means for different peat layers within a row (moisture levels combined) followed by the same letter are not significantly different at P = 0.05 (using Tukey HSD test). ANOVA results in Appendix 3.9a, b and c. Incubations at 25°C.

Increasing 30-day incubation temperatures from 25 to 35°C had a positive effect on respiration of peat samples from both SE6 medium and PI12 deep peat sites, and from the top and base of the acrotelm layers. The significant layer × temperature interaction in the nested factorial analysis of samples from the two sites ($F_{1,2}$ = 44.99, P = 0.022 for SE6 and $F_{1,2}$ = 2379.50, P <0.001 for PI12) likely resulted from the greater respiration response to increased temperature of the top layer of acrotelm peat compared with the base layer. Temperature-induced increases in respiration in the top layer were greater in SE6 peat samples (162%), than in PI12 peat (93%) (Table 4–10).

Increases in respiration due to higher temperature were 2–2.5 times greater than the effects of reduced peat saturation (Table 3–9, Table 4–9). In the field, however, peat temperatures were relatively stable compared to

moisture fluctuations. Temperature increases from 25 to 35°C would only occur if the forest canopy were removed or heavily thinned.

Table 4–10. Mean (\pm 95% CI) respiration of peat samples incubated at 25 and 35°C to simulate mean temperatures under forest canopy cover and no cover, respectively, in the 6 and 12 m peat sites, n = 10.

Acrotelm peat	Respiration (mg CO ₂ g ⁻¹ 30 d ⁻¹)			
layers (cm)	25°C 35°			
	SI	E6		
Top.(0-20)	0.71a (0.08)	1.86c (0.09)		
Base (20-40)	0.30 <i>b</i> (0.02)	0.53 <i>a</i> (0.07)		
	PI	12		
Top (0-20)	1.76 <i>a</i> (0.16)	3.39c (0.27)		
Base (20–40)	0.69 <i>b</i> (0.07)	1.37a (0.17)		

Notes: Means for different sites within a row (layers combined) followed by the same letter are not significantly different at P = 0.05 (using Tukey HSD test). ANOVA results in Appendix 3.10a and b. Peat moisture maintained at 50% saturation.

4.3.3 The Effects of Organic Chemistry and Amendments on Decay Processes

Of the resource quality attributes analyzed in litter and peat, the soluble C fraction (simple sugars, soluble phenolics) had the greatest number of highly significant and positive correlations with peat respiration among the five sites. This was followed by the ratios of lignin:N and C:N, and the other parameters listed in Table 4–11. Respiration of peat from the top of the acrotelm layer was significantly correlated with the greatest number of chemical parameters (6 of 8), while peat from the base of the acrotelm layer had the fewest significant correlations (1 of 8). The proximate C fractions were more strongly associated with respiration in the top than in the base of the acrotelm layer. The stronger association at the surface may have been due to higher root production and the larger mass of intact fine roots (Tables 4–5, 4–6). Peat respiration was more strongly associated with carbon chemistry (proximate fractions) than with macronutrients N and P, in both the top and base layers of the acrotelm.

Alternatively, respiration of fresh litter was most strongly and significantly correlated with N and P concentrations (r = 0.93 and 0.92, n = 240, P < 0.05).

Table 4–11. Matrix of Pearson correlation coefficients for associations among the five sites between 30-day respiration and chemical variables of the organic components in and above the acrotelm layer. Chemical parameters of organic components are listed in order of decreasing strength of association. Ranges of variable concentrations across gradient of peat depth are in parentheses (from Section 4.2.1 and 4.2.2).

Chemical	Correlation	n coefficient r and (minmax, range of v	ariable means)
variable	Fresh leaf litter	Litter layer	Peat (top)	Peat (base)
Soluble C fraction	0.91*	0.92*	0.97*	0.30
	(343.2–181.0)	(343.1–174.6)	(113.2–141.1)	(104.6–148.5)
Lignin:N	-0.90*	-0.76*	0.81*	0.33
	(22.0-57.9)	(30.8-76.7)	(36.5–59.1)	(43.4–56.3)
C:N	-0.89*	-0.75*	0.77*	0.45
	(26.0-51.8)	(36.5-68.6)	(29.8–39.7)	(32.2–44.4)
P	0.92*	0.55	-0.85*	-0.49
	(1.35–0.63)	(0.81–0.40)	(0.74-0.39)	(0.54-0.27)
LCI**	0.24	0.01	-0.79*	0.92*
	(0.66–0.87)	(0.66–0.87)	(0.77-0.98)	(0.85–0.93)
N	0.93*	0.71	-0.63	-0.38
	(19.8–10.6)	(14.1–8.0)	(18.7–14.2)	(17.6-13.3)
Lignin	-0.57	-0.42	0.85*	-0.68
	(435.0-614.7)	(435.9-614.7)	(683.2–839.4)	(764.3-749.8)
Polyphenol	0.54	0.25	0.44	0.25
	(12.2–11.0)	(12.2–11.0)	(9.4–9.9)	(9.8–10.7)
pH	NA	NA	-0.43 (3.95-3.79)	-0.47 (3.57-4.01)
N _{mineral}	NA	NA	0.57 (42.2–55.3)	0.66 (12.4–17.3)

^{*}Significant at P = 0.05, Bonferroni-adjusted probabilities, n = 480. **Lignin:lignocellulose index. NA-not analyzed.

Some chemical parameters were either positively or negatively correlated with respiration, depending on organic component type. Respiration from litters generally decreased across the gradient of increasing peat depth, while respiration of peat from the top of the acrotelm increased across the depth gradient. The opposing trends in respiration accounted for the negative and positive correlations of the same parameter in Table 4–7. The generally

poor correlations between respiration and chemical parameters in peat samples from the acrotelm base were attributed to high respiration rates of PS3 peat. When PS3 data were removed from the analysis, correlation coefficients exhibited a pattern similar to that for peat from the top of the acrotelm layers: significant correlation coefficients for solubles (r = 0.82), lignin:N (r = 0.85) and C:N (r = 0.88).

To further determine the effects of peat organic chemistry on decay, leaves and small roots were incubated under saturated conditions with peat extracts from the medium (SE6) and deep (PI12) peat sites. During 30-day incubations both extracts had a significant positive effect on leaf respiration ($F_{2,4} = 56.57$, P < 0.001), but did not affect root respiration (Table 4–12). The SE6 peat extract was associated with higher mean respiration rates in SE6 and PI12 leaves and roots compared with the PI12 extract.

Table 4–12. Mean (\pm 95% CI) respiration (mg CO₂ g⁻¹ 30 d⁻¹) of intact leaves and small roots incubated in water-based* extracts from SE6 and PI12 peat, and in distilled water, n = 10.

	Incubation treatment				
Origin of samples	Distilled H ₂ O	Peat extract-SE6	Peat extract-PI12		
		1. Leaves			
SE6	8.72a (1.73)	14.85 <i>b</i> (1.77)	13.74 <i>b</i> (1.37)		
PI12	5.45a (0.54)	10.32 <i>c</i> (0.95)	8.06c (0.86)		
		2. Small roots			
SE6	6.75a (0.66)	7.34 <i>a</i> (1.06)	6.55a (1.55)		
PI12	3.51 <i>b</i> (0.42)	3.88 <i>b</i> (1.10)	4.16 <i>b</i> (0.77)		
		3. Extracts alone			
Extracts incub. alone	0.24 (0.02)	0.34 (0.07)	0.52 (0.11)		

Notes: *Extracts are filtered slurries of 2:1 distilled H_2O and fresh peat. Means for different organic components within rows (sites combined) followed by the same letter are not significantly different at P = 0.05 (using Tukey HSD test). ANOVA results in Appendix 3.11a and 3.11b.

The extracts did not affect CO₂ evolution from SE6 and PI12 small roots. Importantly, the PI12 peat extract did not contain substances that inhibited aerobic respiration in peat. The small positive effect of the extracts on leaf and root respiration was likely due to the addition of the soluble C fraction, mineralized N and P and other nutrients, whose effects could not be distinguished.

Respiration of peat from the base of the acrotelm layer of the medium (PS3) and deep (PI12) peat sites was measured for one year following the addition of saturation amounts of C and N amendments (Figure 4–8). The respiration response of peat amended with C was significantly greater in magnitude and duration than for peat amended with N. In addition, the peat samples from the two sites responded differently to the C addition. The initial response to added C was higher for PI12 peat, but PS3 peat responded longer. Over the course of 400 days, the increase in respiration amounted to a CO₂-C loss equivalent to 62% of the C added to PS3 peat, compared to 39% of the C added to PI12 peat. For each peat, the initial respiratory response with added-(C+N) was higher than that with added-C only. However, the elevated respiration of the samples amended with both C and N was similar in duration to that of the peat samples amended with C alone. After 400 days, the amount of C respired was equivalent to 44% of the C amended to the PS3 and PI12 peat samples.

The larger respiration response of peats to added-C than to added-N suggested that microbial communities in the acrotelm layer are primarily heterotrophic and that the rate of peat decay was controlled by the chemical quality of energy-yielding substrates rather than by the availability of macronutrients. The relative importance of available-C and available-N to the microbial communities in the peat samples was quantified using several physiological indices. The energy deficiency index (EDI) is the percent increase in CO₂ efflux over basal respiration due to saturation amounts of added glucose-C. Conversely, the nutritional deficiency index (NDI) of peat is the relative increase in maximum respiratory response due to the addition of N. The EDI of peat samples from both sites was between 51 (PS3) and 389 (P112) times larger than the NDI (Table 4–13). The indices were also affected by site differences. EDI was highest in PI12 peat, while NDI was highest in PS3 peat.

Table 4–13. Energy (EDI) and nutritional (NDI) deficiency indices of acrotelm peat from study sites on 3 m and 12 m peat deposits.

Study site	EDI (%)	NDI (%)	NDI:EDI	
PS3	3669	72	0.020	
PI12	6608	17	0.003	

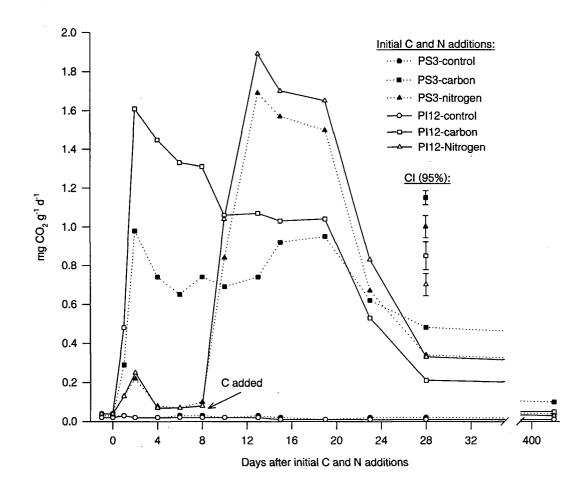


Figure 4–8. Mean daily respiration of peat amended with saturation amounts of glucose (50 mg C g⁻¹) and ammonium nitrate (17.5 mg N g⁻¹), and incubated aerobically for one year. Glucose was added on day 8 to samples initially amended with ammonium nitrate. Peat samples are from the base of the acrotelm layer in both the shallow (PS3) and deep (PI12) peat sites. Error bars represent average CI at P = 0.05, n = 10.

4.3.4 Peat Mass Losses

The results of the respiration incubations were used to estimate mass loss rates of peat from the study sites, assuming saturated conditions, an average ground temperature of 25°C and different C concentrations in each site (Table 4–14). The estimated mass losses (kg m⁻² a⁻¹) were higher in the top of the acrotelm than at the base ($M_{top} = 0.19$; $M_{base} = 0.07$). There was no discernible pattern of peat loss across the gradient of increasing peat depth.

However, when bulk density was incorporated, decay rates of acrotelm peat (k_A) increased considerably across the peat depth gradient, except in PS3 which was similar to PI9.

Peat residence times were extrapolated from the incubation decay rates and compared to the radiocarbon age measurements in Section 4.1. Estimated residence times for the top of the acrotelm layer of incubated peat were greater than radiocarbon ages in all sites, but decreased across the gradient of increasing peat depth, with the shortest periods in PI12 (Table 4–14). The longer residence periods extrapolated from the laboratory incubations indicated that peat from the top of the acrotelm decayed about 3 times faster under field conditions, perhaps due to additions of fresh organic matter and fluctuations in waterlevels. In contrast, residence times in incubated peat samples from the base of the acrotelm layer were comparable to the radiocarbon ages, except PI12 peat which decayed about 5 times slower during the incubations. The small root content of peat from the acrotelm base in PI12 was significantly greater than in the other sites, suggesting continuous inputs of soluble organic C.

Table 4–14. Estimated mass losses of peat samples from the top and base of the acrotelm layers in the five peat forest sites in East Sumatra. Data are means (\pm 95% CI), n = 10.

		Study area and site					
	Depth	3 m deposit PS3	6 m deposit SE6	12 m deposit			
Estimate*	(cm)			PI6	PI9	PI12	
Mass loss	0–20	0.22 (0.03)	0.13 (0.01)	0.18 (0.01)	0.23 (0.01)	0.18 (0.01)	
$(kg m^{-2} a^{-1})$	20-40	0.12 (0.01)	0.04 (0.01)	0.06 (0.01)	0.07 (0.01)	0.07 (0.01)	
Decay quotient (k_A) of peat	0–20	0.0057	0.0043	0.0064	0.0094	0.0103	
	20-40	0.0041	0.0015	0.0021	0.0027	0.0039	
Residence time (years)	0–20	174	232	156	107	97	
	20-40	243	673	470	369	257	

Alternatively, the assumption that 40 cm of peat in the PI12 acrotelm has accumulated over the last 45 years may not be accurate. The young age of peat may indicate rapid turnover (high input and decay) of the entire acrotelm layer, rather than rapid accumulation or a short residence period. The rapid turnover of an existing acrotelm layer is consistent with the historical rates of peat accumulation which suggest slower rates (1–2 mm a⁻¹) during the later stages of peatland development, particularly on the interior plateau of the domed deposit (Supardi *et al.* 1994).

4.4 NET CHANGES IN THE ACROTELM PEAT LAYERS OF THE STUDY AREAS

4.4.1 Peat Physical Properties

The bulk density of peat in the acrotelm layer decreased significantly ($F_{4,5} = 10.31 P = 0.012$) across the gradient of increasing peat depth (Table 4–15). Except for the high value in the top peat layer of PS3, bulk densities did not differ significantly between the top and base of the acrotelm layers. An analysis of particle size distribution explained the differences in peat bulk densities. The percentage of coarse (0.5–2.0 mm) material increased significantly across the site gradient ($F_{4,5} = 66.71$, P < 0.001) and from the base to the top of the acrotelm layer ($F_{1,5} = 36.40$, P < 0.002). The top of the acrotelm peat layer in PI12 pole forest on deep peat had the highest coarse fraction, ranging from 65 to 78% of the total dry mass (Table 4–15). As discussed above, a large proportion of the organic matter consisted of live and dead roots of various sizes. The higher bulk density and lower percentage of coarse fibric material measured in the top of the PS3 acrotelm layer suggested that increased decay has occurred in this layer, relative to the base. This was attributed to accelerated drainage due to canals excavated in the area in the early 1980's.

Bulk density and particle size distribution were used to classify the peat layers according to the USDA system (Soil Survey Staff 1975) (Table 4–15). Due to the high coarse material content, the top and base of the acrotelm peat layer in the pole forest on the deepest peat was classified as Typic Tropofibrist. Much of the organic matter in this layer was recognizable as roots, small wood or leaves. Acrotelm peat in the medium pole forest and mixed forest on Padang Island were classed as Typic Tropohemist, having slightly higher amounts of unrecognizable organic matter than the Tropofibrist peat. The PS3 and SE6 medium depth peat contained high percentages of fine material and was classified mainly as Typic Troposaprist. Only small quantities of PS3 and SE6 peat were recognizable as plant material. The remaining organic matter was highly ripened, with about 90% passing through a 0.5 mm mesh sieve.

Table 4–15. Summary of physical characteristics of the top and base of the acrotelm peat layers used as indices of the degree of decay in the five peat forest sites in East Sumatra.

	Study area and site								
Depth	3 m deposit	6 m deposit							
(cm)	PS3	SE6	PI6	PI9	PI12				
	1. Peat bulk density (g cm ⁻³)								
0–20	0.19 <i>a</i> (0.03)	0.15ab (0.03)	0.14 <i>ab</i> (0.02)	0.12 <i>b</i> (0.01)	0.10 <i>b</i> (0.03)				
20-40	0.14 <i>ab</i> (0.01)	0.15ab (0.03)	0.15 <i>ab</i> (0.03)	0.12 <i>b</i> (0.02)	0.10 <i>b</i> (0.02)				
	2. Peat particle size distribution (% of total dry mass)a) 0.5–20 mm Coarse fraction								
0–20	10.7a (2.9)	17.5 <i>b</i> (2.3)	20.8 <i>b</i> (1.7)	31.1 <i>bc</i> (4.6)	71.4 <i>cd</i> (6.6)				
20–40	9.6a (1.7)	12.5ab (2.2)	15.6ab (2.0)	20.5ab (2.5)	46.0 <i>c</i> (3.9)				
	b) <0.5 mm Fine fraction								
0–20	89.3 (8.1)	82.5 (10.1)	79.0 (11.4)	68.9 (5.8)	28.7 (8.5)				
20–40	90.4 (6.8)	87.5 (11.9)	84.4 (9.6)	79.5 (8.3)	54.0 (11.0)				
	3. Von Post Scale of humification and peat textural class*								
0–20	H8-10, sapric	H6–8, fine hemic	H5–6, hemic	H4-5, coarse hemic	H1-3, fibric				
20–40	H8-10, sapric	H8-10, sapric	H6–8, fine hemic	H5-6, hemic	H1-3, fibric				
		4. Soil classification (USDA 1975)							
0–20	Typic Troposaprist	Typic Tropohemist	Typic Tropohemist	Typic Tropohemist	Typic Tropofibrist				
20–40	Typic Troposaprist	Typic Troposaprist	Typic Tropohemist	Typic Tropohemist	Typic Tropofibrist				

Note: Data are means (\pm 95% CI). Means for different parameters within a row (depths combined) followed by the same letter are not significantly different at P = 0.05 (using Tukey HSD test). ANOVA results in Appendix 3.12. *Based on criteria listed in Table 2–4.

4.4.2 Changes in Peat Surface Topography

In addition to the physical changes in peat properties described above, analysis of the micro-topography of the forest floors revealed the conditions under which recent peat has been preserved in the study sites.

PS3 Study Site

Peat surface levels in PS3 dropped 9 to 12 cm over the two-year monitoring period (Figure 4–9). This drop was consistent with the high rates of litter loss and peat respiration described above. Between tree mounds, the PS3 peat surface was flat with little relief except for the barely distinguishable network of old canals. These were excavated throughout the peat forest in the 1970s to float logs out to the Padang and Sugihan Rivers which flow on either side of the peat deposit. At the beginning of the study period in 1986, the acrotelm peat layer was observed to contain small quantities of litter and small and fine roots, but no root mat. By 1994 the surface litter in PS3 was highly decomposed and sapric peat was fully exposed at the surface. Despite desiccation of the acrotelm peat layer, the waterlogged layer close to the clay-peat boundary in PS3 contained large amounts of intact fine and small dead roots (described above). The differences in root mass between the acrotelm and basal peat layers suggested that edaphic and vegetation conditions had changed considerably in the peat deposit since the first 1–2 m of peat accumulated.

The surface topography of PS3 also showed evidence of net peat decay. Tree mounds of up to 1.5 m in height were mostly hollow except for the matrix of large adventitious roots. Observations made during the two-year monitoring period indicated that changes were partially due to excessive drainage. Many of the tree mounds became desiccated and peat within the matrix of the raised roots disappeared or subsided. Although not quantified during the study, field observations indicated that the high tree mounds in PS3 was due mainly to the degradation of peat surrounding the mounds, rather than to mound growth and litter accumulation.

Extensive tree blow-down also occurred in PS3, particularly during and after the 1987 drought (May-November). Much of the tree blow-down was due to increasing root instability, rather than to pests, disease, lightning or storms. Instability was probably because of dry conditions and peat degradation. Inspection of the felled trees showed that most were cleanly uprooted and very few with broken stems. Consequently, a large portion of the deposit burned during the 1987 El Nino drought (see Chapter 3 and Brady 1989).

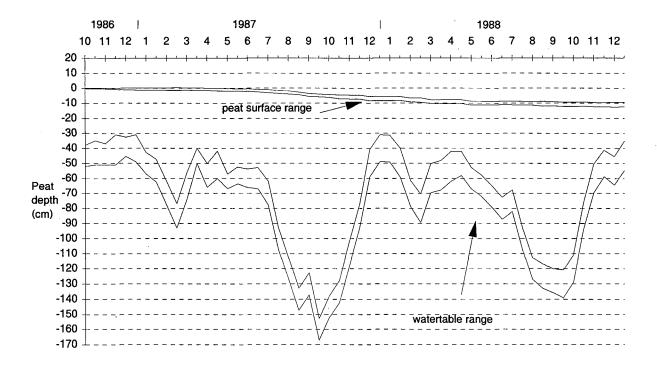


Figure 4–9. Comparison of ground surface changes over 27 months in the PS3 site. Lines represent upper and lower 95% confidence intervals of 10 piezometers used to measure ground surface and water levels. Mean levels are not shown.

SE6 and PI6 Study Sites

The SE6 and PI6 mixed forest sites also contained tree species with buttresses (*Shorea*), stilt roots (*Ganua*, *Palaquium*) and large knee roots (*Alstonia*, *Cratoxylon*). In addition, the mat of surface roots was thin and discontinuous. The tree mounds, however, in the SE6 and PI6 remained intact with the matrix of large and medium-sized roots filled with peat. Peat accumulation in the inter-mound areas, if it was still occurring, was likely to originate largely from aboveground litterfall due to the low abundance of intact fine and small roots. The peat surfaces in SE6 and PI6 did not drop significantly over the 2–3 year measurement period (Figure 4–10). The observations on surface topography, combined with the results above on peat physical properties and the measurements of decay processes, suggested that peat accumulation had ceased under the mixed forest areas over medium peat, and that the surface layer of peat was either in steady state, or in a state of slow net decay.

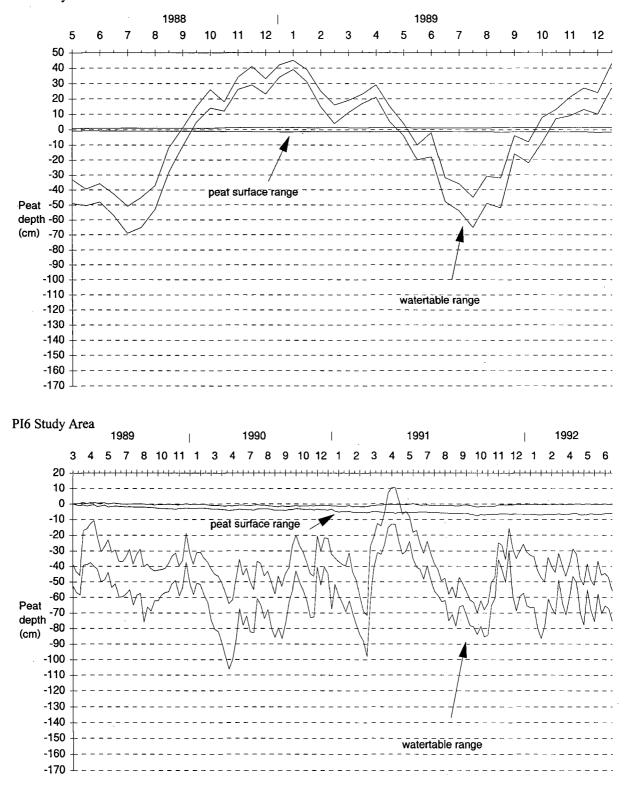


Figure 4–10. Comparison of ground surface changes over 20 and 39 months in the SE6 and PI6 sites, respectively. Lines represent upper and lower 95% confidence intervals of 10 piezometers used to measure ground surface and water levels. Mean levels are not shown.

Surface micro-topography was flattest in the PI9 and PI12 sites. Surface relief between trees decreased from PI9 to PI12 across the Padang Island peat deposit. Tree mounds, from 15 to 30 cm high, were common in the former, but not in the latter. Small mounds (<20 cm) occurred around clumps of *Pandanus artocarpus*. Other dominant trees such as *Calophyllum* spp., *Tetramerista* and *Diospyros* did not form coppices and distinctive mounds of roots and peat. In addition, the root mat under the tall pole forest of PI9 was thinner and less evenly distributed than in PI12. As the water table seldom rose above the peat surface in these sites, there were few natural depressions created by surface drainage water (Figure 4–11). Drainage depressions were likely to be formed where root mats were thin or nonexistent and where the surface peat was more finely textured and could support surface water.

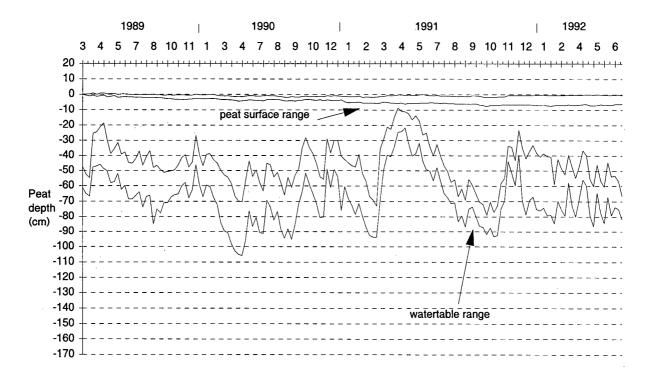


Figure 4–11. Comparison of ground surface changes over 39 months in the PI12 site. Lines represent upper and lower 95% confidence intervals of 10 piezometers used to measure ground surface and water levels. Mean levels are not shown.

Without the presence of a continuous root mat, peat accumulation, if it still occurred in PI9, was likely to be discontinuous across the forest floor. The flat topography in PI12 suggested that peat accumulation between trees

was uniform. Peat surface levels in PI12 dropped up to 7.5 cm in elevation over 3.5 years at some piezometers on Padang Island (Figure 4–11). The level changes, however, were not significant when data from all 10 piezometers were combined. Peat swelling due to water level changes was detected during the study period, but was less than 1 cm and not significant.

 $^{^195\%}$ of the activity, in AD 1950, of the NBS oxalic acid normalized to $\delta^{13}C$ = -19 per mil.

CHAPTER 5

DISCUSSION AND IMPLICATIONS OF THE STUDY

The discussion of study findings focuses on specific component results and on general implications of the study findings. Research results for the age, plant input and decay components of the peat accumulation model are discussed in relation to the framework of alternative and competing hypotheses presented in Chapter 1 (Figure 1–3). For each finding the results are compared to past studies, limitations are discussed and specific research needed to clarify or extend the findings is proposed. The implications of the findings are related to the model assumptions of *Sphagnum* peat accumulation and their application to tropical peat deposits.

5.1 SUMMARY AND DISCUSSION OF FINDINGS

5.1.1 Peat Age

Age of Organic Matter in the Acrotelm Layer

The findings did not support the hypothesis that the gradient of increasing peat depth, as represented by the study sites, could be attributed to variable ages of surface peat. The top of the acrotelm in all samples was of modern (post 1950 AD) age, while peat in the acrotelm base was younger than 660 yBP. Few palynological studies of tropical peat have included the acrotelm layer because of the greater interest in the preserved layers of subsurface peat, and due to the problems of age analysis of young organic materials. Modern ages (103.2 pMC) were measured at 40–50 cm below the surface of basin peat in highland Sumatra (Maloney and McCormac 1995). No other published radiocarbon ages of acrotelm peat in coastal areas of Southeast Asia were found.

Several studies include age measurements of peat within 2 m of the surface and show that ages are highly variable. In Riau Province, peat was 1.4 thousand years BP (ka) at 1.8 m below the surface on the Bengkalis Island 8 m deposit, and 0.7 ka at 0.7 m below the surface on the Siak River 10 m deposit. In contrast, a peat sample from a 4 m portion of the latter deposit was 4.1 ka at 0.7 m below the surface (Diemont and Supardi 1987, Supardi *et al.* 1993). The oldest recorded surface peat was from the high peat deposits near Palangkaraya in Central Kalimantan (Sieffermann *et al.* 1988, Neuzil *In press*). Peat samples from 0.7 m below the surface of deposits 3 to 5 m thick were up to 8.8 ka in age. The authors noted that peat within 0.7 m of the surface was of modern age, but did not provide radiocarbon results. The large age difference between peat in the acrotelm and catotelm layers suggested

that recent aboveground organic matter from vegetation has been preserved in the acrotelm, while a large portion of the upper catotelm layer has decayed, or has been eroded by external forces. Coastal erosion of peat deposits may also explain why some samples of catotelm peat in the rand areas of the Siak and Bengkalis deposits (near the Padang Island study area) were up to 5.7 ka (Supardi *et al.* 1993). To avoid large age differences between acrotelm and catotelm peat, rand areas of the peat deposits were excluded from the present study.

The isotopic fractionation (δ^{13} C) values of all samples ranged from -25 to -31‰, suggesting that the peat deposits have been under continuous forest cover over the last several centuries. Trees in tropical forests have the C_3 photosynthetic pathway and the soil organic matter produced from their litter is known to have δ^{13} C values ranging from -25 to -30 (Volkoff and Cerri 1987). In contrast, tropical grasses which are commonly found in disturbed areas, possess the C_4 photosynthetic pathway for which δ^{13} C values of -6 to -19‰ are common (Cadisch and Giller 1996). Extensive grasslands of *Imperata cylindrica* were common in the disturbed and cleared peat forest areas located in the Sugihan West reference area (Figure 2–1), but were not recorded in the forested study sites.

An additional finding of the age study was that the base of the acrotelm peat layer decreased in age (up to six times) across the gradient of increasing peat depth. The residence time of peat in the acrotelm layer was also affected by root penetration into preserved peat. Small roots were hundreds of years younger than the hemic-textured peat. The effect of root penetration was small in the medium depth peat study areas, but represented up to 71% of the total organic dry mass in the acrotelm layers of the deep peat study areas. As a result, when peat and root fractions were aged separately, the residence time of organic matter from roots in the base of the acrotelm layer was considerably shorter than when the fractions were aged together. Across the gradient of different peat depths, an increasing percentage of the organic inputs preserved in the catotelm layer were of modern age.

The finding of shortened residence times of organic matter in the acrotelm layers of deeper deposits was consistent with the assumption of the two-layered model (eq. 2) for *Sphagnum* peat accumulation. However, the processes that control residence times appeared to differ in *Sphagnum*- and tropical wood-based peatlands. Increasing water levels are thought to reduce the residence time of *Sphagnum* in the acrotelm and increase the amount of plant mass entering the catotelm layer (Clymo 1984). Because of the high rainfall in tropical regions where peatlands occur, it has also been assumed that rising waterlevels reduce decay rates and allow peat to accumulate without much degradation (Esterle *et al.* 1989, Cohen and Stack 1996). The age results of the study

suggested that the effects of rainfall alone could not account for increasing amounts of organic matter entering the catotelm peat layer. In contrast to *Sphagnum* peat deposits, reduced residence time of organic matter in the acrotelm was associated with a decline in mean annual water level and a thickening of the acrotelm layer across the gradient of increasing peat depth in the Sumatra study areas. The reduced residence time and increased preservation of organic matter in the acrotelm base could be attributed more to increased root mass in the base of the acrotelm peat layer, rather than to a rising water table and reduced decay (discussed below).

The increased mass of small intact roots in surface layers of deep peat deposits have been noted in palynological studies in Sumatra (Grady *et al.* 1993) and Borneo (Moore and Hilbert 1992, Esterle and Ferm 1994). The shorter residence times of organic matter in the acrotelm and rapid entry into the catotelm layer were supported by recent findings of several petrographic studies of tropical peat deposits. Moore *et al.* (1996) and Dehmer (1995) proposed that the maceral composition of surface peat in Central Kalimantan indicated little oxidative alteration and a low degree of decay.

Basal Peat Ages

Variable peat accumulation is also determined by basal age which varies within and among peat deposits throughout Southeast Asia. Basal peat ages under the central plateaus of 8 to 10 m deposits along the east coast of Sumatra average about 4.1 thousand years (ka) before present (Table 5–1). Although basal ages were not measured during the present study, comparisons with the nearby Bengkalis Island and Siak River deposits which also contained about 12 m of peat, strongly suggest that the basal peat on Padang Island is probably of similar age.

Basal peat ages from the rand of several deposits in South Sumatra range from 0.9 to 5.5 ka. The variable ages suggested that in some deposits peat initiation occurred simultaneously throughout the entire deposit areas (Diemont and Supardi 1987a, Supardi *et al.* 1993), while in other deposits peat accumulation may have begun in the center and accreted towards the coast (Cameron *et al.* 1989). Coastal accretion rates of up to 20 m a⁻¹ have been estimated in East Sumatra (Chambers and Sobur 1975). The high rate of accretion is supported by the relatively young radiocarbon ages of basal peat (1090 \pm 70 yBP, δ^{13} C -29.8) and wood (880 \pm 70 yBP, δ^{13} C -25.0) found in the Sugihan West peat deposit (Brady, unpublished data) (Figure 2–1). The basal samples were taken from 3–4 m depth peat about 30 km from the coast.

Table 5-1. Radiocarbon ages (ka) of basal peat from deposits in Southeast Asia. Peat depth (m) above basal peat is indicated in parentheses.

	Sample location	in deposit*	Reference		
Peat deposit	Central plateau	Rand			
Sumatra:					
Batang Hari River, Jambi	4.2 (8)	1.2 (2)	Cameron et al. (1989)		
Berbak, Jambi	3.0 (10)	4.5 (3)	Silvius et al. (1984)		
Bengkalis Island, Riau	4.7 (8)	5.5 (3)	Supardi et al. (1993)		
Siak River, Riau	4.5 (10)	4.6 (1)	Diemont and Supardi (1987), Supardi et al. (1993)		
Sugihan River, South Sumatra	na	0.9–1.1 (3)	Brady, unpublished		
Peninsular Malaysia:					
Johore	4.9 (0.5)	na	Haseldonckx (1977)		
Borneo:					
Sebangau River, Central Kalimantan	8.3 (5)	4.8 (1)	Sieffermann et al. (1988)		
Paduran River, Central Kalimantan	na	2.8 (3)	Sieffermann et al. (1988)		
West of Kahayan River, Central Kalimantan	9.1 (7)	9.5 (3)	Neuzil (In press)		
Sambas River, West Kalimantan	9.1 (6)	2.6 (1.5)	Neuzil (In press)		
Baram River, Sarawak	4.3 (13)	1.5 (1)	Esterle (1990), Wilford (1962) in Anderson and Muller (1975)		

^{*}Present locations may not reflect topographical positions during period of peat initiation.

Peat ages were not measured in basal peat of the Padang-Sugihan (PS3) and the Sugihan East (SE6) peat deposits. However, a comparison of basal peat ages in several deposits throughout Southeast Asia showed that

present-day accumulations of peat cannot always be related to the time of initiation (Table 5–1). The weak relationship is particularly evident in deposits that have degraded through erosion or accelerated decay. An extreme example was provided by Rieley *et al.* (1992a), who measured a basal peat age of 11 ka in <1 m of peat along the Kahayan River in Central Kalimantan.

Considering the relatively constant ages for both acrotelm and basal peat in the study areas, peat age alone could not account for the gradient of increasing peat depth from 3 to 12 m. Variable peat accumulation must also be the result of differences in plant input and decay processes as discussed below.

Limitations Related to Age Findings

In addition to root contamination, several other processes can affect the C isotope composition in peat.

Contamination of younger C may result from soil biota incorporating fresh C directly from the air, or by biochemical alteration of dead plant tissue, or from upward and downward percolation of soluble organic materials.

Compared to adjacent forests on mineral soils, the acrotelm peat in the study areas was likely to contain less soil macrofauna because of the mostly wet and frequently flooded conditions (Kaneko and Takeda 1990).

Although unmeasured in the sites, it was assumed that substantial contamination of peat in the acrotelm base by fresh C from soil biota would be small.

The soluble C fraction in peat was partially removed by pretreating the radiocarbon samples with several acid (HCl) washes which also removed carbonates and some holocellulose. Martell and Paul (1974) showed that the acid unhydrolysable fraction of soil organic matter constitutes the major portion of the resistant soil organic components in soils. The high concentrations of lignin (68–84% acid insoluble) in all sites represents the oldest fraction of C in organic matter (Anderson and Paul 1984). Older ¹⁴C dates for lignin than for the cellulose fraction in peat have been reported in studies from the northern (Olson and Broecker 1958) and southern hemispheres (Goh 1978).

The contaminating effect of soluble C fractions may be important when aging preserved peat. Recent radiocarbon studies on gasses in subsurface peat indicate that old gasses at depth can be much younger than the surrounding peat (Aravena *et al.* 1993, Charman *et al.* 1994). The younger gasses were attributed to the downward transport of younger C, probably as part of the dissolved organic C (DOC) in pore waters. However, similar results have not been found in C isotope characterization of organic matter within profiles of tropical soils. Von Fisher and

Tieszen (1995) found no evidence of substantial illuvial translocation of isotopically distinct soil forming material within a soil profile in Luquillo, Puerto Rico. Alternatively, researchers have suggested that ¹⁴C peat ages could be up to 20% older than the real age of the peat due to input of depleted CO₂ emitted from decomposing layers of the deposit below the measured layer (Jungner *et al.* 1995). These studies illustrate the complexity of C processes within deposits of preserved peat. The piezometer measurements taken at the sites (Chapter 3) suggested the existence of both vertical and horizontal hydraulic gradients in the peat profiles. More precise waterlevel measurements would be required to confirm the gradients.

Other possible sources of contamination include old C from active volcanoes, particularly considering the close proximity (200–300 km) of the Krakatau volcanic islands to the study areas. The islands erupted violently in the 1890's, spreading ash worldwide (Whitten *et al.* 1984). However, radiocarbon studies have shown that peatlands adjacent to active volcanoes are not affected by old C from volcanic emissions (Shore *et al.* 1995).

The use of radiocarbon dating techniques on the young organic matter in the acrotelm layers of the sites was appropriate for the objectives of this study. However, the method is not appropriate for more detailed age studies in acrotelm peat. Many factors affect the concentration of ¹⁴C in plants before and after their death including: atmospheric ¹⁴C variations, alteration effects, source or reservoir effects, contamination and pretreatment (Bowman 1990, Coleman and Fry 1991). In particular, the enrichment of the atmosphere with bomb ¹⁴C in the 1950s and 1960s has precluded the use of radiocarbon dating of post-1950 organic materials (Goh 1991). Other dating methods such as ¹⁴C accelerator mass spectrometry (AMS) and the continuous rate of supply (CRS) model using ²¹⁰Pb are available for dating young peat (Appleby *et al.* 1988). However, sampling acrotelm peat at finer spatial scales (e.g., 5 cm layers) would likely result in large sample errors due to spatial variability (Townsend *et al.* 1995). The large errors may not be overcome because of the expense of AMS measurements. Dates based on ²¹⁰Pb can be biased and inaccurate because lead can be mobilized by organic-rich waters of peatlands (Urban *et al.* 1990).

5.1.2 Plant Organic Matter Inputs to Acrotelm Peat

Aboveground Litter Inputs

The analysis showed that the mass and resource quality attributes of fine litterfall declined across the gradient of increasing peat depth. The findings therefore, did not support the hypothesis that the gradient of different peat depths can be directly attributed to increased additions of aboveground plant matter (Figure 1–3). Changes in litterfall mass and chemistry were significantly correlated with changes in peat forest characteristics. Across the gradient of increasing peat depth, fewer plant species and lower stand height and basal area were associated with reduced resource quality in the top of the acrotelm peat layer.

Litterfall rates in the undisturbed SE6, PI6, PI9 and PI12 sites were comparable to the data sets of litterfall for other low stature and low fertility forest soils in Southeast Asia summarized by Proctor (1984) and Vogt *et al.* (1986) and listed in Table 5–2. The total litterfall rate in SE6 mixed forest was at the low end of the range of litterfall in the non-peat forest types listed in Table 5–2, while PS3 litterfall was high. The maximum PS3 annual rate of 1.42 kg m⁻² was substantially higher than the highest total litterfall rates of the primary lowland forests listed, except that of a mangrove forest in Malaysia (Proctor 1984). The high PS3 litterfall was within the range of litterfall in other tropical forests on low fertility soils including: Caatinga soils (Jordan and Herrera 1981, Jordan 1987) and inundation forests (Adis *et al.* 1979, Franken *et al.* 1979) in South America, and cypress swamp forest in the southern U.S.A. (Ewel and Odum 1984). The estimated annual litterfall rates in PI9 and PI12 pole forest were lower than in other lowland forest types, with the exception of the lower limit of a fresh water swamp forest in Malaysia (Furtado *et al.* 1979). No published studies could be found that report such low litterfall production in any forest types in Southeast Asia. In Caatinga forest on mineral soil in Venezuela, Jordan and Murphy (1982, in Proctor 1984) reported low annual litterfall production between 0.4 and 0.6 kg m⁻².

Low litterfall rates in the tropics have been related to nutrient and moisture effects (Whitmore 1984). Some studies show decreasing litterfall production with declining soil fertility (van Schaik and Mirmanto 1985), while others report no correlations (Jordan and Herrera 1981, Proctor *et al.* 1983b, Scott *et al.* 1992). The high litterfall in PS3 may be attributed to earlier disturbances rather than to differences in peat depth compared to the other sites. Mean litterfall in PS3 was almost double that in the other sites, with the highest rates occurring during an extended dry period in 1987. Although undetected at the beginning of the study, previous logging resulted in changes in forest composition and, as indicated by lower water table levels (Chapter 3), the peat became drier after logging in the

1970's and drainage canals were excavated in the early 1980's. The proportion of secondary tree species such as *Macaranga* spp., *Campnosperma* spp. and *Licuala spinosa* increased during the study period. Lim (1987) measured higher litterfall rates in logged-over forest than in undisturbed lowland forest in Malaysia, and attributed the increase to more secondary forest species including Euphorbiaceae, Myrtaceae and Rubiaceae.

Table 5–2. Comparison of total fine litterfall and leaf fall rates in the study areas and rates measured in other lowland forests on poor soils.

					Range of litter production		
Location	Forest type	Lat.	Rainfall (mm a ⁻¹)	Alt. (m)	Total litterfall (kg m ⁻² a ⁻¹)	Leaf litterfall (kg m ⁻² a ⁻¹)	Source
Indonesia:							
Padang Island	Low pole (PI12)	1°N	2300	12	0.35-0.67	0.29-0.52	This study
Padang- Sugihan	Chablis forest (PS3)	3°S	2400	5	1.07–1.42	0.63-0.92	This study
Malaysia:							
Tasek Bera	Freshwater swamp	3°N	2000	30	0.62–1.09	0.52-0.87	Furtado et al. (1979)
Pasoh	Lowland Dipterocarp	3°N	2100	100	0.92	0.68	Gong (1972)
Pasoh	Lowland Dipterocarp	3°N	2100	100	0.75–1.02	0.54-0.74	Lim (1978)
Pasoh	Lowland Dipterocarp	3°N	2100	100	1.06	0.63	Ogawa (1978)
South Banjar	Mangrove	3°N	1900	0	1.39–1.51	0.57–1.07	Proctor (1984)
Sarawak: Gunung Mulu	Kerangas Forest	4°N	5700 ·	200	0.80-1.04	0.50-0.62	Proctor <i>et al.</i> (1983)

Note: Litterfall data from Peninsular Malaysia and Sarawak are from Tables 5, 7 & 8 in Proctor (1984).

The effects of low water levels and abundant pioneer species in PS3 exacerbated the effects of the extended dry period which occurred along the east coast of Sumatra in 1987 (Chapter 3.2). Others have reported relations between litterfall rates and seasonal rainfall, with the highest rates usually, but not always, measured in the driest periods (Wright and Cornejo 1990). The highest annual litterfall rates during dry periods have been found on

oligotrophic soils in tropical regions of South America (Jordan 1989) and Australia (Stocker *et al.* 1995). The low litterfall rates in the pole forests are more typical of drier deciduous or montane tropical forests (Proctor 1984).

Changes in the physical and chemical characteristics of litterfall in the study areas were related to the changes in forest composition and structure across the gradient of increasing peat depth. The large broad-leaved and pioneer vegetation found in PS3, SE6 and PI6 provided fine litter with relatively high concentrations of N and P and soluble C fraction. Litter in PI9 and PI12 on deep peat was provided mainly by smaller, slower growing trees with medium to dense wood and small, thick-cuticled leaves. These included species from the genera *Calophyllum*, *Eugenia* and *Tristania*. The tree stands in PI9 and PI12 exhibited xeromorphic features including a smooth even canopy, reduced leaf size and steeply inclined leaves with higher albedo, typical of other oligotrophic tropical forests (Brünig 1970, Brünig and Klinge 1977, Whitmore 1984).

Similar physical changes in leaf litter have been noted in studies on poor soils. Brünig (1974) described the xeromorphic nature of leaves from trees found in Kerangas heath forests over nutrient-poor soils in Sarawak.

Leaves were smaller, harder and thicker than those in mixed topical forest on mineral soils and are physiognomically similar to those in peat forests. Turner *et al.* (1995) studied a Kerangas community on highly acidic, base-poor soils in Malaysia and recorded several tree species that were also found in PI12 study site. The trees were characterized by small leaves with low nitrogen, phosphorus and total chlorophyll concentrations and chlorophyll a/b ratio. The xeromorphic nature of the leaves is also reflected in the internal structure as emphasized by greater lamina thickness, higher incidence of hypodermis and greater development of pallisade (Peace and Macdonald 1981). Xeromorphic leaf structure has been attributed to at least three factors including: periodic drought, insect grazing and nutrient stresses.

Studies by Brünig (1970, 1971, 1974, 1990) and Baillie (1975, 1976) of Kerangas and peat forests on Borneo suggest that the xeromorphic nature of leaves may be in response to periodic water stress. Despite high annual rainfall, dry periods occur in the moist tropics and may be sufficiently high to exhaust the available water in certain soils. As demonstrated in the rainfall frequency analysis in Chapter 3.2.1, rainless periods of about 16 days occur in the study areas annually. Over any given 10-year interval, rainless periods may extend up to 92 days. No studies could be found for tropical peat forests, but a limited number of studies have examined the rate of water loss from leaves of Kerangas forests in Malaysia. The experiments have shown that those species examined from Kerangas forest were no more drought resistant (defined by the maintenance of high leaf conductance at low water

potential) than the much less xeromorphic species of lowland rainforest (Peace and Macdonald 1981, Turner *et al.* 1995). The findings of the Kerangas studies are supported by other studies of vegetation with xeromorphic features. Little restriction of transpiration rates were found in the caatinga and floodplain forests in South America (Medina *et al.* 1990, Oren *et al.* 1996) and in temperate bogs (Small 1973).

No firm conclusions about the water relations of peat forest plants can be drawn from the few studies completed to date as a small number of species from limited areas have been examined. Peat forest physiognomy may not be well adapted to resist water stress. The adaptive significance of the peculiar characteristics of the forest canopy, tree crown and leaves is probably related to minimizing heat loads on those occasions when transpirational cooling is restricted (Whitmore 1984). Still, peat forests do experience drought from time to time (1982-83, 1987, 1992). The large percentage of dead intact fine root mass in the acrotelm layer (up to 71% of acrotelm peat mass in P112) was observed to be in response to frequent peat drying during rainless periods, and may indicate low drought resistance in the peat forests. There are also important differences between Kerangas and peat forests which may affect moisture relations. Soil depth is important in determining the rate at which plant available water is depleted. Kerangas forests, which are generally developed on shallow soils, are more likely to be frequently affected by drought than are the forests on deep peat (Baillie 1976). Root systems of many of the peat forest species were observed to extend below dry period waterlevels (see Chapter 3.5.1). The concept of physiological drought appears to be inadequate to explain the xeromorphic characteristics of the peat vegetation.

Janzen (1974) proposed that xeromorphic leaves may be an adaptation to deter insect grazing.

Xeromorphic leaves containing large amounts of phenolic compounds could be of importance in low productivity forests if these features deter grazing insects. It has not been shown that xeromorphic leaves in tropical peat forests contain greater concentrations of secondary compounds than do leaves of other lowland evergreen forests. The concentration of soluble polyphenols in leaves from all of the study areas ranged from 1.0 to 1.9% using a tannic acid standard (Table 4–4), and did not differ significantly across the gradient of increasing peat depth. Higher concentrations of polyphenols have been found in other oligotrophic forests in Southeast Asia. Turner *et al.* (1995) recorded a mean concentration of 10.0% soluble tannin in leaves from a Kerangas community in Peninsular Malaysia. Anderson *et al.* (1983) recorded a mean concentration of 2.3% for a mixed Kerangas community, which was the lowest of the four forest types studied in Gunung Mulu National Park, Sarawak, but was higher than that found in leaves in the study areas. Of the four forest types in the Gunung Mulu study, litter from the Kerangas forest

was considered to have the lowest resource quality attributes for saprotrophs. However, six-month litter losses in the Kerangas forest were similar to those in the other forest types and did not differ between fine and coarse mesh bags. Anderson *et al.* (*ibid.*) also found that, compared to most acidic soils in temperate deciduous forests, the Gunung Mulu forest floors contained low biomass of soil macro-fauna and a lack of specific groups associated with litter comminution. Of relevance to this study, total population densities and biomass of soil and litter macro-fauna were among the highest in the Kerangas forest, compared to the other forest types with higher resource quality attributes.

Inspection of living leaves in the course of leaf harvests as part of the biomass estimation, as well as leaves lying on the peat, did not show signs of heavy attack by animals. High water table levels were likely to have a negative effect on macro-fauna, but this has not been studied in detail (Kaneko and Takeda 1990). Moreover, there may be little adaptive advantage to lower grazing pressure (*sensu* Janzen 1974) in the peat forests. Most young trees in the deep peat sites were produced vegetatively from the roots of mature trees. *Calophyllum* seeds were observed to germinate and seedlings 10–15 cm in height were abundant on the forest floor following dry periods. However, all of the taller *Calophyllum* plants examined were suckers growing from roots of nearby trees. The importance of insect grazing cannot be excluded, but the comparison of resource quality attributes and observations on vegetative reproduction in the sites suggested that macrofauna is not a primary factor governing the selection of peat forest species with xeromorphic features.

Xeromorphic vegetation with nutrient-poor foliage has also been associated with impoverished or shallow soils and with high insolation. Several studies have proposed that soils with low nutrients and high insolation lead to low productivity due to photoinhibition, exacerbated by nutrient deficiency (Peace and McDonald 1981, Medina *et al.* 1990). An understanding of the internal cycling of minerals and the amount of nutrients that leak from leaves may help to determine whether xeromorphy assists in the conservation of nutrients by plants.

In this study, soil N and P declined across the gradient of increasing peat depth, but only P was significantly correlated with P concentrations in litterfall. Vitousek (1984) and Silver (1994) reviewed studies from lowland tropical forests and concluded that fine litterfall can be predicted by P levels, but not N, particularly on nutrient poor soils. The litterfall N and P concentrations and annual litterfall nutrient content in PS3 and SE6 were similar to those found in other medium depth peat deposits in Malaysia (Ahmad-Shah *et al.* 1992). No published studies of litterfall nutrients from deep peat deposits could be found. The annual litterfall N (5.4–23.6 g m⁻²) and P (0.3–1.6 g m⁻²) content in all sites were generally in the same range of N (2.8–22.4 g m⁻²) and P (0.14–1.4 g m⁻²) in

litterfall from other tropical rain forests in Asia, Africa and Central and South America (Dantas and Phillipson 1989, Silver 1994). Lower foliar concentrations of N and P have been found in plants on nutrient-poor Kerangas soils in Malaysia (Anderson *et al.* 1983, Proctor *et al.* 1983, Turner *et al.* 1995). Low P in litterfall has been associated with an increased ratio of fibrous material to protoplasm (Small 1972a, Turner 1995). Lignin (acidinsoluble) concentrations in litter from all of the study sites (435–615 mg g⁻¹) were significantly higher than those measured in litter from Kerangas forests in Southeast Asia (30–40%)(Anderson *et al.* 1983) and from oligotrophic forests in North America and Europe (120–430 mg g⁻¹)(Berg 1986, Taylor *et al.* 1991). On other poor soils in the tropics, researchers have found patterns of reduced leaf litterfall quality (Cuevas and Medina 1986, Bongers and Pompa 1990).

Although litter quality decreased across the gradient of increasing peat depth, the mass:nutrient ratio widened with lower nutrient returns (Figure 5–1), which indicated greater nutrient-use efficiency (the ratio of mass to nutrients circulated in litterfall) with lower nutrient circulation. The high biomass: P ratio in the Padang Island sites indicated that P was cycled through litterfall more efficiently compared to the other study areas on thinner peat. The biomass: N ratios in litterfall suggested that N was used less efficiently by plants than P.

Medina and Cuevas (1989) measured low P return in the fine litterfall and high P-use efficiency in low caatinga forests in Amazon forests near San Carlos. The dry mass:P ratio was over 5000, compared to 1700 for the PI12 site. In a review of 62 tropical forests, Vitousek (1984) calculated dry mass:P ratios in forests exceeding 7000 (Figure 5–1). The P-use efficiency in PI12 was moderate compared to these studies, due mainly to the extremely low rate of litterfall.

More recently, Lugo *et al.* (1990a) calculated N-use efficiency ratios for forested wetlands ranging from approximately 70 units for freshwater riverine, to over 300 for mangrove forests. The low N-use efficiency of litterfall in freshwater riverine forests was comparable to that of PS3 and SE6, while the higher N-use efficiency of litterfall in freshwater basin forest types compared to that of litterfall in PI9 and PI12 on deep peat. The highest N-use efficiency found was in North Carolina peatland sites with high litterfall and low N return (Figure 5–1)(Bridgham *et al.* 1995). While nutrient-use efficiencies increased across the gradient of increasing peat depth, litterfall concentrations of N and P in the study area vegetation were not excessively low compared to other tropical forests, particularly for P.

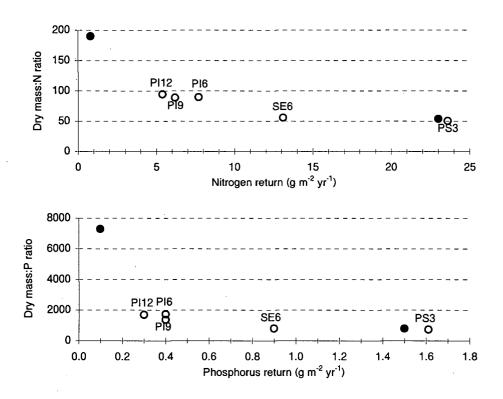


Figure 5–1. The mass:nutrient return ratio relative to nutrient return in litter fall for nitrogen and phosphorus in five sites (open circles) along gradient of increasing peat depth. Maximum and minimum data (closed circles) from world tropical forests (Vitousek 1984) are included for comparison.

The N:P ratios of annual nutrient return in litterfall widened across the gradient of different peat depths from 14.7 in PS3 to 16.8 in PI12, indicating the increasing importance of P as a limiting nutrient in deeper peat deposits. Considerably higher ratios of N:P have been found in other peatlands. Bridgham and Richardson (1991) measured a N:P ratio of 26.4 in the short pocosin peatlands of North Carolina. The study results were consistent with findings of other studies which suggest that indices of soil P are related to litterfall processes, but other measures, particularly total soil N, may not be as relevant to nutrient cycling by the vegetation (Bridgham *et al.* 1995).

Xeromorphic leaf types are commonly found in environments where N and especially P are deficient (Beadle 1966, Small 1972a). Of the three factors discussed above, nutrient deficiency, particularly P, appeared to best explain the xeromorphic features of the peat forest vegetation in the study areas. Nutrient limitations in the study sites, as shown by the crude analysis of litterfall nutrient-use efficiencies, were high, but not extreme

compared to other tropical forests and forested peatlands of similar stature. The very low litterfall rates and xeromorphic features in PI12 suggested that leaf sclerophylly may correlate with leaf longevity and the conservation of P and other important nutrients. In a habitat with lower productivity, the plant should produce better protected leaves as a consequence of selection for leaves with a longer half-life. If sclerophylly correlates with leaf longevity, the advantage would be increased photosynthetic efficiency—more photosynthate produced on a leaf area per unit N or P basis (Small 1972a, 1972b).

Limitations Related to Litter Findings

Further understanding of nutrient limitations in peat forests requires that elements other than N and P be assessed. The effects of moisture and nutrient limitations on litterfall can only be disentangled by further detailed investigations similar to those performed in tropical Kerangas (Turner *et al.* 1995), caatinga (Medina *et al.* 1990) and floodplain (Oren *et al.* 1996) plant communities. Comparisons of the published litterfall rates from other low fertility forests in the region to the annual litter production from one-year litterfall measurements in the study areas must be considered preliminary until multi-annual collections are taken. Variation among collection periods was high in all sites (CV = 20-30%) and reflected the wide variation in rainfall during the collection periods. Stocker *et al.* (1995) assessed annual patterns of litterfall in a lowland tropical forest in Australia and concluded that a minimum of three years of continuous collection are required to accurately assess seasonal variability.

Belowground Plant Inputs

In contrast to the pattern of aboveground litterfall in the sites, root mass and production in the acrotelm layer increased substantially across the gradient of increasing peat accumulation. The findings supported the hypothesis in Figure 1–3 that the gradient of different peat depths, as represented by the study sites, could be directly attributed to increased additions of belowground plant matter. Changes in the organic chemistry of small roots were also significantly correlated with several of the resource quality attributes measured in the top of the acrotelm peat layer. Similar to the trends found in aboveground litterfall and peat, total N and P and the lignin fraction were positively correlated between roots and peat. Opposite to the pattern in litterfall and peat, the soluble C fraction in small roots and peat was positively correlated across the five sites. The concentration of soluble C fraction in root mass and peat mass increased 2.4 and 1.3 times, respectively, from PS3 on medium peat to PI12 on deep peat. Because the bulk density of the acrotelm peat layer declined across the gradient of increasing peat depth, the total amount of soluble C fraction in peat declined by 23% from PS3 to PI12.

The presence of a large living root mass in the surface layer of Sumatran peat forests was reported during early expeditions (Polak 1933, Sewandono 1938) and more recently during land development surveys (Ministry of Transmigration 1988). Thorenaar (1927) provided detailed diagrams and descriptions of root forms of various tree species in the peat forests around Palembang and noted the mass of knee and loop roots that formed root mats under tree species such as *Alstonia, Calophyllum, Xylopia, Tetramerista and Durio*. In Borneo, Anderson (1961a) described the presence of a continuous platform of radiating roots above the water table in Sarawak peat forests.

Also in Sarawak, Brünig (1974) described the presence of a shallow root mat in Kerangas forest over Kerangas soils. Richards (1952) noted the common presence of stilt roots, adventitious roots and pneumatophores such as knee or loop roots in peaty inundated forests throughout the tropics. The forests described by Richards contain many tree species found in the deep peat sites including *Calophyllum, Ganua, Palaquium, Tristania and Gonystylus*. Several studies have also noted the abundance of dead roots in the surface and subsurface layers of peat. Anderson and Muller (1975) noted the abundance of roots and rootlets throughout the peat profile of a deposit in Sarawak, particularly in the upper 2–4 m. Brady *et al.* (1996) noted the presence of a thick mat of roots over ombrogenous peat in the Timika lowlands of Irian Java.

Despite the root observations mentioned above, no quantitative studies of roots in the peat deposits of Southeast Asia could be located for comparison to the study areas. The root measurements in the study sites, however, were consistent with studies in tropical South America which showed that most live small roots in soils of low fertility occur in superficial root mats (Berish 1982, Klinge 1973, Stark and Jordan 1978). The highest mass of small (<10.0 mm diam.) roots was in PI12 (9.0 kg m⁻²⁾ and was at the high end of the values for small roots from moist tropical forests (range 1.1–12.8 kg m⁻²; Vitousek and Sanford 1986). Large quantities of small roots were recorded in the Caatinga forest types of Venezuela which are also characterized by nutrient-poor soils. Jordan and Escalente (1980) and Klinge and Herrera (1978) measured 4.2–12.8 kg m⁻² of small roots in thick root mats over mineral soil. Small root production estimated in the top 40 cm of peat in PI12 (1.59 kg m⁻² a⁻¹) was considerably higher than the rates published for other broad leaved evergreen tropical forests. Jordan and Escalante (1980) estimated, using ingrowth bags, an annual net root production rate of 0.11 kg m⁻² a⁻¹ in a root mat overlying a sandy Oxisol soil near San Carlos, Venezuela. Prior to this study, the highest published rates for tropical forest was 0.15 kg m⁻² a⁻¹ in the top 10 cm of an Oxisol site in Venezuela (Vitousek and Sanford 1986) and 0.29 kg m⁻² a⁻¹ in the top 20 cm of a wet forest site in Puerto Rico (Kangas 1991).

The study findings showed that the root:shoot ratio (R:S) increased across gradient of increasing peat depth. In PS3 on medium depth peat, small litterfall (1.2 kg m⁻² a⁻¹) was significantly higher than small root ingrowth (0.05 kg m⁻² a⁻¹) during the study period. In contrast, litterfall in PI12 on deep peat (0.5 kg m⁻² a⁻¹) was significantly lower than root ingrowth (1.6 kg m⁻² a⁻¹). Several models have been developed to account for changing R:S in plants, each focusing on different aspects of growth including: allometric relationships, functional equilibrium, hormones, transport resistance and functional balance (Wilson 1988, Agren and Wikstrom 1993). The latter model is mechanistic, based on the supply, transport and utilization of carbon and nutrients in roots and shoots. The functional balance approach has gained wide acceptance and is used below to evaluate the factors that may control R:S of plants in the study sites. The approach assumes that the translocation of carbon from shoots and nutrients from roots depends on differences in concentrations and resistance. Among other factors, the model is affected by water, major and minor nutrients, light, CO₂, temperature, defoliation, root pruning and toxicity. Some of these effects on root growth and mortality are discussed below.

Roots of Pandanus artocarpus, Cyrtostachys lakka, Calophyllum spp. and Cratoxylon arborescens were observed to form a dense, vertically-oriented matrix of small roots. When pulled from the peat, some of the small vertical roots were up to 3 m in length. In addition to rooting below the water table, many of the peat forest species exhibited other features indicative of flood tolerance. These include adventitious roots, hypertrophied lenticels, large diameter roots with aerenchyma and smaller, longer-lived leaves (Gomes and Kozlowski 1988). Plants may tolerate flooding using several strategies. Well known strategies include increased root alcohol dehydrogenase (ADH) activity under anaerobic conditions and increased gas transport to soil via plant roots. Several researchers have found that plants have different thresholds to low redox (Eh) conditions and may respond by inhibiting root elongation (Pezeshki et al. 1996). Bald cypress (Taxodium distichum) trees of the swamps in the Southeast USA have been found to tolerate flooding by increasing anaerobic respiration, ADH activity and ethylene production (Pezeshki 1991, Terazawa and Kikuzawa 1994). Some plant roots are able to diffuse O₂ from the atmosphere via a continuous system of aerenchymatous lacunae into sediments (Waisel and Eshel 1991). Oxygen transport is well correlated with a rise in Eh of soil around roots (Armstrong et al. 1992, Grosse et al. 1992). Pressurized gas transport may aid survival of wetland species during the initial period of soil flooding before acclimatization to waterlogging. Although the roots of the peat forests in East Sumatra exhibit numerous features associated with flood tolerance, processes such as alcoholic fermentation and gas transport have not been studied.

Root growth and the R:S of flood tolerant plants have been shown to respond to different hydroperiods. Several studies suggest that for many plants R:S is greater under conditions of periodic flooding, particularly after the plant is physiologically and morphologically adapted (*i.e.*, roots larger diameter, less branched and more succulent) to flood conditions. Megonigal and Day (1992) found increased growth, R:S allocation and root depth by bald cypress with a shift from continuous to periodic flooding. This finding is consistent with the lower frequency of flooding and higher R:S found in PI12 and PI9, compared to the sites on 3 and 6 m peat deposits which flooded up to 4 months annually.

The high root mortality observed in the deep peat study sites was partially controlled by seasonal rises in the water table which were of sufficient duration to kill the roots. Most roots in the acrotelm had numerous scars where root branches died in response to flooding or drought-caused moisture stress. New roots branches were observed to resprout above the scars. Although not verified during the study, field observations during the frequent wet and dry periods in Sumatra suggested that root production rates may have been higher than those measured using the ingrowth bags. Rapid response of roots to moisture changes has been observed in other low fertility forests (Kozlowski et al. 1991). Megonigal and Day (1992) found that highly flood tolerant trees are generally drought sensitive. Under drought stress in a Florida swamp, cypress shoots were irreparably damaged in 3-4 hours. The authors concluded that cypress may be more sensitive to inadequate moisture than excessive moisture. Other researchers have also observed considerable fine root mortality in dry conditions. Kavanagh and Kellmen (1991) measured up to 50% mortality of the total small root mass during a seasonal dry period in a tropical forest. They found the growth of fine roots to be more sensitive to moisture availability than high nutrient concentrations at the beginning of the wet season. In the Douglas-fir forests in New Mexico, Gower et al. (1992) measured increased fine root production during periods of higher moisture (after spring snow melt) and then significant root mortality in the summer when moisture was low. Studies elsewhere support the findings of high root growth and mortality under periodic flooding in the study sites on deep peat. The response suggested that the net effect of water stress was to limit growth more than photosynthesis, making water analogous to nutrients in the functional balance model of R:S control. Root mortality from flooding or drought may reduce leaf growth as assimilates would be redirected towards the roots via a relative deficiency of mineral nutrients in the shoot (Wilson 1988). The differences in the hydrological regimes among study sites were not, however, sufficiently large to account for the much smaller root mass and R:S found in the 3 and 6 m study sites. Other factors affecting root growth must be considered.

Similar to the study sites in East Sumatra, most studies show an inverse relationship between small root mass and soil nutrient status. Low soil availability of nitrogen and phosphorus are believed to be major factors governing below-ground root mass and root turnover (Cuevas and Medina 1983, Vogt *et al.* 1986, Jordan 1989). Seedlings taken from a Singapore forest, and of the same genera found in the study sites (*Calophyllum*, *Garcinia* and *Antidesma*), responded to P by increasing dry mass in stems and roots (Burslem *et al.* 1995). The studies suggest that the proportion of assimilate spent on the production and maintenance of fine roots is greater on infertile sites than on fertile sites (Nambiar and Sands 1993). The response of plants to nutrient deficiency is in the same direction predicted by the functional balance model of R:S control. Under nutrient deficiency, the model predicts a build-up of carbohydrate levels and that growth of the root will be more than that of the shoot (Wilson 1988).

Recent studies on low fertility sandy soils at Maracá Island in Brazil showed no structural features such as root mats or small sclerophyllous leaves that are often associated with forests on nutrient poor soils (Scott *et al.* 1992, Thompson *et al.* 1992). The absence of a root mat was partially explained by the relatively high rates of litterfall which contained large amounts of P, K, Ca and Mg and the rapid decay of fine litterfall. The presence of surface root mats has also been explained as an adaptation for nutrient conservation in climates where strong leaching could occur (Stark and Jordan 1978, Jordan 1989).

It is also possible that root mats provide an aerated medium for nutrient collection which also lacks the toxins found in the saturated peat below. Thompson *et al.* (1992) proposed that features of soil chemistry such as high acidity or phenol toxicity are the most likely cause of root mats in Kerangas forests. However, the functional balance model of R:S control suggests that the same mechanism that enables root growth to benefit in comparison to shoot growth where nutrients are deficient, will suppress root growth more than shoot growth when levels become toxic (Wilson 1988). Furthermore, acidity and phenolics did not vary significantly in the Sumatra peat forests across the gradient of increasing peat depth and associated mass of surface roots.

The study findings showed that across the gradient of increasing peat depth, resource quality attributes of organic matter appeared to vary more than hydrological conditions in the acrotelm peat layer. These differences suggested that nutrition may be more important than moisture in controlling R:S in the deeper peat sites.

Researchers have observed that allocation to roots is more affected by variations in soil N availability than by soil moisture (Nambiar 1990, Nambiar and Sands 1993). Canham *et al.* (1996) suggested that there may be fewer

constraints on plants to optimize root allocation for N uptake than there are for water uptake. Thus, species adapted to moist infertile soils are likely to have more opportunistic patterns of root allocation.

The larger mass of younger intact roots in PI12 suggested that roots were increasingly important for peat accumulation in the catotelm layer of the deeper deposits. The results represent the first published estimates of plant production in the coastal peat deposits of Southeast Asia. The annual combined aboveground and belowground rates of small litter input (0.74–2.1 kg m⁻² a⁻¹) were generally higher in the study sites than in North American and European *Sphagnum* peatlands, which have been found to range from 0.3 to 1.0 kg m⁻² a⁻¹ (Jones and Gore 1978, Clymo 1987, Moore 1989). The input rates in the study sites were comparable to production rates for ericaceous shrubs on peatlands in Canada (1.9 kg m⁻² a⁻¹) and for temperate swamp and marsh vegetation such as *Phragmites*, *Typha* and *Cyperus* (1.5–2.0 kg m⁻² a⁻¹), as indicated in a summary of primary production in wetlands by Bradbury and Grace (1983). Many wetland communities have considerable belowground biomass, but the production of this component has rarely been measured with any accuracy.

The varying patterns of above and belowground litter inputs across the gradient of increasing peat depth were not expected and were not consistent with the assumptions of the model of *Sphagnum* peat accumulation. The model assumes that vegetation inputs are restricted to the acrotelm, change little from year to year and that productivity is relatively constant during peat accumulation. The study results were consistent with a key assumption of the *Sphagnum* peat model that increasing peat deposit depth is due to the increased amount of dry mass entering the catotelm layer. The findings suggest, however, that peat accumulates in tropical deposits more because of larger amounts of fresh roots entering the catotelm, rather than from rising water levels in the acrotelm layer as assumed by the *Sphagnum* model.

The importance of roots in organic matter dynamics has often been overlooked. Vogt *et al.* (1986), in a study of organic matter dynamics and nutrient cycling in the temperate coniferous forests of Northwestern USA, identified the serious consequences of ignoring root inputs. Their studies showed that organic matter and nutrient turnover in the forest floor could be under estimated by 20 to 80 percent if root input into detritus production was ignored. Wallen (1986) studied the role of vascular plants in a subarctic peat bog and concluded that up to 95% of total net annual production occurs below the soil surface, represented mostly as turnover of fine root biomass. The presence of living roots may have an inhibitory or stimulatory effect on organic matter decomposition (Cheng and

Coleman 1990, Vogt et al. 1991, Bloomfield et al. 1993). The effects of varying quantities of root mass on peat decay in the study areas is discussed in Section 5.1.3.

Limitations of the Root Findings

Root production and mortality are highly complex processes (Kurz and Kimmins 1987, Vogt et al. 1991). An advantage of using the root ingrowth method was that a large number of bags could be prepared and sampled. However, the accuracy of the root ingrowth method was limited by several factors. Placement of the bags in peat can result in: 1) physical disturbance of roots surrounding the bags, 2) aeration of peat and roots surrounding the bags and 3) differences in the physical properties between the ingrowth peat medium and the surrounding peat. The first and second factors were addressed by cutting as few roots as possible and carefully placing the mesh bags. The frequent water level fluctuations in the sites were likely to restore the chemical and hydrological conditions after the bags were buried. The third factor was addressed by using peat from each site and imitating the peat density in the mesh bags to that in the incubation layers. In addition to root ingrowth measurements, several more precise methods have been developed to measure root growth in peat including: sequential sampling of live and dead roots (Fairley and Alexander 1985, Finer et al. 1993), root observations using rhizotron viewing devices (Wallen 1993) and indirect techniques using stable or radioisotopes (Milchunas et al. 1985). Despite the limitations of the mesh-bag ingrowth method for use as an index of root production, the large differences in small root production between study sites demonstrated that belowground litter was an important source of organic input for peat accumulation, particularly in the deeper deposits in East Sumatra.

The measurements and analyses above represent a preliminary study of belowground organic matter processes in peat. The results are, however, the first reported measurements of root structure and function across the gradient of increasing peat depth in Southeast Asia. While the results suggest moisture and nutritional factors associated with changes in small root growth, the study was not intended to elucidate the causative factors governing root structure and function. A complete study of root growth would have to include, but not be limited to, experimental control of such processes as nutrient availability and uptake, transpiration, nutrient and photosynthate translocation and retranslocation, and toxicity response.

5.1.3 Organic Matter Decay

The state factor approach of Jenny (1941) provides a powerful conceptual framework for understanding the controls over ecosystem processes. This approach has been applied to the processes of decay and organic matter formation. Swift *et al.* (1979) proposed that physical (P), chemical (Q) and biological (O) factors govern organic matter decay in a hierarchical manner, each operating at different scales of space and time according to: macroclimate, soil physico chemical conditions, the quality of organic matter inputs and the activities of invertebrates and microorganisms. The model has been applied to organic matter decay in the humid tropics (Anderson and Swift 1983, Anderson and Flanagan 1989, Lavelle *et al.* 1993) and provides the framework to discuss the decay of litter and acrotelm peat in the five Sumatra peat forests. Macro and micro-climate effects are excluded from the discussion because rainfall, temperature and topography in the everwet study areas were uniform among the study areas (assessed in Chapter 3).

Decay of Aboveground Litter

Fine and small aboveground litter decayed at different rates among sites, but wood did not. Litter decayed initially at rates up to 10 times faster in PS3 medium peat than in PI12 deep peat. Despite low litterfall rates in PI12, slow decay resulted in the largest litter layer of all sites. The findings supported the hypothesis that slower rates of aboveground litter decay are associated with the gradient of increasing peat depths in East Sumatra (Figure 1–3).

Measurements of litter layer mass for other peat forests could not be found. Thick accumulations of litter are not common in other tropical wetlands. Furtado and Verghese (1981) measured a low forest floor mass of 0.47 kg m⁻² in a freshwater swamp forest in Malaysia. Similarly, Proctor *et al.* (1983a) measured litter layer mass of 0.54 to 0.65 kg m⁻² in an organic Kerangas soil in Gunung Mulu, Sarawak. In comparison, the litter layer mass in all peat study sites was higher. Vogt *et al.* (1986) calculated a global average forest floor mass (2.25 \pm 0.49 kg m⁻²) from studies in 16 locations in tropical broadleaf evergreen forests. The mean value is just over half of the litter mass in PI12 (4.81 \pm 0.56 kg m⁻²). The survey by Vogt *et al.* focused on forests over mineral soils and defined litter mass as including all organic material (LFH) over the mineral soil layer. In this study, the litter layer consisted of all intact litter above the surface layer of peat. The highest litter layer mass recorded in the survey by Vogt *et al.* was 5.40 kg m⁻² for aboveground litter including a root mat in Colombia. The total mass of the root mat and litter layer in PI12 was about three times greater at 17.80 kg m⁻².

Similar to litter mass, published litter decay rates for other peat forests in Southeast Asia could not be found. Litter decay in the medium depth study sites was comparable to other forests on nutrient poor soils. Decay in PI12 on deep peat was lower than any published value in tropical Asia. Anderson *et al.* (1983) measured a k_L value of 1.3 for total small litter in an oligotrophic Kerangas forest in Gunung Mulu National Park, Sarawak. Furtado and Verghese (1981) measured a high k_L value (1.93) in the freshwater swamp forest in Malaysia. Both of the forests types contained vegetation similar to that in SE6 (*Eugenia, Palaquium, Pandanus* spp.), but had thinner organic soils. The lowest decay rates documented for Southeast Asia were from a dipterocarp forest near Penang Malaysia where Gong and Ong (1983) recorded a k_L of 0.97 for small litter. Decay values as low as in P112 (k_L = 0.11) have not been recorded in other tropical regions (see Vogt *et al.* 1986). Cuevas and Medina (1988) measured k_L values from 0.22 to 0.87 in Caatinga and Bana forests over poor soils in Venezuela, while a k_L of 0.13 was recorded in a tropical evergreen forest site with a perched water table in Colombia (Fölster *et al.* 1976). The global mean k_L value for tropical broadleaf evergreen forest for all soil types is 0.42 (Vogt *et al. ibid.*), which is about midway between the range of decreasing rates across the gradient of increasing peat depth in my study (k_L = 1.00 to 0.11).

Moisture fluctuations appeared to exert greater control over litter decay than did resource quality in the SE3 and PS6 medium depth peat sites. Litter in these sites contained relatively high initial N, P and soluble fraction, and exhibited a linear decay pattern with a residence time of about one year. Litter decay appeared to be inhibited more during dry periods than during wet periods due to flooding. The lowest accumulations of forest floor litter occurred in the study sites that experienced the greatest flooding during wet periods. In contrast, litter layer mass was greatest in PI12, where flooding was rare. Litterbag studies in other areas prone to flooding have shown greater mass loss than in unflooded sites (Day 1982, 1983). Other researchers have found that decay is most influenced by moisture at low moisture contents during dry periods (Heal *et al.* 1978, Osborne and Macauley 1988, Cornejo *et al.* 1994). Studies of *Rubus* litter decay in peat bogs indicate that even with high rainfall and waterlogged peat, low moisture can inhibit respiration of surface litter for about 20% of the time. Birch (1959) proposed that drying causes fragmentation or increased porosity of organic structures, which upon rewetting, promotes increased leaching and microbial activity of soluble organic material. Taylor and Parkinson (1988) observed significant effects of wetting and drying in temperate forest litter, but questioned whether the effect can be separated from the variation in moisture content through space and time.

The high variability of decay values in litter under similar moisture conditions was probably due to changes in plant species and resource quality attributes. Litter CO₂ emissions were positively correlated with N, P and solubles concentrations, and negatively correlated with lignin: N ratios. Decay was slowest in PI12 litter which also showed the lowest respiration response to moisture differences. Moreover, because of species changes, PI12 litter contained the lowest initial concentrations of N, P and solubles and the highest ratio of lignin: N. Several studies have shown how litter decay rates are positively correlated with nutrient content and negatively with litter quality (Meentemeyer 1978, Swift et al. 1979). Litter nutrient concentrations were discussed in Section 5.1.2 above. The lignin concentrations of litter in the study sites (436–615 mg g⁻¹) were considerably higher than other oligotrophic forests in the region including Kerangas forests in Gunung Mulu (396 mg g⁻¹, Proctor et al. 1983a) and on Pulau Sibu (282 mg g⁻¹, Turner et al. 1995). Differences in laboratory methods, however, may limit comparisons between studies. The relatively high concentrations of lignin in all sites suggested that other resource quality attributes were more important. In contrast to lignin, total polyphenol concentrations (expressed as tannin equivalents) in litter were low (10.0 to 12.2 mg g⁻¹) compared to litter in other forests on poor soils in the region (24.9 mg g⁻¹ in Gunung Mulu and 100 mg g⁻¹at Pulau Sibu). The low polyphenol concentrations in litter from the study sites were not consistent with other published values. Differences in laboratory procedures may account for the comparatively low values in the study areas. The polyphenol results should be reassessed in future studies.

As discussed above, the populations of litter-feeding macrofauna, such as Isopoda, Diplopoda, Mollusca and earthworms were likely to be low in the water-saturated litter and peat of the study areas. The importance, therefore, of macrofauna in litter decay across the gradient of peat accumulation was likely to be small. In the Gunung Mulu Kerangas site, Anderson *et al.* (1983) found no difference in litter decay using fine and coarse mesh bags. Coulson and Butterfield (1978) suggested that the absence of macrofauna in peatlands is an important factor leading to low decay and peat accumulation.

The role of microorganisms in litter decay across the gradient of peat depth was not evaluated directly. Several indicators, however, suggested that microbial populations in litter were generally low and declined across the gradient of increasing peat depth. The k_L quotients for N and P in litterfall and in the litter layer were greater in all sites than the same k_L quotient for litterfall and litter layer mass. Higher k_L values for N and P suggest that nutrients are lost rapidly from litter, rather than immobilized by litter microflora (Scott *et al.* 1992). Declining rates of litter decay across the gradient of increasing peat depth were associated with increases in small roots which

formed a continuous root mat under the litter layer in PI12. The presence of a root mat has been known to enhance litter decay in some tropical forests (Cuevas and Medina 1988). Several studies have shown that root mats support well developed vesicular-arbuscular mycorrhiza (VAM) or ectomycorrhiza. St. John and Uhl (1983) described VAM in the root mat of a Caatinga flooded forest in the Amazon. Mycorrhiza were found on roots in the study sites, but were not studied in detail. Differences between litter decay rates in field and laboratory incubations were not significant, suggesting that detailed studies are required to understand the role of mycorrhizae in tropical peatlands.

The extremely slow decay of PI12 litter may also be due to energy and physical limitations. The decline in N, P and solubles concentrations in litter across the gradient of increasing peat depth was associated with an increase in small roots and a concomitant increase in the concentration of solubles in peat. Extracts of PI12 peat added to PI12 leaves during the 30-day incubations caused an increase in respiration.

In contrast, the results of the leaf incubations with extracts from medium and deep peat sites suggested that the chemical and biological properties of PI12 peat with low resource quality attributes did not inhibit the decay of litter with higher resource quality attributes. Other factors that have been known to limit microfauna activity in litter, such as pH (Benner *et al.* 1985) and polyphenol concentrations (Bharat *et al.* 1988), did not vary significantly across the gradient of increasing peat depth. Polyphenol concentrations were also high in peat in which respiration and N-mineralization rates were high. The addition of phenolic metabolites (tannic acid) and leaf filtrates from hill and lowland forests litter did not significantly inhibit ammonification and nitrification in three Malaysian forest soils (Chandler 1985).

The preliminary evidence from the study suggested that the measured declines in litter mass loss and in rates of respiration across the gradient of increasing peat depth were more strongly associated with differences in plant species and their declining resource quality attributes, rather than with changes in water table levels or decomposer organisms. A detailed evaluation of microbial populations in the peat forest litter is required to fully evaluate their role in litter decay.

Among study sites, 30-day and 1-year respiration rates of acrotelm peat samples increased across the gradient of increasing peat depth, suggesting that surface peat decayed faster in the deeper peat deposits. Despite higher rates of decay, the macrostructure of the acrotelm layer was better preserved in PI9 and PI12 deep peat sites compared to PS3 and SE6 sites on medium depth peat. The fibric content acrotelm layer increased from 11 to 72% across the gradient of increasing peat depth. Moreover, the increased decay rates in the acrotelm were associated with decreasing N and P concentrations in the peat. These results were unexpected and did not support the hypothesis (Figure 1–3) that increasing peat depth among the study areas was associated with slower rates of acrotelm peat decay (Clymo 1965, Damman 1979) and a decline in soil nutrition (Anderson 1983). There are five possible explanations for the discrepancy found in the deeper peat deposits between intact macrostructure, declining nutrients and increasing rates of decay in the acrotelm layer. They relate to age (1), environmental controls (2 and 3), organic matter quality (4) and soil organisms (5):

- (1) The thicker deposits were in a state of net decomposition. This was not supported by the radiocarbon age results which indicated that the top of the acrotelm layers in the five study sites were of modern age. The base of the acrotelm in the deep peat sites was younger than in the medium depth sites, suggesting that none of the deposits were degrading. Some peat deposits in Indonesia have been determined to currently be degrading. For example, acrotelm ages in the high peat deposits in central Kalimantan have been dated at several thousands of years BP (Siefferman et al. 1988, Rieley et al. 1992a).
- (2) The deeper peat areas received less moisture. Rainfall rates were similar among sites (Chapter 3). The water level measurements taken during the study, however, suggested that mean water table levels were slightly lower in the deeper peat deposits, compared to the medium depth deposits containing SE6 and PS3 sites. Surface flooding did not occur in PI9 and PI12 deep peat sites, but water table levels occasionally rose to the surface and frequently saturated the top of the acrotelm layer. Moisture levels, however, could not explain differences in decay among study sites. The limited effect of moisture on decay was demonstrated using a standard organic material in all sites. The use of cotton strips demonstrated that readily decomposable material decayed rapidly in all sites above and below the water table. Decay patterns, however, of the more resistant organic matter undergoing preservation in the acrotelm were variable. Using CO₂ emissions from aerobically incubated peat as an indication of decay, the largest differences in respiration occurred between samples from the top and base of acrotelm peat, followed by

samples from the different site differences. The changes in respiration with depth reflected the effects of increasing peat age and preservation, rather than of saturation.

The limited effect of moisture on decay has been noted in surface peat at other sites. In Swedish peatlands, *Sphagnum* decayed at faster rates in flooded hollows compared to hummocks, in spite of the greater wetness.

Differences in decay the between different *Sphagnum* species found in the hollows and hummocks completely overruled the effects of microhabitat (Johnson and Damman 1991, Hogg 1993, Hogg *et al.* 1994).

In addition to species effects, continued peat decay under saturated conditions is controlled by aeration in the rhizosphere. It has been shown in other saturated soils that plants can sustain an essentially permanent increase in sediment redox potential (Amrstrong *et al.* 1990, Sorrel and Armstrong 1994). Sediments can also be oxidized by transpiration driven water table movements (Dacey and Howes 1984). As discussed above, the roots of many plants in the deep peat sites contained features associated with gas transport. The ability of the plants, however, to oxidize the rhizosphere cannot be determined without measurements of the redox potential and oxygen content of peat in the study areas. Sorrel and Armstrong (1994) discuss the difficulties of assessing gas transport into the rhizosphere.

(3) The deeper peat deposits have received greater external nutrient inputs. Nutrients enter ombrogenous peat deposits by wet and dry atmospheric deposition, and from flooding by mineral-laden water. Atmospheric inputs to peat should have been higher in the study sites in South Sumatra (3–6 m sites) because they are close to the large urban centre of Palembang. A large fertilizer plant and refinery complex is located approximately 50 km from the study area. The effect of atmospheric inputs on tropical peat processes has not been studied. The effects of low and high atmospheric supply of N on the vitality of *Sphagnum* have received preliminary attention in European (Aerts *et al.* 1992, Jauhiainen *et al.* 1993) and North American (Rochefort *et al.* 1990) peatlands.

River flooding would also more likely affect the thinner peat deposits in South Sumatra and Riau. Cecil *et al.* (1993) described the allogenic and autogenic controls on sedimentation in the central Sumatra basin and concluded that the deep peat deposits have not been exposed to fluvial sediment influx from adjacent rivers. Similar type studies should be performed in the South Sumatra peatlands to determine whether sediment influx occurred and was an important factor limiting peat accumulation.

(4) Sites on thicker peat received litter additions of higher resource quality. The resource quality attributes measured during the study showed that both litter quantity and quality declined significantly across the gradient of

increasing peat depth. As discussed above, the residence time of litter in PI12 was longer than in any other published studies in the tropics.

Peat decay was strongly associated with changes in resource quality attributes across the gradient of increasing peat depth, with the PI12 site on the deepest peat having the highest rates. The site gradient was most reflected by changes in plant species. While rates of litter decay were most strongly associated with site differences in initial N and P, acrotelm peat decay was correlated across the gradient of increasing peat depth with resource quality attributes in the order: soluble C fraction > P and lignin > lignin: N > C:N > LCI. Peat decay was not correlated with organic or mineralized N, nor with changes in pH and polyphenol content. Among the resource quality attributes measured, the strongest positive correlation was between decay and the soluble C fraction. The increase in soluble C fraction was most likely related to the large increase in small roots in across the site gradient of increasing peat depth. The positive effects of small root inputs on organic matter decay has been observed for several plant species and soil types (Cheng and Coleman 1990, Bradley and Fyles 1995b, Bradley and Fyles In press).

Roots are a source to the soil of labile compounds, amino acids and enzymes, all of which may play the role of co-metabolites in the decay of refractory litter (Melillo *et al.* 1989, Bradley and Fyles 1995b). The finding of a higher initial respiration response in PI12 peat to added C may have been due to its greater soluble C content (~2.4 times), compared with the sapric-textured PS3 peat. The greater root mass in PI12 deep peat may have supported larger or more active microbial populations which responded more rapidly to the added energy source. The higher energy deficient index (EDI) of microbial communities in PI12 peat suggested that a larger pool of energy deficient biomass evolved in the root-rich peat. Bradley and Fyles (1995b) found a significant and positive relationship between available C and the energy-only limited microbial fraction in a mineral forest soil planted with tree seedlings. They proposed that the higher quantities of root-derived available C favoured the development of zymogenous microbial populations in soils with a high EDI.

In contrast to EDI, the nutritional deficiency index (NDI) was higher in PS3 than in PI12 peat, suggesting that the former contained a proportionally larger fraction of nutritionally deficient microbial biomass. Bradley and Fyles (1995b) found that nutritionally limited soil microbial biomass did not correlate with available C and total microbial biomass. The NDI-to-EDI ratio, which reflects the energy to nutrient deficiency of microbial biomass.

was well below one in each site and was lowest in PI12 peat (Table 4–13). The low values suggested that in all sites only a small proportion of the microbial community was nutritionally limited.

(5) An alternative explanation is that the rapid decay in the acrotelm layer of PI12 on deep peat was unrelated to the process of organic matter preservation as peat in the catotelm layer. The greater respiration rates in PI12 were not consistent with the assumption for *Sphagnum* peatlands, that decreasing rates of organic matter decay in the acrotelm, rather than increasing plant inputs, controls accumulation (Clymo 1965, Damman 1979). The importance of plant inputs and organic matter decay in acrotelm peat is further explored in Section 5.2 using a model of peat accumulation adjusted to the study sites conditions.

Limitations Related to Decay Findings

Peat respiration measurements under field conditions are required to confirm the site differences in rates found in the laboratory. The study focused on N and P concentrations in litter and peat. Nutrients such as Ca, K and Mg have been associated with decay processes in other tropical forests on nutrient poor soils (Anderson *et al.* 1983, Scott *et al.* 1992) and should be evaluated in peat forests where their stocks are derived solely from atmospheric inputs.

5.2 THEORETICAL IMPLICATIONS OF THE STUDY

The study results provide an example of a test of the peat accumulation model (eq. 1 and 2) in Southeast Asian peat deposits, where peatland productivity is less well known than in the northern hemisphere. Simulation modeling is commonly used to verify the theoretical assumptions about ecological processes using the results of field and laboratory studies. Several steps were taken below to simulate the processes of peat accumulation and decay in East Sumatra using the model (eq. 1) of *Sphagnum* peat accumulation (steps 1–2), which was verified using information from other coastal peat deposits in the region (step 3) and expanded to incorporate the results of the three component studies in Chapter 4 (steps 4–7):

- 1) Assuming steady state conditions, use acrotelm age and depth results (Chapter 4.1) to determine rates of organic inputs to catotelm peat (p_C) ;
- 2) Use p_C in peat accumulation model (eq. 1) to calculate catotelm decay (k_C) in study sites of increasing peat accumulation (x_C);

- 3) Verify catotelm p_C and k_C constants with age and depth results from other peat deposits in East Sumatra:
- 4) Expand peat accumulation model (eq. 1) to incorporate the functional organic layers found in the study sites including a litter layer, the top and base of the acrotelm and the catotelm layer;
- 5) Run expanded model using catotelm p_C and k_C from steps 1-3 above and acrotelm organic inputs (p_A) and decay (k_A) from the field and laboratory studies in Chapter 4.2 and 4.3, respectively;
- 6) Evaluate simulation results and revise various acrotelm p and k constants with results of acrotelm age and depth study (Chapter 4.1), rerun model; and
- 7) Use results to identify similarities and differences between assumptions of accumulation models for *Sphagnum* peatlands and the forest peatlands in East Sumatra.

Acrotelm Accumulation

Rates of organic inputs and decay from the study can be compared with theoretically-derived values from numerical relationships established for peat deposits elsewhere. Under steady state conditions, the rate of acrotelm accumulation equals the total input of organic matter to the catotelm (Clymo 1983). Accumulation rates for the study sites were calculated from the age and depth (from the surface) of the acrotelm base, and I assumed that radiocarbon ages at the base reflected the residence time of accumulated organic matter. The rates were similar for all sites (0.08–0.20 kg m⁻² a⁻¹), except for PI12 (0.89 kg m⁻² a⁻¹) which was considerably higher due to the modern age of peat at 40 cm. The high rate in PI12 assumes that peat has accumulated at a rate of 9 mm a⁻¹ and is unrealistic compared to published rates of 1–2 mm a⁻¹ for upper layers of other peat deposits in Sumatra (Supardi *et al.* 1993) and Kalimantan (Sieffermann *et al.* 1988). The implications of the high PI12 accumulation rate are discussed below.

Accumulation rates similar to those of the study sites were found in other deep peat deposits in Sumatra for which age measurements were available. Acrotelm accumulation rates in deep peat (8–10 m) deposits at Siaksriindrapura and Bengkalis near Padang Island (Diemont and Supardi 1987, Supardi *et al.* 1993) are included in Figure 5–2, and correspond to the rates of the 3–6 m sites, but not the PI12.

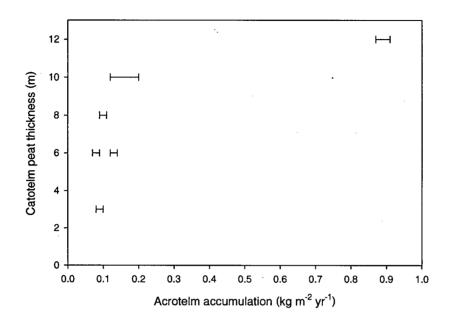


Figure 5–2. Range of acrotelm accumulation rates across gradient of increasing peat depth based on mean (±1 SD) radiocarbon ages at 40 cm below the surface. The wide range of rates for PI12 is based on assumption that acrotelm layer may be 45 to 200 years old. Acrotelm rates of other peat deposits in Sumatra on Bengkalis Island (8 m) and Siaksriindrapura (10 m) are included for comparison. Radiocarbon ages were not obtained in PI9 peat.

The estimated acrotelm accumulation rates were also compared with an estimate of catotelm input from the Siaksriindrapura peat deposit, which is the only deposit in Sumatra for which incremental age, depth and bulk density data are available (Diemont and Supardi 1987). The acrotelm accumulation rates in all sites but PI12, were comparable to the catotelm input rate (p_C) of 0.14 kg m⁻² a⁻¹ calculated for the top 3 m of the Siaksriindrapura peat deposit using Clymo's (1984, p. 651) equation to calculate p_C and k_C with age and depth data. The estimated acrotelm accumulation rates were higher than the modal value of 0.05 kg m⁻² a⁻¹ for peatlands in the northern hemisphere (Clymo 1984).

Assuming steady state conditions, the annual rate of acrotelm accumulation is equal to the total input (p_C) of organic matter to the catotelm, which according to the general peat accumulation model (eq. 1), is also equal to the total annual decay of accumulated mass in the catotelm layer

$$\frac{p_C}{k_C} \left(1 - e^{-k_C t} \right) = x_C \tag{1}$$

where x_c is the cumulative mass of catotelm peat per unit area, p_c is the rate of addition of dry mass (kg m⁻² a⁻¹) and k_c is the decay rate coefficient (% a⁻¹) of catotelm peat. With known p (acrotelm accumulation rates), x (total peat mass per unit area in each deposit) and bulk density (0.06–1.50 g cm⁻³) values, the model was used to estimate an average decay rate (k) of 0.00022 a⁻¹ required to maintain steady state conditions over time. The results in Figure 5–3 show that negative exponential decay over time is proportional to the mass remaining. The large accumulated mass in PI12 shows the greatest speed of descent. Few peat deposits in Sumatra exceed 12 m so this site appears to be close to steady state where the rate of addition of plant matter at the surface is balanced by losses at all depths and the rate of accumulation is zero. Clymo (1984, 1991) described the pattern of concave age against depth-ascumulative mass curves for peat deposits in the northern hemisphere. This result suggests that to compensate for decay occurring throughout the entire peat profile, the rate of organic inputs from the acrotelm must remain constant or increase, but cannot decrease in proportion to the height of the deposit (Winston 1994).

The decay coefficient of 0.00022 a⁻¹ is equivalent to a residence time of approximately 4.5 kyr, which is comparable to the age of basal peat in the Sumatra deposits (4.0–4.5 kyr). The catotelm decay rate estimated for the study sites was surprisingly similar to the rate calculated (0.00024 a⁻¹) for the Siaksriindrapura peat deposit using the data of Diemont and Supardi (1987) and Clymo's (1984, p. 651) equation for p_C and k_C .

The estimated catotelm decay rate for the study sites is on the high side for decomposed peat in the northern hemisphere for which values of about 10⁻⁴ to 10⁻⁷ seem to be common (Ingram 1983). No direct measures of decay were available for tropical peat deposits, but it is reasonable to believe that decay would be greater in tropical peats where mean annual temperatures are considerably higher. Higher decay rates are also matched by relatively higher rates of plant input. The system however, is certainly more complex than represented here due to the relatively young age of the deposits in East Sumatra and the assumption of steady state conditions.

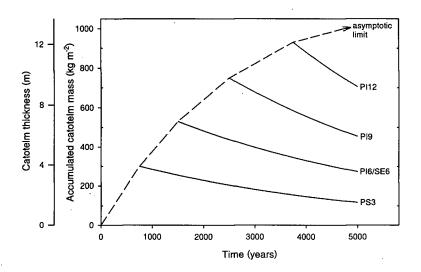


Figure 5–3. Simulated catotelm accumulation (dashed line) and decay (solid lines) over time in raised peat deposits in East Sumatra. A decay coefficient of 0.00022 a⁻¹ is used in the general peat model (eq. 1).

Expanded Peat Accumulation Model

The general model of production and decay (eq. 1) in the catotelm does not reflect organic input and decay processes in the acrotelm layers of tropical forested peatlands where allogenic and autogenic site conditions have the greatest effects. I have modified the model in eq. 1 to account for these processes and the effects to be expected if the processes considered so far are combined. This can be shown in a simulation based on the peat accumulation model (eq. 1) in which the rate of accumulation of dry matter was determined by the rate of plant additions and the integrated rate of loss at all heights in the peat deposit. The modified model had five compartments of mixed organic matter: (1) a layer of aboveground litter, (2) a top layer of acrotelm peat, (3) a basal layer of acrotelm peat, (4) a top layer of catotelm peat, and (5) a basal layer of catotelm peat. The depth of the acrotelm layer was specified at 40 cm which also determined the cumulative mass (x) of each compartment (Chapter 4.2). The rates of organic input (p) and the decay coefficients (k) were from the component studies in Chapter 4.2 and 4.3. The simulation periods (n) varied according to the radiocarbon age of the acrotelm base (45-660 years) at each peat forest site. The steady state model for the litter layer is:

$$\sum_{i=1}^{n} \frac{p_L}{k_L} \left(1 - e^{-k_L t} \right) = x_L \tag{3}$$

where x_L is the cumulative mass of litter per unit area above the top of the acrotelm layer, p_L is the rate of addition of plant dry mass (kg m⁻² a⁻¹) and k_L is the decay rate coefficient (% a⁻¹).

The top of the acrotelm incorporates a fraction of decayed litter (x_L) , receives live small roots (p_{ATr}) , and is in steady state during the accumulation period:

$$\sum_{i=1}^{n} \frac{x_L + p_{ATr}}{k_{AT}} \left(1 - e^{-k_{AT}t} \right) = x_{AT}$$
 (4)

where x_{AT} is the cumulative mass of dry matter in the top of the acrotelm layer and k_{AT} is the decay rate of peat in the top of the acrotelm.

The base of the acrotelm incorporates a fraction of peat from the acrotelm top (p_{AT}) , receives live small roots (p_{AB_T}) , and is also in steady state:

$$\sum_{i=1}^{n} \frac{x_{AT} + p_{ABr}}{k_{AB}} \left(1 - e^{-k_{AB}t} \right) = x_{AB}$$
 (5)

where x_{AB} is the cumulative mass of peat in the acrotelm base and k_{AB} is the decay rate of peat in the acrotelm base.

The top of the catotelm layer (x_{CT}) incorporates peat at the acrotelm base inundated by the rising water table (x_{AB}) , small live roots growing into the catotelm (p_{Cr}) and is in steady state during the accumulation period:

$$\sum_{i=1}^{n} \frac{x_{AB} + p_{Cr}}{k_{CT}} \left(1 - e^{-k_{CT}t} \right) = x_{CT}$$
 (6)

where x_{CT} is the cumulative mass of peat per unit area in the top of the catotelm layer from the radiocarbon age at the acrotelm base to the present and k_{CT} is the decay rate coefficient of saturated catotelm peat.

Annual additions to the base of the catotelm layer (x_{CB}) consist only of that portion of peat at the top of the catotelm inundated by the rising water table. During the simulation, net catotelm peat accumulation occurs in the top of the catotelm while the base of the catotelm decays:

$$\sum_{i=1}^{n} \frac{x_{CT}}{k_{CB}} \left(1 - e^{-k_{CB}t} \right) = x_{CB} \tag{7}$$

where x_{CB} is the cumulative mass of peat per unit area in the catotelm layer from the radiocarbon age at the acrotelm base to the present and k_C is the decay rate coefficient of saturated catotelm peat.

Equations 3–7 were used to get the results presented in Figure 5–4 for four of the peat forest sites in East Sumatra. The PI9 site was not included in the simulation because radiocarbon ages were not measured. The model incorporates the p and k constants developed from the field and laboratory studies of the litter and acrotelm layers. The k coefficient of peat in the old and new catotelm layers was calculated using eq. 1 as shown in Figure 5–3, The mass of p entering the new catotelm was assumed to be the same as p in the acrotelm base. It was also assumed that the old catotelm layer was below the root zone and did not receive any p. The results showed that the peat surface in PI12 aggraded over the simulation period, while the surfaces of the other study sites degraded. The simulations did not adequately reflect the present conditions in the study sites because the radiocarbon age and depth analysis of peat profiles in deposits adjacent to the study sites indicated that the peat deposits in East Sumatra continue to aggrade (Diemont and Supardi 1987, Supardi $et\ al.\ 1993$, Neuzil $et\ al.\ 1n\ Press$). The same analysis of peat accumulation trajectories also indicates that the rapid accumulation in PI12 was unrealistic. Supardi $et\ al.\ (1993)$ calculated that present day accumulation rates should be no greater than 1–2 mm a^{-1} , or about 5 kg m⁻² over the 45-year simulation period. Also, using the k and p values taken directly from the field and laboratory studies did not maintain steady state conditions in the litter and acrotelm layers.

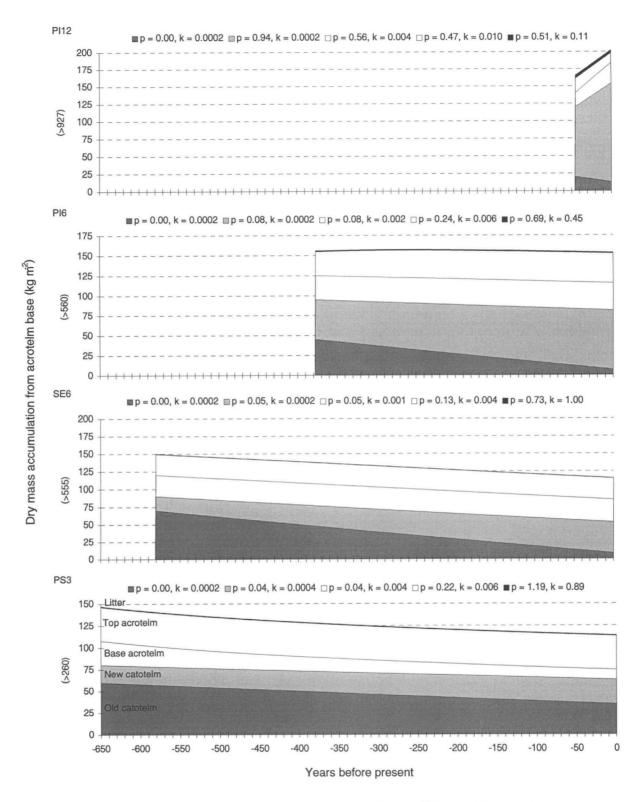


Figure 5–4. Reconstruction of dry mass accumulation starting from the 14 C age of the acrotelm base to the present time in four peat forest sites in East Sumatra. Measured organic inputs $(p, \text{kg m}^{-2} \text{ a}^{-1})$ and decay coefficients $(k, \% \text{ a}^{-1})$ are for \blacksquare old catotelm, \blacksquare new catotelm, \square acrotelm base and acrotelm top, and \blacksquare litter layer. Mass of peat below acrotelm base at start of simulation is parenthesized in left margin.

The model was re-calibrated using age-corrected production and decay variables and the results are shown in Figure 5-5. The radiocarbon ages of the peat and roots in the top and base of the acrotelm layers were used to modify the field and laboratory measurements of production and peat decay. For example, the decay rate coefficients in Table 4-14 for PS3 peat (based on CO_2 emissions from peat), were increased 286% for the top layer, but were reduced 172% for the bottom layer of the acrotelm to reflect the age of the peat measured by radiocarbon analysis. After adjusting the k coefficients, rates of p were also modified in the model to maintain steady state conditions in the litter and acrotelm layers during the simulation periods.

The age-corrected simulation in Figure 5–5 showed that all sites aggraded slowly (0.1–0.2 kg m⁻² a⁻¹). The relative importance of aboveground litter in the acrotelm layer increased proportionally across the gradient of increasing peat depth from 1.2% of the acrotelm mass in SE6, to 10.6% in PI12. Despite the larger proportion of litter in the PI12 acrotelm layer, aboveground litter inputs do not likely contribute significant amounts of dry mass to the catotelm layer. The presence of a continuous mat of fine and small roots was observed to act as a physical barrier that would prevent substantial quantities of decayed litter from being submerged by the rising water table as peat accumulates. Conversely, the small proportion of aboveground litter in the acrotelm of PS3 and SE6 sites likely had an important role in peat accumulation because of the absence of a root mat to keep litter above the rising water table.

The results suggest that different plant communities may have dissimilar processes of peat formation.

Covington and Raymond (1989) studied root:shoot ratios (R:S) in mangrove peat and proposed that high R:S were due to the presence of a root mat that prevents the input of aerial debris to peat. Shearer and Moore (1995) analyzed fragments of peat from Kalimantan and could not find angiosperm xylem tissue, leaves, cuticle, reproductive organs, seeds and stems. They attributed the absence of plant components to high rates of decomposition in aerial litter above the peat surface.

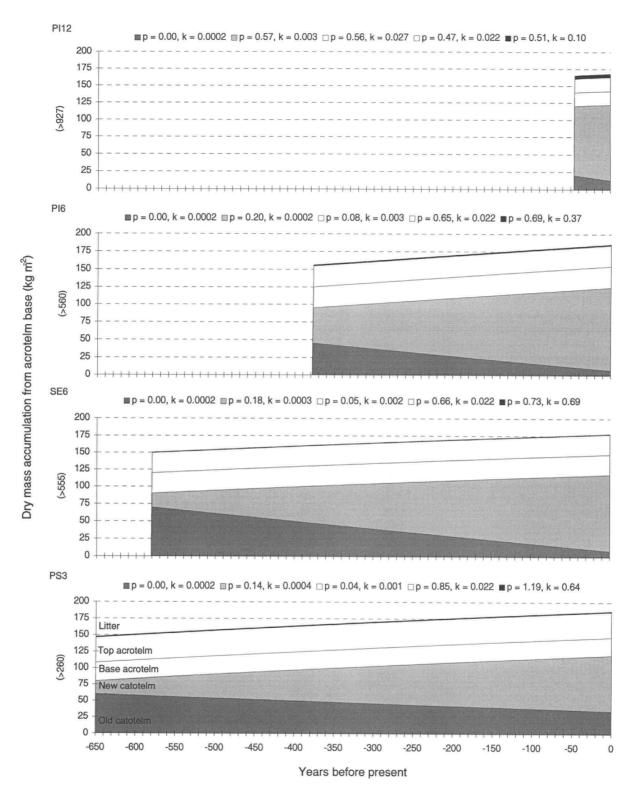


Figure 5–5. Age-corrected reconstruction of dry mass accumulation from the 14 C age of the acrotelm base to the present time in four peat forest sites in East Sumatra. Organic inputs $(p, \text{kg m}^{-2} \text{ a}^{-1})$ and corrected decay coefficients $(k, \% \text{ a}^{-1})$ are for \blacksquare old catotelm, \blacksquare new catotelm, \square acrotelm base and top, and \blacksquare litter layer. Dry mass of peat below acrotelm base at start of simulation is parenthesized in left margin.

The age correction increased p rates in the acrotelm top and catotelm top layers of PS3, SE6 and PI6 sites. The increase in p suggested that the root ingrowth study underestimated root production in these sites. Conversely, the age-correction increased the k coefficient in the acrotelm layer of all sites with the largest increase in PI12. This suggested that peat decay in the top of the acrotelm was faster than measured by CO_2 emissions during the incubations, despite the similar environmental conditions. The only age-corrected decline in k occurred in PS3, suggesting that decay under field conditions was slower than in the laboratory incubation.

The high rate of peat accumulation in PI12 during the first simulation was based on the modern age of the entire acrotelm layer, but did not reflect actual rates of peat accumulation. The young age of the dense root mat suspended over the catotelm in PI12 suggested a short residence time for organic matter inputs before they are preserved as peat in the catotelm below. The acrotelm in PI12, however, because of high production of small roots, remained fibric-textured from the top to the base at the water table level. Unlike in the medium depth peat deposits where root production was lower, the constant input of small roots in the acrotelm of deep peat deposits may have prevented the plant structure at the base of the acrotelm from collapsing, and thereby maintaining conditions for rapid hydraulic conductivity. The fibric textured acrotelm in PI12 may have limited further water table rises, leading to cessation of peat accumulation and the formation of the flat central plateau characteristic of peat deposits in Sumatra. If the fibric texture of the acrotelm inhibits further water table rises, the young age of the organic matter may reflect rapid turnover within the layer, rather than a short residence time before the lower portion of the layer is preserved as peat below the rising water table.

A similar process of stagnation has been observed in temperate peatlands. Ingram (1982) and Clymo (1984) observed that peat initially accumulates at some constant high rate that continues until the rise in water table cannot keep up with the potential increase in peat depth. Thus, the accumulation rate of catotelm peat in the centre of a peat deposit may not depend on the growth rates of the plants there; it may be more closely linked to the horizontal dimensions of the peat deposit than to the texture of surface peat layer (*Sensu* Granlund's water mound theory, Ingram 1982, 1983, Winston 1994).

Age and fraction analyses showed that the acrotelm peat layers in the study sites were constant or increased in depth across the gradient of increasing peat depth. This finding is inconsistent with the assumptions for *Sphagnum* peat accumulation, where an increase in the total depth of peat is associated with a decrease in the depth of the acrotelm layer. Recent petrographic analyses of Indonesian peat also question the rising water table effect.

Grady et al. (1993) analyzed the maceral content¹ of peat from different layers of a deep deposit near

Siaksriindrapura, Riau, and assumed that increased fungal degradation² of plant cells in peat was evidence of higher oxygen levels in peat during degradation. The fungal degradation suggested that the root-dominated fibric peat found in deep deposits is more aerobic than that of the wood-dominated sapric peat found in thinner deposits.

Similar to the findings of my study, the maceral evidence of Grady et al. suggests that peat accumulation and cessation in deeper peat deposits may be associated more with drier surface or acrotelm conditions and changes in species composition, than with a rising water table as assumed by the two-layer model. Vertical sequences of peat have also been analyzed from other deposits in Sumatra (Esterle and Ferm 1994) and in Kalimantan (Moore and Hilbert 1992, Dehmer 1993). The studies show how peat layers differ both in texture, because of species changes, and in the degree of decay as determined by texture analysis. The study results were consistent with a key assumption of the *Sphagnum* peat model that increasing peat deposit depth is due to the increased amount of mass entering catotelm layer. Larger amounts of fresh material are found in the catotelm of the deep peat study areas than in the medium depth areas. The fresh material consists mainly of small and fine roots, rather than aboveground litter.

The varying importance of plant inputs and organic matter decay across the gradient of peat accumulation indicated that the assumptions of the model for accumulation in *Sphagnum* peatlands would not apply directly to the peat deposits in East Sumatra. The study results suggested that increasing peat accumulation was associated with several significant changes in the acrotelm peat layer including: reduced flooding and lower mean water table levels, declining resource quality of plant inputs, and an increase in the root:shoot ratio. The increased input of small roots of poor resource quality appeared to be the most important process contributing to peat accumulation among the study areas. The high root inputs, however, also appeared to promote the eventual cessation of peat accumulation in the deep peat deposits. Here, much of the acrotelm layer was occupied by a thick, fibric mat of small and fine roots. The large mass of young roots and high decay rates suggested a short turnover period during which fibric-textured peat would be sustained throughout the acrotelm layer. As a result, the root mat, which also acted as a barrier to aboveground litter inputs, may have increased and eventually restricted further water table rise, which is the primary means by which peat accumulates. This hypothesis is speculative and requires examination of other deep peat deposits in Sumatra and Borneo.

FOOTNOTES

¹A petrographic technique first developed to study coal.

²Indicated by higher levels of inertinite (high O/C ratio) and degraded huminite maceral groups. The greater degradation of huminite cellular debris is interpreted to be the result of fungal activity that increases in response to increasingly aerobic conditions (Grady *et al.* 1993).

CHAPTER 6

GENERAL SUMMARY AND IMPLICATIONS OF THE STUDY FOR CONSERVATION AND MANAGEMENT

6.1 KEY FINDINGS OF THE STUDY

In this study I attempted to determine whether the variable accumulation of peat among the 3, 6 and 12 m deposits along the coast of East Sumatra might, in part, be explained by age, vegetation and edaphic differences.

Peat Age

The top of the acrotelm in all samples was of modern (post 1950 AD) age, while peat at the base of the acrotelm was younger than 660 yBP. The findings did not support the hypothesis that the gradient of increasing peat depth, as represented by the study sites, could be attributed to variable ages of surface peat.

An additional finding of the age study was that the base of the acrotelm peat layer decreased in age (up to six times) across the gradient of increasing peat depth. The residence time of peat in the acrotelm layer was also affected by root penetration into preserved peat. Small roots were hundreds of years younger than the hemic-textured peat. The finding of shortened residence times of organic matter in the acrotelm layers of deeper deposits was consistent with the assumption of the two-layered model (eq. 2) for *Sphagnum* peat accumulation. The processes, however, that control residence times appeared to differ in *Sphagnum*- and tropical wood-based peatlands. The reduced residence times of organic matter in the acrotelm with increasing peat depth were mainly because of increased root mass in the base of the acrotelm peat layer, rather than due to reduced decay rates (discussed below).

Peat Forest Vegetation

Four of the five study sites were floristically and structurally distinct from each other and included chablis, mixed tall pole and low pole forest types. While the chablis and mixed peat forests are common in East Sumatra, the pole forests have not been described in detail previous to the study. Changes in forest types across the gradient of increasing peat depth included decreases in species, canopy height and layering, basal area and leaf area. The gradient was also associated with increasing stem density, root suckering and clumping of tree distribution. Tree

buttresses and adventitious roots were more common in medium depth sites, while a continuous mat of fine and small roots was present in the deepest peat sites

Organic Matter Inputs to Peat

The relative contributions of aboveground and belowground vegetation inputs to peat were estimated. The single canopy and low species composition in the deep peat forest, compared to the medium depth peat forests, were associated with increasing root mass and a decrease in the quality and quantity of aboveground organic matter litter inputs to peat. The input of organic matter from fine and small roots in the deep peat sites was greater than aboveground litterfall. Repeated field observations indicated that root production and mortality were highly sensitive to soil watertable and moisture.

Peat Edaphic and Environmental Factors

The study of peat water level fluctuations generally supported the hypothesis that water table fluctuations and surface moisture were negatively related to peat depth. However, correlations between peat water levels and rainfall were weak in all study sites, possibly due to lateral flows through subsurface peat and moisture losses from evapotranspiration. The study was not of sufficient length to confirm that average peat water levels have dropped in response to a long-term decline in rainfall in East Sumatra.

Surface peat temperatures under the forest canopy were constant throughout the year, but increased significantly upon forest clearing. Dry peat conditions were observed to occur regularly in all sites during low rainfall periods. The driest conditions were recorded in the acrotelm of the study site on the deepest peat. During dry the periods peat was not sufficiently dry to burn belowground. It was, however, sufficiently dry to kill large quantities of fine roots in the surface layer of peat.

Organic Matter Decay

Surface layers of peat were more humified in the medium depth peat areas than in the deep peat areas, while the degree of decomposition in subsurface layers of unmanaged peat formations was similar in moderate and deep peats. The differences in the degree of decomposition between the surface and subsurface peat layers were greater in the Padang Island deep peat formation than the South Sumatra medium depth peat formations. This was determined by the lower bulk density and larger amount of fibric matter in the surface layer of the deep peat area.

Organic matter quality, as characterized by concentrations total N and P and the proximate C fractions in this study, was lower in both the litter layer and surface peat layer in deep peat study areas, than in those of the moderate depth areas. The lower quality litter in the deep peat was associated with slower rates of decay as measured by mass losses of organic components, estimates of litter layer turnover periods, and surface topography changes. However, peat decay, as reflected by respiration, was greater in the deeper peat sites which contained large quantities of intact fine and small roots.

Organic matter decay was also limited by moisture conditions. Decay in medium depth peat areas was more strongly associated with moisture fluctuations than with differences in organic matter quality, but was restricted by both extreme wet and dry conditions. Despite the saturated peat conditions during wet periods, organic matter decayed rapidly. High cotton substrate losses were recorded, and N mineralization occurred in the saturated peat. High rates of N mineralization have not normally been associated with saturated soil conditions in temperate soils (Alexander 1977, Tate 1977, 1980, Tate and Terry 1979).

Model of Peat Accumulation

The varying importance of plant inputs and organic matter decay across the gradient of peat accumulation indicated that several of the assumptions of the model for accumulation in *Sphagnum* peatlands would not apply directly to the peat deposits in East Sumatra. In particular, the age and fraction analyses showed that the acrotelm peat layers in the study sites were constant or increased in depth across the gradient of increasing peat depth. This finding is inconsistent with the assumptions for *Sphagnum* peat accumulation, where an increase in the total depth of peat is associated with a decrease in the depth of the acrotelm layer. The study results were, however, consistent with a key assumption of the *Sphagnum* peat model that increasing peat deposit depth is due to the increased amount of mass entering the catotelm layer. The study results suggested that increasing peat accumulation was associated with several significant changes in the acrotelm peat layer including reduced flooding and lower mean water table levels, declining resource quality of plant inputs and an increase in the root:shoot ratio. The increased input of small roots of poor resource quality appeared to be the most important process contributing to peat accumulation among the study areas. The high root inputs, however, also appeared to promote the eventual cessation of peat accumulation in the deep peat deposits.

6.2 THE SUSTAINABILITY OF OMBROGENOUS PEAT

If peat accumulation is controlled largely by the quantity of belowground organic matter inputs, as evidence in the study suggests, then the peat forests where root mats have declined or disappeared by natural or artificial causes will remain in equilibrium or subside, but will not expand. Net accumulations of peat will likely occur where high water levels and thick root mats still exist, and possibly in altered areas where these conditions are re-established.

The study results provided direct evidence that the disturbed medium depth peat formations in East

Sumatra are currently in a state of accelerated degradation due to drainage and forest disturbances. Results from the study were sufficient to conclude that the unmanaged medium and deep peat forest deposits are not presently degrading, but did not provide evidence to confirm that the peat forests continue to accumulate peat. The results of the simulation modeling, corrected with radiocarbon ages, suggested that peat continues to accumulate in the medium depth sites, but has reached steady state in the deepest peat sites

6.3 LIMITATIONS OF THE STUDY

The thesis study had several limitations in design and implementation. A primary limitation in the study design was the use of a retrospective approach. Because the sites were used to compare across a gradient of increasing peat depth, assumptions were made about their historical conditions (*i.e.*, peat depth and class, drainage characteristics and vegetation).

The use of two plots per site limited the confidence that the selected study sites were representative of the peat deposit studied. In addition to site replication, field measurements were occasionally modified because of logistical problems that restricted access to the remote site locations. Sites were necessarily remote being located in the central plateau of the deposits and as a consequence access was sometimes restricted. Common to field research programs in remote areas, the study sites were subject to the vagaries of nature which included forest fires, flooding, wind throw and damage by wildlife (in this case by Elephants).

6.4 CHARACTERISTIC SCALES OF ENVIRONMENTAL FLUCTUATIONS AND POSSIBLE FUTURE CHANGES

This study of organic matter dynamics focused on processes in relatively small volumes of peat and short time scales. In contrast, the spectrum of temporal variation for hydrological phenomena has periods ranging from less than a day for surface evaporation rates, to more than 10000 years for Holocene cooling. In undisturbed peatlands, the dense forest cover, combined with the convex-shaped topographical configuration associated with peat development (ombrogenous raised bog), provides a buffer against rapid, local moisture and temperature fluctuations. Watertable levels and soil temperatures in peat forest show little response to the small-scale climatic fluctuations of seasonal rainfall. The development peat deposits is therefore more likely to be influenced by moisture and temperature changes occurring over longer time periods and larger areas. These include patterns of seasonal rainfall, long-term drought, geomorphological processes, sea level changes and historical climate changes. A complete understanding of the effects of organic matter input processes on peat swamp dynamics would require the integration of all the space and time scales described above.

A generally accepted hypothesis associates peat accumulation in the tropics with historically high levels of annual, evenly distributed rainfall in combination with basin-shaped topography completely lacking in natural drainage (Andriesse 1988). The threshold level of rainfall under which peat will remain stable or accumulate has not been established for tropical peatlands. It is unlikely, regardless of the topography, to be much below 2000 mm a⁻¹ with no more than 2 to 3 continuous dry months. In addition to the lower limits of rainfall, air temperatures may have also controlled peat accumulation rates. Lower temperatures, such as occurred during the early Holocene, would promote reduced evapotranspiration and allow greater water storage in peat. Payette (1988) hypothesized that temperate peat bogs in Eastern Canada were strongly affected by temperature increases over the past 5000 years and as a result of increasing evapotranspiration, peat accumulation ceased about 2000 years BP. He emphasized, however, that any attempt to further differentiate between the effects of temperature and rainfall changes on peat accumulation would be difficult.

Various predictions have been made on the effects of future climate changes on the hydrological cycle in the tropics (Henderson-Sellers 1981, 1987, Henderson-Sellers and Gornitz 1985). Brünig (1991) addressed the effects of climate changes in South East Asia. He speculated that CO₂ induced global temperature increases will

result in more severe droughts in the region. This could lead to increased moisture stress, faster rates of organic matter decomposition and increased evapotranspiration, all of which would promote accelerated peat degradation. Alternatively, Solomon and Tharp (1985) argued that increased CO₂ levels will cause reduced seasonality in the tropics due to increased cloud cover and rainfall from higher convection rates. This would enhance organic matter storage because of wetter conditions, increased water use efficiency and increased primary production of plants.

6.5 CONSERVATION AND MANAGEMENT IMPLICATIONS

The evidence collected in this study suggests that the surface layers of unmanaged deposits of medium and deep peat in East Sumatra are presently in steady state or continuing to accumulate peat. The disturbed site is in a state of net peat decomposition and releasing carbon, albeit very slowly, perhaps in the order of 10 Mg ha⁻¹ a⁻¹. This is cause for concern, considering that the Sumatra peatlands are one of the few terrestrial ecosystems of significant size that could be managed to store carbon. Compared to forested peatlands, those altered by artificial drainage and/or annual crop production loose considerably more carbon, in the range of 100 to 200 Mg ha⁻¹ a⁻¹ (Armentano and Menges 1986).

Because of their carbon sequestering function, the coastal peatlands should be preserved (Harger 1992). However, given the increasing pressures in Indonesia on land for food production, forest products and settlement areas (Appendix 1), the preservation option is unlikely. The question then is how to manage peatlands for development in such a way as to minimize the loss of organic carbon from the ecosystem? Given the increasing concerns about minimizing releases of carbon to the atmosphere, and the ability of tropical peatlands to effectively act as large net sinks or net sources of carbon, decisions to develop peatlands should include recognition of the shift of the carbon balance towards a net release of carbon. This will inevitably occur following disturbances which alter the balance between organic matter inputs and decay. Such alterations are caused by natural or human activities in and around peatlands and lead to the following changes:

- Increases in the decomposability of organic matter puts (labile organic matter, high N and P, low lignin) from vegetation due to species changes;
- Decreases in allocation of belowground biomass production due to species changes and increased nutrient release and availability;

- 3) Increases in moisture losses by convection and evapotranspiration due to forest canopy removal;
- 4) Lowering of peat water levels through drainage;
- 5) Increasing peat micro-relief, which promotes more rapid lateral drainage;
- 6) increased inputs of nutrient laden sediments and water from water bodies originally separated from the peat formation; and
- 7) increased inputs of nutrients from atmospheric deposition from urban/industrial sources.

Management initiatives to control these factors are discussed below:

Vegetation Composition

Wyatt-Smith (1959), Anderson (1983) and others have shown that the peat forests in Southeast Asia are a valuable timber resource because of their good regenerative capacity, timber quality and high productivity. Forestry is likely to be the most sustainable use of peatlands. Forest harvesting, however, may result in changes to the quality and quantity of organic matter inputs from vegetation. Harvesting methods that leave forest cover relatively intact and productive are essential if the peatlands are to remain. Of equal concern, but perhaps more difficult to achieve, is the need to limit species invasions. Increases in the resource quality attributes of organic matter inputs from vegetation due to species changes would alter the balance between organic matter input and losses. As a result, forest harvesting should be conducted so as to minimize the invasion of fast growing pioneer and secondary species. This will require careful harvest planning to ensure that sufficient trees remain to exploit newly created canopy gaps. If enrichment planting is performed, species indigenous to peatlands, or other species with massive allocation to roots should be used.

Belowground Biomass Allocation

Forest species changes may lead to reduced belowground biomass allocation. Many lowland forest species show considerable morphological plasticity in adapting to changing growing environments. For example.

Calophyllum ferrugineum in the tall pole forest was commonly found with few loop roots, whereas in the low pole forest individual trees contained extensive networks of loop roots extending laterally across the peat surface.

Despite the importance of conserving forest species known to allocate large amounts of biomass belowground, neither basic silviculture, not the morphological plasticity of most lowland and peat swamp species has been

studied. It would be difficult to determine which species would be appropriate for planting in the absence of field trials under swampy conditions. It may be more practical to test whether more widely known species are capable of adapting to swampy conditions and of allocating increased biomass belowground.

In deep peat areas that have been developed for settlement and agricultural purposes, efforts should be placed on the establishment of permanent tree crop cover. Intercropping with green manure of low resource quality will add organic matter to the peat in addition to that from the trees. To simulate natural peat forest conditions as closely as possible, tree species should be selected both for high belowground biomass allocation and for low quality litter.

Microclimate

Increasing temperature had the greatest effect on peat decay. Land and forestry practices should be controlled to maintain as much vegetation cover over the peat surface as possible. Clear felling should be avoided to prevent high insolation at the peat surface.

Peat Water Levels

Lowering of peat water levels by drainage will normally lead to increased decay, particularly below the root mat. The need to maintain high water levels requires no further emphasis as it is the primary factor promoting peat accumulation in the medium depth peatlands. However, the study has shown that natural drainage changes may occur and this can lead to the natural degradation of some peatlands. Observations of both natural and artificial drainage changes revealed that the effects are often extensive, in most cases affecting the entire raised peat formation.

Development activities designated for areas within a peat deposits and involving drainage canals, may affect the hydrological balance of large areas of the raised peat formation and should be assessed accordingly. For example, ground studies and analysis of aerial photographs have indicated that drainage of the Padang-Sugihan peat deposit has led to large changes in the hydrological regime, vegetation and peat components of the 77 000 ha peat swamp forest (Brady 1989). Unless the seven main canals and hundreds of secondary canals are closed, the area will continue to over-drain as described in Chapter 2 and 3. There will continue to be tree species replacement, and

the peat will decompose further until a new steady state is attained. During these changes the peat deposit will continue to be particularly vulnerable to aboveground and belowground fires.

Peat Surface Topography

Development activities such as peat mining, road building and ditches may lead to an increase in the topographical relief of the peat surface within the peat swamp. If hydrological alterations occur, water flows should be directed towards the central expanse, rather than towards the lagg where the water would be lost from the peat deposit.

Terrestrial and Aquatic Inputs to Peat

Increased inputs of nutrient laden sediments and water from water bodies originally separated from the peat formation may accelerate peat decomposition. To conserve peatland functions, development activities involving irrigation or tidal flushing must be designed to control the input of water and sediment from streams, rivers and coastlines outside the peat formation. The natural fringe of mangrove forest adjacent to coastal peat deposits should be maintained to act as a buffer for sediment and water flows.

Recent attention has been given to the use of natural wetlands in both controlling and treating non-point source pollution (Olson 1992). Trials should be performed to determine whether wastes that are low in nutrients and high in organic matter (e.g., pulp mill effluent) can be disposed of in peatlands without causing increased peat decay.

Atmospheric Inputs to Peat

Increased concentrations of chemical elements in dry and wet atmospheric deposition will likely affect the imbalance between organic matter inputs and decay. Increased N and P deposition may act to enhance decomposition processes. Alternatively, increases in other elements such as sulphur may promote further increases in peat acidity (decline in pH). This could further inhibit soil biological activities. The effects of "acid rain" have now become a concern in urban and industrial areas of Indonesia. Their effects on peat forests have not been assessed.

6.6 ADDITIONAL RESEARCH NEEDS

There are several additional studies required to improve our understanding of organic matter dynamics in the tropical peatlands and the effect on the short-term and long-term sustainability of ombrogenous conditions. Of greatest importance is the need to better understand plant-water relations in peatlands (Brünig 1991). Direct evapotranspiration measurements would allow a more accurate assessment of the effects of vegetation on peat moisture and watertable levels. Patterns of peat elevation changes, waterlevel fluctuations and seasonal climate will be better understood if long-term monitoring information is recorded at permanently established locations in the peatlands. Monitoring studies are also required to measure the below-surface interflow of water through peat. This information would enhance understanding of the movement of mineralized nutrients in peat formations and the possible effects on vegetation distribution and growth.

Further understanding of nutrient limitations in peat forests requires that elements other than N and P be assessed. Several studies of nutrient dynamics in low fertility tropical forests have suggested that Ca, Mg, K and secondary chemicals such as polyphenols may play important roles in decay processes and nutrient cycling (Medina and Cuevas 1989, Palm and Sanchez 1990, Bloomfield *et al.* 1993, Burselm *et al.* 1995). While the pyroloysis studies by Calvert *et al.* (1989) and Dehmer (1995) provide details of the organic chemical compounds found in the lignin and cellulose fractions of Indonesian peats, the effects of individuals or groups of these compounds on decay at the peat surface remains to be studied. In particular, the water-soluble C fraction, which was strongly correlated with an increase in small root mass in peat from the deep peat sites, is vaguely linked to the amount of available C (Melillo *et al.* 1989). Although there is no absolute measure of soil labile C pools, more refined indices have recently been developed. For example, Bradley and Fyles (1995a) described a quantitative measure of the glucose equivalent of available C in soils.

Multi-annual aboveground and belowground litter collections are required to confirm the study findings, particularly in PI12 which showed low rates of leaf litterfall and exceptionally high rates of small root production. Variation among collection periods was high in all sites and reflected the wide variation in rainfall during the collection periods. A minimum of three years of continuous collection would be required to accurately assess seasonal variability (Anderson and Ingram 1993, Stocker *et al.* 1995).

CHAPTER 7

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APPENDIX 1. SUSTAINABILITY OF TROPICAL COASTAL PEATLANDS: THE PROBLEM OF POPULATION GROWTH AND PEAT FOREST USE IN SUMATRA

1.1 GEOGRAPHY AND POPULATION DISTRIBUTION IN INDONESIA

The Republic of Indonesia is a large archipelago of about 17000 islands (Donner 1987). Together with Australia to the south and Peninsular Malaysia to the north, Indonesia separates the Indian Ocean from the western Pacific Ocean. The islands, which occupy a total land area of approximately 192 million ha (Mha), include the large islands of Borneo, Sumatra, New Guinea, Sulawesi and Java, plus many smaller islands. The archipelago extends 5200 km from west (95°E) to east (141°E) and 1900 km from north (6°N) to south (11°S).

Sumatra is the westernmost island of Indonesia. It is the second largest island with a surface area of 47.4 Mha (Figure 3–1). Positioned diagonally across the equator, the distance from the north west to the south east ends of Sumatra is approximately 1750 km (Whitten 1984). The average width of the island is 300 km. Much of the east coast is bordered by the Malacca Strait which separates Sumatra from Peninsular Malaysia and Singapore.

Indonesia's population is currently the third largest in Asia after China and India. It has grown rapidly this century. In 1905 there were 37 million people. Between 1970 and 1981, the annual growth rate was 2.3 percent. The population in 1995 was estimated at 195 million (World Bank 1996). Recent estimates show the growth rate declining to 2.1 percent (Sutter 1989). The island of Java contained the majority of Indonesia's population (99.5 million) in 1985 as listed in Appendix Table 1–1 (Hill 1991). Sumatra contained the second largest population (32.7 million) in 1985. Sutter (1989) estimated that this figure had risen to 38 million by 1990. The two provinces of

South Sumatra and Riau, in which this study took place, had populations in 1985 of 5.4 and 2.5 million, respectively.

Appendix Table 1–1. Population and annual average growth rate in Indonesia, Java and Sumatra from 1920–85. Modified from Hill (1991).

	Population estimate, millions, and annual average growth rate (percent)				
Region	1920–30	1961–71	1971–80	1980–85	
Indonesia	49.4–60.7 (2.1)	97.1–119.2 (2.1)	119.2–147.5 (2.3)	147.5–163.9 (2.1)	
Java.	35.0-41.7 (1.8)	63.1–76.1 (1.9)	76.1–91.3 (2.0)	91.3–99.5 (1.7)	
Sumatra	6.1-8.3 (3.1)	15.7–20.8 (2.9)	20.8-28.0 (3.3)	28.0-32.7 (3.1)	
- South Sumatra	ND	ND (2.2)	ND (3.3)	5.4 (3.2)	
- Riau	ND	ND (2.9)	ND (3.1)	2.5 (3.0)	

Note: ND - no data

1.2 POPULATION GROWTH AND THE DEVELOPMENT OF INDONESIA'S OUTER ISLANDS

Current population projections indicate that Indonesia will reach 216 million people by the year 2000 and 320 million by 2030 (Sutter 1989). A static population of 400 million has been projected by the year 2140 (Donner 1987). Seventy-four percent of the population is located in rural areas and this pattern is expected to continue indefinitely (Myers 1991a, 1991b). Population growth rates in Sumatra have been higher than the national annual average (3.12% compared to 2.13% from 1980–85), and are expected to continue, with the population of the island doubling to 70 million people by 2030 (Sutter 1989). This will result in an increase in population density from the current level of 79 people/km² to 144/km² (RePPProt 1988). This remains considerably lower than the densely populated island of Java that had, in 1985, an average population density of 753 persons/km² (Hill 1991).

Along with the increases in population and economic development is an increasing demand for land, particularly for urbanization, agricultural expansion and population resettlement. On the Island of Java, approximately 30 000 ha of flat, fertile land is converted annually from agriculture to industry or occupied land for population growth (Jakarta Post, May 3, 1991). The remaining agricultural land is intensively used. Up to 62 percent of the farm households in Java are on less than 0.5 ha of land compared to 27 percent of farm households in Sumatra (World Bank 1988). As a result of these pressures for land, Indonesia's outer islands have been undergoing accelerated development. From 1979 to 1988, approximately 359 100 ha of new land was developed for rice

production, of which 45 percent was in Sumatra. Government targets called for an additional 375 000 ha of newly-developed land to be made available for rice production in the five years between 1989 and 1993. Approximately 43 percent of this land will be developed in Sumatra for transmigration settlements, tree crops, coffee, cocoa, oil palm, rubber and agro-processing (RePPProt 1988, Sutter 1989).

1.3 SUMMARY OF FOREST COVER STATUS IN INDONESIA

Current estimates of forest cover in Indonesia vary by over 30 percent, ranging from 114 Mha (Dick 1991) to 110 Mha (World Bank 1990) to 86 Mha (Myers 1991a, 1991b). These are based on annual clearance rates of 0.62, 0.90 and 1.20 Mha respectively. The World Bank (1990) clearance rates ranged from 0.70 to 1.20 Mha annually, and illustrate the uncertainty of using 1982–83 forest cover data. Dick (1991) questions the higher rates. He notes that in compiling such data, careful consideration must be given to: 1) separating planned clearance estimates from actual forest areas cleared, 2) the additive effect of reclearing previously disturbed land, particularly by small holders, and 3) the inclusion of previously cleared land. The sources of deforestation are listed in Appendix Table 1–2.

Appendix Table 1-2. Estimates of major sources of deforestation from 1979 to 1989. After Dick (1991).

	Annual clearance		
Sources of deforestation	(ha)	% of total	
Regular transmigration	78 500	12.6	
Swakarsa* transmigration	178 500	28.6	
Estate crops	11400	1.8	
Swampland development	30400	4.9	
Forest harvesting	120000	19.2	
Traditional agriculture	134500	21.7	
Forest fires	70000	11.2	
Total annual clearance	623300	100.0	

^{*}Swakarsa refers to transmigrants receiving partial or no assistance from Government.

Sumatra has experienced the highest deforestation rate in Indonesia as a result of peatland development, estate crops and the large number of spontaneous transmigrants emigrating from Java (Dick 1991). At a minimum,

23.3 Mha or 49 percent of Sumatra's land area of 47.4 Mha remains forested (RePPProt 1988). Of this forested area, at least 1.8 Mha were selectively logged between 1974 and 1987.

The forest cover of Sumatra peat deposits, based on 1982–83 aerial photography, has been estimated by different authors to range between 4.6 and 5.5 Mha (RePPProt 1988, Whitten *et al.* 1984). Whitten *et al.* (1984) calculated that by 1982, as much as 37 percent of Sumatra's peat deposits had been opened. By the end of 1988, approximately 3.2 Mha of Indonesia's peatland had been developed (Sutter 1989, Republic of Indonesia 1990). Maltby and Immirzi (1992) estimated that 82 percent of Southeast Asia's 24 to 43 Mha of peatlands remain unaltered. The figures mentioned above are estimates based on large-scale evaluations and extrapolations, and will be further refined by Indonesia's Forest Inventory Program which will be completed in the mid-1990's.

1.4 HISTORY OF USE AND FUTURE DEMANDS FOR PEATLAND DEVELOPMENT

Much of the peat forest along the east coast of Sumatra has remained inaccessible and largely intact until recently due to the intractable peat surface and flooding during much of the year. The future will be different, however, because the past two decades have witnessed a dramatic acceleration of development activities in these forests. Prior to the 1960's, the peat forests along Sumatra's east coast were sparsely populated and unexploited. They contain a relatively low diversity of flora and fauna compared to the nearby mixed lowland forests on mineral soils. In his account of Sumatra in the early 19th century, Marsden (1986) describes the peatlands around Palembang, South Sumatra as "flat marshy land ... entirely unfit for the purposes of cultivation." The predominant economic activity in the coastal peatlandss until the mid part of this century was subsistence fishing in the rivers and hunting and gathering in the forests. Before the beginning of this century, the Buginese from South Sulawesi, the Banjarese from South Kalimantan and the Javanese emigrated to the east coast and involved themselves in subsistence agriculture and small-scale trading and commerce (MAB 1983). Records of medium-scale commercial forestry activities date back to the turn of the century. Sewandono (1937, 1938) and van de Koppel (1938) describe the harvesting of Calophyllum poles from peat forests in the Bengkalis area of Sumatra for export to Singapore where they were used for building construction in the late 1800's and early 1900's. Oil exploration and development began in the east coast peatlandss in the 1950's and 60's, but did not result in large-scale impacts (Hill 1991).

Development of the Sumatran peatlands began on a large-scale during the 1960's. After exhausting the accessible timber stocks in the lowland forests over mineral soils, forest companies moved their operations into the

peat forests. In the 1970's, forest clearing began for settlements and agricultural production. This occurred mainly through a government-sponsored transmigration program, but also through unassisted immigration of settlers, mainly from overcrowded Java. These activities are described below.

1.4.1 Forest Conservation

Of the 10.2 Mha of forest in Sumatra officially designated as protected from commercial development, the peatlands of the east coast contain 397 500 ha (Sutter 1989). A further 200 500 ha of peat forest has been proposed for protection (RePPProt 1988). These areas, located in South Sumatra, Jambi and Riau Provinces, contain large expanses of peat over 3 m in depth (Euroconsult 1984). They are described in general in RePPProt (1988) and by Silvius (1986), and in further detail by: Giesen and van Balen (1991) and Verheugt and Purwoko (1989) for Riau, Silvius *et al.* (1984) for Jambi, and Nash and Nash (1985a and 1985b) and Verheugt *et al.* (1989) for South Sumatra.

The RePPProt (1988) study proposed that the Ministry of Forestry revise its current classification of forest production and conservation classes and update the area in each class according to current forest conditions in Sumatra. An up-to-date survey would show that the forests in some of the classes have been damaged or cleared for other land uses. Recent surveys have revealed that 14 to 17 percent of the forests within the current reserves and protected areas have been cleared (World Bank 1990). Nash and Nash (1985a and 1985b) provide details of the degradation occurring in a protected wildlife reserve in South Sumatra. The RePPProt study recommends an increase of forested area under protected status from 10.2 to 15.9 Mha. A portion of this area would be peatlands as they remain relatively intact compared to adjacent lowland forests on mineral soil.

In a survey of coastal wetlands of Sumatra's east coast, Silvius (1986) concluded that the coastal mangrove forests and peatlands further inland have high conservation value for wildlife. The reserves are also valuable for the regulation of regional climate, ground water storage and coastal productivity and diversity (Maltby 1986, Verheugt et al. 1989).

1.4.2 Harvesting of Natural Forests

Sumatra's peat forest were classified into forest use classes in 1983. To date, all of the areas classified as Production and Limited Production forests have been awarded to concessionaires for harvesting (RePPProt 1988).

According to Whitten *et al.* (1984), peat forests constitute one of the largest remaining intact forest types in Sumatra. Data from the last island-wide aerial surveys in 1982–83 showed that 3.5 of the 5.9 Mha of the remaining lowland forests in Riau were in peatlands. In Jambi Province, 585 100 ha of the 2.4 Mha of remaining forest were in peatlands, and in South Sumatra 678 200 ha of the 3.3 Mha remaining were peat forests (Dick 1991). Since 1982–83, almost all of the commercially viable peat forest areas in South Sumatra have been selectively logged (personal observations). As domestic and international demands for timber and wood products continue to rise, it has been predicted that the peat forests in Jambi and Riau will be logged over by the end of the century (Sutter 1989).

The considerable infrastructure now developed in Sumatra's peatland areas will ensure that this will occur. Riau has 20 sawmills in the peatlands, and a pulp and paper plant and numerous plywood factories nearby. Jambi has 10 sawmills, while in South Sumatra there are 20 sawmills, one paper mill, and numerous plywood factories within the borders of the peatlands to the north of Palembang. In addition to the government licensed harvesting and processing operations, illegal forestry activities are extensive. These occur most often in logged-over peat forests where the abandoned transportation corridors and facilities can be used (personal observations). Nash and Nash (1985a) estimated that 2.2 million m³ of logs were removed annually from the Padang-Sugihan Wildlife Reserve near Palembang¹ (one of the locations for the study). Along the Siak River that flows through peatlands in Riau Province, 30 illegal sawmills were observed by the authors of the RePPProt (1988) study.

Tree harvesting in the peat forests follows the Indonesian Selective Harvesting System (TPI). The diameter limit ranges from 35 to 60 cm diameter at breast height (dbh), and at least 25 large diameter trees must be left standing per ha for the next harvest in 35 years. Primarily designed for mixed lowland forests, this system was adapted to the peat forest conditions mainly through a reduction in the diameter limit to 40 cm. Peat forests have been highly valued in the region for their large numbers of commercial species. However, few concessionaires in peat forests have performed enrichment planting or silvicultural work such as thinning or weeding after harvesting (personal observations). Silvicultural treatments have been developed and used successfully in Malaysian peat forests (Lee 1972, 1977, 1979, Wyatt-Smith 1963b) while other tropical forest-types are harvested under "natural" forest management systems (Schmidt 1987, Whitmore 1984a, Gomez-Pompa *et al.* 1991).

According to World Bank (1990) estimates, Indonesia's current annual timber harvest of 27 million m³ is projected to increase by the year 2001 to between 34.7 and 48.3 million m³, depending on economic growth rates

and changes in forest management efficiency. The rise in demand will lead to increasing harvesting pressure on Sumatra's peat forests.

1.4.3 Tree Crop and Timber Plantations

By 1988, over 7 Mha of tree crops, including oil palm, rubber, coconut, and beverage crops, had been planted throughout Indonesia (Sutter 1989). Fifty-five percent of the area was in Sumatra. An additional 4.4 Mha of tree crops are planned by the year 2000 (World Bank 1990). Few large-scale plantations have been established in the peatlands. Blasco *et al.* (1983) and Laumonier *et al.* (1986) note some small-holder plantations of rubber, coconut and sago (*Metroxylon* sp.) in the peatlands in Riau and South Sumatra. There are approximately 20 000 ha of tree crop plantations on Padang Island in an area close to where the thesis study was performed; these were established in the 1960's and 70's. The plantations on peat greater than 3–4 m have proven to be unproductive and most have been abandoned (RePPProt 1988, personal observations).

Since 1986, the expansion of tree crop plantations has been vigorously promoted. More recently, the development of timber estates has been promoted to supply wood for a growing pulp and paper industry and lumber to augment supplies from unmanaged forest. In the fifth five-year development period (1989–94), 1.5 Mha of timber estates were projected to be planted. In addition, a total of 2.7 Mha of land has been set aside for future plantations (Review Indonesia 1992). For various reasons the program has not been as popular as initially projected. By May 1992, a total of 326000 ha had been planted with only two years remaining to achieve the 1.5 Mha target.

Despite the slow start, the Government views the timber estate program seriously as a way to boost exports of pulp, paper and lumber, as a way to further promote regional development, and as a promising model for new and existing transmigration schemes (Hill 1991). Further incentives will likely be offered to encourage the achievement of estate development targets.

To date, the tree crop and timber plantations have not replaced natural forests to the same extent as transmigration settlements did during the 1970's and 80's. There are also no known plans to locate estates in the peatlands. However, the conversion of natural forested areas to plantations may become more attractive in the future. The idle, degraded land upon which most of the currently planned estates will be located may prove difficult to rehabilitate for high timber production rates². If this occurs, the peat forests may be exploited and further reduced in area. Much of the land allocated for the timber estates in Sumatra and Kalimantan is in lowland areas

immediately inland of the coastal peat forests. Estates are planned for the forested areas in Riau between Pekanbaru and the east coast, and in South Sumatra near Palembang. One operation in Riau has plans to extend its existing estate into the peatlands and has begun feasibility studies (T.C. Whitmore, personal communication).

A common concern among Indonesia's environmental community is that many of the difficult lessons learned about peatland development by the Ministry of Transmigration may not be passed on to the Ministry of Forestry in their efforts to promote timber estates and that, as a consequence, the peatlands will undergo further degradation³. One of the most basic requirements is to develop soil maps at a scale sufficient to distinguish between shallow, medium and deep peatlands. None of the current mapping systems have provided information at this scale (RePPProt 1988).

1.4.4 Transmigration

Much of the development that has taken place in the peat forests of Sumatra and Kalimantan has been for government sponsored transmigration programs. By 1988, over 3.28 Mha of peat forest, mainly in Sumatra and Kalimantan, had been felled to establish transmigration settlements (Republic of Indonesia 1990). In the early 1980's, Government development plans called for the conversion of an additional five to six million hectares of this forest type to agriculture before the end of the century (Whitten *et al.* 1987a). However, these plans were postponed in 1986 when the transmigration program was curtailed for technical, economic and political/environmental reasons. These are described further in reviews of the transmigration program by the World Bank (1988) and Secret (1986).

The conversion of forests to agricultural land in the peatlands of South Sumatra has been part of a nation-wide program to resettle people from Indonesia's central islands to the lesser-developed outer islands. Operating for almost half a century, the Indonesian transmigration program has been referred to as the largest and most ambitious colonization scheme in history (Caufield 1985). Despite the continuity of the program it's goals have changed considerably over time. Originally, transmigration was seen as a way to reduce the pressures of the rapidly increasing populations on the Islands of Java, Bali and Madura. With annual population growth rates averaging over three percent, the government saw transmigration as the only solution at hand. By the early 1980's, officials recognized that the program was not successfully relieving population pressures. Java's population continued to increase and the number of people relocated annually could never keep pace with the increases. The Indonesian government then began to define additional goals for the transmigration program. These included the use of

population resettlement for promoting national development and security, occupying remote regions along national boundaries and for increasing national agricultural output. New agricultural lands were also being developed to meet the escalating food requirements of the increasing population. Importance was also placed on increasing the agricultural output of cash crops to generate increased export revenues. Recently, this latter goal has taken on increased importance and has been expanded to include transmigrants settling and working in newly established industrial timber plantation estates and complexes. Using transmigrants for economic expansion will likely become increasingly important to help reduce Indonesia's dependence on petroleum exports. In the early 1980's, receipts from oil and gas represented about 57 percent of Government revenues and about 82 percent of total export earnings (World Bank 1988, 1990). With the decline in oil prices in the mid-1980's, oil and gas export revenues declined to 39 percent of total exports. This has led to the development of additional sources of export earnings.

From 1969 to 1989, the Ministry of Transmigration had resettled approximately 3.1 million people to the outer islands, of which 1.8 million people went to Sumatra (Sutter 1989). The majority of the relocation programs were directed towards creating agricultural communities to produce food and cash crops in regions cleared of forest. However, many transmigrants were insufficiently trained in agriculture, particularly for peatland conditions. A study by Hanson and Koesoebiono (1979) showed that 45 percent of all transmigrants had never grown rice before. The lack of farming skills has been a major impediment to new settlements in areas of cleared peat forest, considering the generally poor growing conditions for plants provided by the cleared peat soil. Where farmers could not successfully cultivate their allotted land, dependency on an off-site income was common. As a result, the remaining peat forests surrounding the South Sumatra transmigration settlements have been heavily logged (personal observations from 1986 to 1990), and, in most established settlement areas, this form of income for transmigrants has dwindled. Local forests have been exhausted of commercially valuable trees and the farmers now seek other sources of income to supplement their agricultural activities.

By the end of the fourth five-year plan in 1988, approximately 1.28 Mha of swamp forest had been converted for government sponsored settlements and agriculture programs in Indonesia, including 598000 ha in South Sumatra (Sutter 1989). Plans for new swamp development projects are unclear. However, land planning studies have identified an additional 690000 ha of swamp lands with agricultural potential (Elshof 1990).

Forest degradation resulting from transmigration is probably the most severe of the various types of disturbance that occurs in peat forests. Large tracts of land are cleared and burned, resulting in the destruction of

vegetation and productive topsoil. Large-scale degradation problems have often occurred on these sites, inhibiting agricultural production (MOT 1988). Few settlers farming on the deeper peat formations (>1 m) in the cleared swamp areas have been able to establish both economically and ecologically sustainable agricultural systems.

Removal of the forest canopy, followed by land drainage and cultivation, have resulted in severe moisture and fertility problems in the exposed peat that are not conducive to the sustained production of food crops.

In addition to government sponsored transmigration, unprogramed, spontaneous settlement activities have occurred in the swamp lands. Knox and Miyabara (1984), Collier (1979, 1980), Hanson (1981), Hanson and Koesoebiono (1979), Whitten *et al.* (1987) and the World Bank (1988) have reported that such activities account for as much or more land conversion from forest to agriculture than the organized settlement programs. Ross (1985) discussed the problem of off-site land degradation adjacent to transmigration settlements and estimated that up to five times the total land area cleared for settlements is cleared off-site by both the transmigrant settlers and spontaneous migrants. Dick (1991) concluded that the spontaneous transmigrants (*Swakarsa*), not managed but explicitly encouraged by the Government, are the single largest agent of land use change in Indonesia. He calculated that this group is responsible for clearing 178500 ha of forest annually. A World Bank (1990) report places this annual figure higher at 500000 ha, or 55 percent of the total annual deforestation rate in Indonesia.

1.4.5 Crop Production on Peat

Acceptable levels of agricultural production have been attained in some peatland areas in Sumatra and Kalimantan. Annual production rates of up to five tonnes of unhulled rice per hectare have been recorded (IRRI 1984a, 1984b, Knox and Miyabara 1984). These rates are comparable to those attained in the upland regions of Sumatra. Production success has been most common in areas of thinner peat (less than 0.5 m thick), with small fluctuations in local hydrological conditions and non-toxic subsoils underlying the peat.

Under these conditions some swamp settlement areas have become relatively self-sufficient in food production. As a result, over the past 15 to 20 years they have become successful communities, combining moderate to high levels of crop production with successful agricultural marketing schemes (personal observations, World Bank 1988).

There are large portions of the Sumatran peatlands which, following forest conversion, present unsuitable or marginal conditions for agriculture. These areas have been described in detail by Andriesse (1988), Brady and

Kosasih (1991), Driessen and Sudjadi (1984), Whitten *et al.* (1987) and World Bank (1988). The areas are characterized by: thick, unripened organic peat (between 1 and 15 m deep), wide fluctuations in hydrological conditions leading to floods and drought, and an underlying toxic mineral substrate of acid sulfate clay. Under these conditions, agricultural production and the development of self-sustaining settlements have had little success. Despite government-sponsored site preparation and subsidies to transmigrants, many settlements in cleared peatland have failed to prosper over the past 20 years (World Bank 1988). Moreover, many settlements required continued long-term support following the initial two-year subsidy period. Such settlements are marginal in the sense that land reclamation costs are high, crop yields are low, and soil and water management is difficult and not well understood (Andriesse 1988, Driessen and Rochimah 1976).

In 1983 it was reported that at least 32 (10%) of the Indonesian transmigration settlements had failed, 60 were in need of rehabilitation and 2000 families (approximately 10000 people) had abandoned their new homes (GOI 1983). In 1985 it was estimated that there were 229831 people at risk due to the failure of 37 settlements (GOI/IIED 1985). The transmigration area adjacent to SE6 study area (Air Sugihan Kiri) contains eight settlement divisions. In 1983, five divisions were classified by the Transmigration Ministry as failures due to poor soil and hydrological conditions (GOI 1983).

In response to these problems, the Ministry resettled selected transmigrants a second time. In the mid1980's, 125 000 people were moved from their communities due to poor soil conditions and flooding (World Bank
1988). What remained behind were abandoned tracts of cleared forest land that contributed to the rapidly increasing area of degraded land throughout Indonesia (Donner 1987).

Many of the problem sites are located in areas of thick peat (1–6 m). Agricultural production rates have been generally low and crop failures or decimation by pests have been common (GOI/IIED 1985, Otten 1986, Whitten *et al.* 1987). These areas do not support rice production unless the soils are intensively conditioned by the addition of mineral soil or by regular burning to produce ash. They must also be located directly adjacent to canals for drainage and irrigation. In deep peat areas, cassava, sweet potato and pineapple are grown instead of rice. Even the more tolerant species have often shown poor rates of growth and vulnerability to climatic extremes (personal observations). The low and unstable rates of plant productivity have been attributed to the low levels of available nutrients and high amplitude and frequency of soil moisture fluctuations (Andriesse 1988, Chambers 1979, Coulter 1957, Driessen and Ismangun 1972, Driessen and Soepraptohardjo 1974). Driessen and Sudjadi (1984) observed

that Indonesian coastal peats pose formidable problems for agriculture because of their extremely high porosity and low mineral content, with mineral cycling often occurring only in the top few centimeters. Ismunadji and Damanik (1984) found that plant growth in tidal swamps varied enormously depending on the soil. Annual crop yields in deep peat can be as high as 10 Mg/ha for root-crops such as cassava. These yields are comparable to those of the same crop types on the fertile soils of Java (Donner 1987).

Another concern is the disappearance of peat soil upon cultivation. Farmers living in the South Sumatra peatlands claim that since their arrival in 1981, 10 to 30 cm of peat has disappeared annually. In many areas where the peat was originally thin (<1 m) such as at Cintamanis, Talang and Saleh settlements, over-drainage, cultivation and peat burning has lead to the complete loss of peat and exposure of underlying clay (personal observations, Chambers 1979).

1.4.6 Sod Peat Development for Energy

The use of peat as sod for thermal energy production has been given close consideration in Indonesia (Ministry of Mines and Energy 1987, Republic of Indonesia 1984). A nation-wide survey of peat resources was performed in 1984. The survey calculated that the total of 8.8 Mha of deep peat (>2m) in Indonesia is equivalent to 65 billion barrels of oil. This was greater than the known oil and gas reserves at the time of the survey. Peat sod development represents the most severe form of disturbance to peat ecosystems, where both the vegetation and underlying peat layers are removed.

In the mid-1980's, a pilot project was established in Kalimantan to harvest and burn peat sod experimentally. No commercial operations have been initiated to date and no proposals for Sumatra's peatlands could be located. Indonesia's first peat-fired power plant of 100 megawatts is planned planned for Pontianak, West Kalimantan (Jakarta Post, 19 March 1993).

1.5 CONSEQUENCES OF PEATLAND DEVELOPMENT

Some of the observed ecological effects resulting from forest alteration and drainage in the shallow and medium depth (0.2–3 m) peatlands of Sumatra and Southeast Asia are summarized below. Secrett (1986) provides a more detailed review of the environmental impact associated with the transmigration program on peat and mineral soils.

1.5.1 Altered Forest Regeneration

Poor natural regeneration of native tree species has been observed following moderate to high levels of selective harvesting (Euroconsult 1984, Kostermans 1958, Lee 1977a, Sutisna 1985, Sutisna and Soeyatman 1985, Sutisna et al. 1988, Wyatt-Smith 1959, Wyatt-Smith and Foenander 1962). The degraded peat and Kerangas forests are susceptible to invasion by persistent and flammable secondary species (Brady and Kosasih 1991, Riswan 1981). Slow or arrested forest regeneration has occurred in abandoned cleared areas (Brady and Kosasih 1991, Kartawinata and Vayda 1984). Kochummen and Ng (1977) observed that tree species of commercial value have yet to appear in any quantity in abandoned and degraded peat areas in Malaysia.

1.5.2 Aboveground and Belowground Fires

Fires are becoming more common over larger areas and burning is at higher intensities in altered peat forests (Malingreau *et al.* 1985, Anderson 1983, Brady 1989, Brady and Kosasih 1991). As a result of smoke from forest, scrub and peat fires, the Palembang Airport in South Sumatra closed for up to two months in 1982 (Whitmore 1984a), 1987 and 1991 (Brady 1989, personal observations in 1991) and for shorter periods almost every dry season. Forest regeneration in burned areas has been observed to be extremely poor (Brady and Kosasih 1991, Riswan and Kartawinata 1991).

1.5.3 Variable Crop Production

Poor crop production or crop failure has been common in the peatlands. This has been attributed to both moisture stress (Brünig 1971, Chambers 1979) and nutrient deficiencies (Chew 1970, 1971, 1973, Chew and Yeong 1974, Chew *et al.* 1976a, 1976b, Coulter 1957, Driessen and Sudjadi 1984, Ismunadji and Supardi 1984).

1.5.4 Degradation and Flooding

Rapid decomposition and loss of OM have been common in agricultural areas (Chambers 1979, Chambers and Abdullah 1977). Excessive drainage has resulted in the lowering of water table levels by up to two meters in some places. Where peat has subsided substantially, flooding often occurs due to the reverse flow of water in the system of drainage canals during periods of high river water.

1.5.5 Invasion of Weeds

Where peat forests have been cleared and burned, there is often a rapid invasion of persistent grass such as alang-alang (*Imperata cylindrica*) or ferns (*Achrostichum*, *Nephrolepis* spp.). Losses in crop yield due to weed competition can amount to 50 percent (Koswara and Rumawas 1984, Lee 1977b).

1.5.6 Accelerated Loss and Degradation of Organic Matter

Forest clearing and drainage canal construction cause erosion and runoff of carbon compounds and nutrients to adjacent estuaries, the ocean and the atmosphere (Chambers and Sobur 1977).

1.5.7 Acid Toxicity

A consequence of degradation is the exposure of acid sulphate clays which underlie peat in many areas of the coastal swamps. Once oxidized, the clays become toxic and remain infertile for long periods (Pons and Driessen 1975, Pons and van Breeman 1981).

Limited success in agricultural production has been attained in the Sumatran swamp forests on deep peat which has been cleared for development. Land abandonment is common where the thick peat has proven unmanageable, or where complete peat elimination, through burning and biological oxidation, has exposed the underlying toxic substrate (GOI 1983).

FOOTNOTES

¹Personal field observations of illegal log removal activities from 1986-88 indicate these wood volume figure to be excessive.

²At the time of writing, none of the feasibility studies prepared for the planned timber estate projects provides a scientific basis for biomass yield predictions based on site-specific information on soils, topography and climate.

³Some of these lessons are reviewed in Hardjono (1986), Whitten et al. (1987), World Bank (1988, 1990).

APPENDIX 2. VEGETATION INFORMATION

2.1 SPECIES COVER-ABUNDANCE SCALE

Species Cover-Abundance Scale (modified from Braun-Blanquet 1932, 1965):

Class	Abundance	Cover range (%)	
4	Any number	45–60	
3	Any number	30–45	
2	Any number	15–30	
1	Any number	5–15	
0.5	Numerous	< 5	
0.1	Few	< 5	

2.2 LIST OF PLANTS IN PEAT FOREST STUDY SITES (ALL PLOTS)

NOTE: NI = scientific name of taxa not identified

Genus	Species	Family	Vernacular name	Form
Aglaia	argentata	Meliaceae		tree
Alocasia	longiloba	Araceae	keladi Air	herb
Alstonia	scholaris	Apocynaceae	pulai	tree
Antidesma	puncticulatum	Euphorbiaceae	nyamuk-nyamuk	tree
Aporosa	sphaeridophora Merr.	Euphorbiaceae		tree
Ardisia	NI	Myrsinaceae	jambu hutan	tree
Ardisia	NI	Myrsinaceae	jari lima	shrub
Artabotrys	suaveolens Bl.	Annonaceae		climber
Aspelnium	nidus	Dennstaedtiaceae		fern
Asplnium	longissimum Bl.	Dennstaedtiaceae		fern
Baccaurea	bractea Muell. Arg.	Euphorbiaceae	geronggang	tree
Beilschmedia	kunstleri Gamble	Lauraceae	medang	tree
Blumeodendron	elateriospermum J.J.S.	Euphorbiaceae		tree
Blumeodendron	NI	Euphorbiaceae		tree
Blumeodendron	tokbrai (BI) Kurz	Euphorbiaceae	semodol	tree
Bruguiera	sp. 1	Rhizophoraceae	bakau-bakau	tree
Bruguiera	NI	Rhizophoraceae	bakau-bakau	shrub
Buchanania	NI	Anacardiaceae		tree
Calamus	NI	Arecaceae	rotan	climber
Calophyllum	costulatum	Clusiaceae	bintangur putih	tree
Calophyllum	ferrugineum var.	Clusiaceae	bintangur merah	tree
Calophyllum	sundaicum	Clusiaceae	bintangur hitam	tree
Campnosperma	auriculatum (Bl.) Hook. f.	Anacardiceae	terentang	tree
Campnosperma	coriaceum (Jack.) Hall. f.	Anacardiaceae	terentang	tree
Canarium	sp. 1	Burseraceae	pakam	tree
Chisocheton	divergens	Meliaceae	merewah	tree
Cotyllelobium	melanoxylon Pierre	Dipterocarpaceae	resak	tree
Cratoxylon	NI	Hypericaceae	gerunggang	shrub
Cyrtostachys	lakka	Arecaceae	pinang merah	palm
Dehasia	incrassata	Lauraceae	medang	shrub
Dillenia	excelsa	Dilleniaceae	kecimpur	shrub
Dillenia	obovata	Dilleniaceae	simpur	

Genus	Species	Family	Vernacular name	Form
Dillenia	NI	Dilleniaceae	simpur talang	tree
Diospyros	maritima	Ebenaceae	hitam, k./malam, k.	tree
Diospyros	maritima/siamang	Ebenaceae	serang	tree
Disepalum	anomalum	Annonaceae	pisang-pisang	tree
Drypetes	NI	Euphorbiaceae	mensira hutan	tree
Drypetes	NI	Euphorbiaceae		tree
Dyera	costulata Hook. f.	Apocynaceae	jelutung	tree
Elaeocarpus	NI	Elaeocarpaceae	harum	tree
Elateriospermum	NI	Euphorbiaceae	kekait	tree
Endospermum	diadenum	Euphorbiaceae		tree
Endospermum	moluccanum Becc.	Euphorbiaceae		tree
Eugenia	NI	Myrtaceae	gelam	shrub
Eugenia	NI	Myrtaceae	gelam tikus	tree
Eugenia	NI	Myrtaceae	jambu-jambu	tree
Eugenia	NI	Myrtaceae	kelat	tree
Eugenia	NI	Myrtaceae	kelat merah	tree
Eugenia	NI	Myrtaceae	kelat putih	tree
Eugenia	NI	Myrtaceae	kemodan	tree
Eugenia	NI	Myrtaceae	sisik tempalo	tree
Eugenia	spicata Lam.	Myrtaceae	beti-beti	tree
Euphoria	malaiensis Radlk.	Sapindaceae	bedara	tree
Fagraea	elliptica Roxb.	Loganiaceae		tree
Fagraea	racemosa	Loganiaceae		shrub
Fagraea	auriculata	Loganiaceae	terung	tree
Fibraurea	chloroleuca Miers.	Menispermaceae	akar	epiphyte
Ficus	NI	Moraceae		epiphyte
Ficus	retusa L.	Moraceae	uyah-uyahan, k.	epiphyte
Ficus	sundaica Bl.	Moraceae		tree
Ficus	sundaica	Moraceae	ara, k.	epiphyte
Flagellaria	indica	Flagellariaceae	rotan dini	herb
Forestia	mollissima	Commelinaceae		shrub
Freycinetia	javnica	Pandanaceae	pandan	shrub
Freycinetia	sumatrana	Pandanaceae	pandan	shrub
Ganua	motleyana Pierre	Sapotaceae	ketiau	tree
Garcinia	dioica Bl.	Cluciaceae		tree
Garcinia	parvifolia	Clusiaceae	kelat merah	tree
	- *			

Genus	Species	Family	Vernacular name	Form
Garcinia	rigida	Clusiaceae	kelat jambu	tree
Garcinia	rostrata	Clusiaceae	ribu-ribu (lombok)	tree
Garcinia	NI	Clusiaceae	jambu	shrub
Garcinia	NI	Clusiaceae	jambu air	shrub
Garcinia	NI	Clusiaceae	kandis	tree
Glochidion	NI	Euphorbiaceae		tree
Gluta	aptera (King) Ding Hou	Anacardiaceae	renghas	tree
Gluta	NI	Anacardiaceae	renghas	tree
Gomphia	serrata	Ochnaceae		tree
Gonystylus	bancanus	Thymelaceae	ramin	tree
Gonystylus	macrophyllus	Thymelaceae	ramin	tree
Gynotroches	axillaris	Rhizophoraceae		tree
Hanguana	malayana	Flagellariaceae		shrub
Histiopteris	incisia	Polypodiaceae	paku resam	herb
Horsfieldia	subglobosa var. brachiata	Myristicaceae	pendarah	tree
Horsfieldia	NI	Myristaceae	mendarahan	shrub
Ilex	cymosa	Aquifoliaceae	mensira hutan	tree
Ilex	pleiobrachiata	Aquifoliaceae	mensira hutan	tree
Jackia	ornata	Rubiaceae	seluma terong/selumar	tree
Knema	cinerea var. sumatrana	Myristicaceae	pendarah jantan	tree
Koompassia	malaccensis Maing. ex.	Leguminoseae	menggeris	tree
Lasianthus	apicalis	Icacinaceae ?	garam-garam	tree
Licuala	spinosa	Arecaceae	palas	palm
Litsea	glutinosa C.B. Roxb.	Lauraceae	garu/medang	tree
Litsea	NI	Lauraceae	medang asam	tree
Litsea	ochreaceae	Lauraceae	medang lundu	tree
Litsea	paludosa	Lauraceae	medang	tree
Litsea	NI	Lauraceae	keladi	shrub
Litsea	NI	Lauraceae	medang kuning	tree
Litsea	NI	Lauraceae	medang putih	shrub
Lucinea	montana	Rubiaceae	akar larak	epiphyte
Macaranga	tanarius (L.) M.A.	Euphorbiaceae	mahang	tree
Macaranga	triloba M.A.	Euphorbiaceae	mahang	tree
Mangifera	indica	Anacardiaceae	pelam	tree
Mangifera	NI	Annacardiaceae	asam tampang	tree
Maranthes	corymbosa Bl.	Rosaceae	milas	tree
•	•			

Genus	Species	Family	Vernacular name	Form
Maranthes	NI	Rosaceae	milas putih	shrub
Melanochyla	bracteata King	Anacardiaceae	gelam hijau (pianggu)	tree
Melanochyla	NI	Anacardiaceae	renghas	tree
Memecylon	sumatrense	Melastomataceae	delik	shrub
Merillia	caloxylon	Rutaceae	kemuning hutan	tree
Mezzettia	lepotopoda Oliv.	Annonaceae		tree
Mezzettia	parviflora Oliv.	Annonaceae	gambiran	tree
Microtropis	sumatrana	Celastraceae	delik	tree
Myristica	iners Bl.	Myristicaceae	mereweh	tree
Nauclea	orientalis L.	Rubiaceae	bengkal	tree
Neoscortechninia	kingii	Euphorbiaceae	buntalan hitam/nangka	tree
Nepenthes	NI	Nepenthaceae	akar tempuyung	epiphyte
Nepenthes	reinwardtiana	Nepenthaceae	akar tempuyung	epiphyte
Nephrolepis	biserrata/hirsutula	Dennstaedtiaceae	paku uban	fern
Notaphoebe	kingiana	Lauraceae	medang lendir	tree
Palaquium	NI	Sapotaceae	jambu hutan/balam	tree
Palaquium	rostratum Burck.	Sapotaceae		tree
Palaquium	ridleyi K. et. G.	Sapotacaeae	pitis	tree
Palaquium	NI	Sapotaceae	mayang-mayang	tree
Palaquium	NI	Sapotaceae	nyatu-nyatu	tree
Pandanus	artocarpus	Pandanaceae	benkuang (Laki)	tree
Pandanus	kurzii	Pandanaceae	pandan	shrub
Pandanus	NI	Pandanaceae	pandan	shrub
Parastemon	urophylus A. DC.	Rosaceae	malas/kuning, k.	tree
Payena	leerii	Sapotaceae	sonder	tree
Polyalthia	hypoleuca	Annonaceae	banetan/gerunggung	tree
Polyalthia	sumatrana King.	Annonaceae	banditan	tree
Pometia	pinnata	Sapindaceae	pakam	tree
Pothos	NI	Araceae		tree
Psychotria	polycarpa Hook.f.	Rubiaceae		epiphyte
Pteridium	aquilinum	Dennstaedtiaceae	paku-paku	fern
Rhizophora	NI	Rhizophoraceae	bakau-bakau	tree
Sageraea	lucida	Annonaceae	kapas-kapas	tree
Salacca	edulis or conferta	Arecaceae	salak	palm
Santiria	apiculata Benn.	Burseraceae	babi kurus	tree
Santiria	laevigata Bl.	Burseraceae	parak-parak	tree

Genus	Species	Family	Vernacular name	Form
Santiria	NI	Burseraceae	kompas	tree
Schleichera	oleosa (Lour.) Merr.	Sapindaceae	siasam	tree
Scindapsus	NI	Areceae		tree
Shorea	leprosula	Dipterocarpaceae	meranti batu	tree
Shorea	NI	Dipterocarpaceae	meranti	tree
Shorea	ovalis (Korth) Bl.	Dipterocarpaceae	meranti	tree
Shorea	smithiana	Dipterocarpaceae	meranti bakau	tree
Shorea	teysmannia	Dipterocarpaceae	Meranti Bunga	tree
Shorea	accuminata	Dipterocarpaceae	meranti bunga	tree
Shorea	scabrida	Dipterocarpaceae	meranti bunga	tree
Stemonurus	malaccensis Steum.	Icacinaceae	•	tree
Stemonurus	scorpioides	Icacinaceae	basah-basah	shrub
Stemonurus	secundiflorus	Icacinaceae	garam-garam	tree
Stenochlaena	palustris (Burm.) Beed.	Dennstaedtiaceae	paku sayur	fern
Sterculia	NI	Sterculiaceae	kelumpang/teratai	tree
Sterculia	stipulata	Sterculia	kelumpang/nyatu	tree
Syzygium	anticepticum	Myrtaceae	nasi-nasi	shrub
Syzygium	zeylanicum	Myrtaceae		shrub
Terminalia	foetidissima	Combretaceae	garam-garam	tree
Tetractomia	NI	Rutaceae	mendara putih	tree
Tetramerista	glabra Miq.	Theaceae	punak tembaga	tree
Thoracostachyum	bancanus	Cyperaceae	selensing/pisu	herb
Timonius	flavescens	Rubiaceae	sentulang	tree
Timonius	NI	Rubiaceae		tree
Trichosanthes	globosa	Cucurbitaceae		climber
Tristania	obovata	Myrtaceae	pelawan	tree
Uncaria	NI	Rubiaceae	kait-kait	climber
Uvaria	NI	Annonaceae		climber
Vatica	ŇI	Dipterocarpaceae	resak	tree
Xanthophyllum	heteropleureum Chodat.	Polygalaceae	kemuning hutan	tree
Xylopia	ferruginea	Annonaceae	jangkang	tree
Xylopia	malayana	Annonaceae	jangkang	
Xylopia	NI	Annonaceae	jangkang	tree
Ziziphus	rufula	Rhamnaceae	•	shrub
NI	NI	NI	akar pengcuali	epiphyte
NI	NI	NI	akar saputunggul	epiphyte

Genus	Species	Family	Vernacular name	Form
NI	NI	Orchidaceae	anggrek	shrub
NI	NI	NI	bakong api	shrub
NI	NI	NI	bantayan	tree
NI	NI	NI	bentain	tree
NI	NI	NI	degemo, k.	shrub
NI	NI	NI	jangguk geli	herb
NI	NI	NI	jolok bulan	tree
NI	NI	NI	kali tiga	shrub
NI	NI	NI	keladi hutan	shrub
NI	NI	NI	linau	herb
NI	NI	NI	malam-malam	tree
NI	NI	NI	manggis	tree
NI	NI	NI	mareh putih	epiphyte
NI	NI	NI	medang telur	tree
NI	NI	NI	pancuali, k.	epiphyte
NI	NI	NI	pasir	shrub
NI	NI	NI	pasir-pasir	tree
NI	NI	NI	patam	tree
NI	NI	NI	pelam-pelam	tree
NI	NI	NI	resam-resam	shrub
NI	NI	NI	rinau	tree
NI	NI	NI	rumput landingan	shrub
NI	NI	NI	sakat	shrub
NI	NI	NI	sawinggan	tree
NI	NI	NI	sedarahan	tree
NI	NI	NI	sedarkan	tree
NI	NI	NI	segintan	tree
NI	NI	NI	Senasi	tree
NI ·	NI	NI	senuduk	tree
NI	NI	NI	setombak	tree
NI	NI	NI	simbar	shrub
NI	NI	NI	surau	tree
NI .	NI	NI	telado	tree
NI	NI	NI	tepis	tree

APPENDIX 2.3 LARGE FOREST LITTERFALL IN STUDY SITES

Large litterfall (>2 cm diam.) was not measured quantitatively during the study. Observations were made of litterfall patterns in each site and are discussed below.

PS3 Chablis Forest

This site contained the highest amount of large woody litter of all the study sites. Woody litter originated from both the canopy and subcanopy and from single tree falls and patches of trees blown down. The subcanopy layer at 4 m consisted almost entirely of *Licuala spinosa*. This palm grows from a coppice and produces new stems constantly. The forest floor in the plots was covered with a loose mat of 10 to 15 cm diameter *Licuala* stems in various stages of decay.

Single and multiple windthrow of large canopy trees were more common in the chablis forest type than in the other sites. The rate of windthrow in PS3 was also observed to increase over the study period from 1985 to 1994. The increase appeared to coincide with the progressive peat drying which occurred due to drainage of peat water into the adjacent canals (250 m from the study site).

In October 1989, 12 mature canopy trees blew over in plot two. Unlike windthrow in SE6 mixed and PI9 pole forest types, the trees blew over by uprooting rather than stem breakage. The uprooting resulted in the formation of large hummocks and hollows. This suggested that the dry, well-drained peat provided less rooting stability than naturally wet peat. At the base of many uprooted trees the entire mat (up to 10 m in diameter) of medium and large diameter lateral roots was pulled from the peat surface.

A comparison of conditions in SE6 and PS3 suggested that drainage of the Padang-Sugihan peat forest promoted tree windthrow. Increased canopy roughness due to selective logging could have also contributed as this would produce greater air turbulence.

SE6/PI6 Mixed Forest

This forest type possessed an open forest floor and shrub layer, with little medium-sized woody litter.

Single tree falls were common and stems of large trees were frequently found on the forest floor. However, large open patches caused by windthrow were not common in the uneven canopied mixed forest. Tree falls causing

uprooting were also not common. This observation suggests that the root forms found in the peat forests provide adequate stability.

Woody litterfall rates have not been published for other peat forests in Southeast Asia., but have been measured in other tropical forest types. Whitten *et al.* (1984) surveyed litter studies in Southeast Asia and estimated that annual coarse litterfall ranged from 9 to 15 Mg ha⁻¹ in a variety of forest types. Vogt *et al.* (1986) summarized world-wide litterfall studies specifically for tropical broad leaved evergreen forests and estimated the range to be 0.5–5.7 Mg ha⁻¹ annually. The lower limit of this range might apply to PI12, while the upper limit may apply to SE6 on medium peat.

PI9 Tall Pole Forest

The forest floor was covered with a dense shrub layer and a moderate amount of woody litter, mostly derived from the shrubs. Individual fallen trees were not common, but tree-fall patches were most frequent in the tall pole forest type. This may be due to the height of the pole trees and the uneven canopy surface. During high winds it was common to observe the tall *Calophyllum* spp. trees bending to angles reaching 45°. The windthrow patches were rectangular in shape measuring approximately 10 m x 50 m. Inside the patches, the forest floor was covered by fallen trees. Most trees did not uproot during windthrow, but snapped within 2 m of their base. A hummocky surface resulting from uprooting was rarely seen.

Broad estimates from aerial photographs of Padang Island indicated that visible forest windthrow patches ranged from 2 to 10 percent of PI9, but none in PI12. Brünig (1964, 1973) and Anderson (1961b, 1964a, 1966) found large areas of forest damaged from windthrow, lightning strikes and insect infestation in tall peat swamp forests in Borneo. They noted that less natural damage occurred in the low pole forests in the same regions (Padang forest).

PI12 Low Pole

The forest floor was mostly bare, without herb or shrub cover and with very little undecomposed woody litter. Fallen trees resulting from windthrow were rarely observed. The absence of windthrow may have been due to the low, even canopy characteristics of this forest type. The dense mat of tree roots common in this forest would also contribute to the stability of the stands.

APPENDIX 2.4 EFFECTS OF THE 1991 EL NINO DROUGHT ON LITTERFALL PATTERNS

During the latter half of 1991, rainfall declined below the normal pattern due to the 1991-1992 El Nino Southern Oscillation event (NOAA 1991-92). The drought ended in December 1991. Trees in the PI9 and PI12 pole forest flowered profusely during the 1991 drought, as the mixed forest trees did in the October to November 1987 El Nino drought in PS3. In particular, *Calophyllum* spp. flowered heavily. By March 1992, the forest floor was littered with seed of which *Calophyllum* drupes were most numerous. The heaviest seed production was observed in PI12. Field surveys indicated 300 to 400 new *Calophyllum* seeds per 10 m² of the forest floor in PI12 in March 1992. By April 1992, many of the seeds in PI12 had germinated. *Calophyllum* seedlings and saplings were not observed in the relevé plots in 1989.

The El Nino drought in 1987 also affected the study sites on Padang Island (NOAA 1987–1988). In response to the dry conditions, seed production and germination probably followed a similar pattern in late 1987 as was observed in 1991 and 1992. Considering the absence of seedlings in the relevé plots before the 1991 drought, it is also possible that the crop of 1992 seedlings did not survive. Most 1 to 3 m tall *Calophyllum* in PI9 and PI12 saplings were observed to have originated vegetatively as root suckers, rather than as seedlings.

APPENDIX 3. STATISTICAL ANALYSIS

Appendix 3.1. F statistics for ANOVAs of resource quality attributes of peat with study sites and acrotelm layers as main effects and plots nested within study sites.

Dependent variable	Source	df	MS	F	P
Dry mass (kg m ⁻²)	Site	4	544.240	10.276	0.013
	Layer	1	40.960	1.243	0.316
	Site x Layer	4	131.560	3.992	0.081
	Plot (Site)	5	52.960	1.031	0.405
	Layer x Plot (Site)	5	32.960	0.642	0.669
	Error	80	51.360		
C (mg g ⁻¹)	Site	4	10.269	17.302	0.004
	Layer	1	172.738	100.598	0.000
	Site x Layer	4	4.594	2.676	0.155
	Plot (Site)	5	0.594	0.559	0.731
	Layer x Plot (Site)	5	1.717	1.618	0.165
	Error	80	1.061	٠	
N (mg g ⁻¹)	Site	4	0.725	3150.609	0.000
,	Layer	1	0.155	337.478	0.000
	Site x Layer	4	0.008	16.500	0.004
	Plot (Site)	5	0.000	0.048	0.999
	Layer x Plot (Site)	5	0.000	0.096	0.992
	Error	80	0.005		
N mineral	Site	4	472.646	2.153	0.211
(mg N 100 g ⁻¹ a ⁻¹)	Layer	1	29 494.628	148.422	0.000
	Site x Layer	4	368.095	1.852	0.257
	Plot (Site)	5	219.519	53.580	0.000
	Layer x Plot (Site)	5	198.722	48.504	0.000
	Error	80	4.097		
P (mg g ⁻¹)	Site	4	0.461	28.676	0.001
	Layer	. 1	0.309	46.417	0.001
	Site x Layer	4	0.015	2.302	0.193
	Plot (Site)	5	0.016	5.006	0.000
	Layer x Plot (Site)	5	0.007	2.075	0.077
	Error	80	0.003		
continued					

Appendix 3.1 continued

Dependent variable	Source	df	MS	F	P
pН	Site	4	1.005	5.960	0.038
	Layer	1	0.159	0.822	0.406
	Site x Layer	4	0.317	1.635	0.299
	Plot (Site)	5	0.169	1.852	0.112
	Layer x Plot (Site)	5	0.194	2.126	0.071
	Error	80	0.091		
Solubles (mg g ⁻¹)	Site	4	70.500	358.504	0.000
	Layer	1	0.035	0.278	0.621
	Site x Layer	4	2.697	21.653	0.002
	Plot (Site)	5	0.197	0.667	0.650
	Layer x Plot (Site)	5	0.125	0.422	0.832
	Error	80	0.295		
Holocellulose (mg g ⁻¹)	Site	4	379.687	157.056	0.000
	Layer	1	457.233	79.551	0.000
	Site x Layer	4	285.676	49.703	0.000
	Plot (Site)	5	2.418	0.327	0.896
	Layer x Plot (Site)	5	5.748	0.776	0.570
	Error	80	7.402		
Lignin (mg g ⁻¹)	Site	. 4	152.751	98.996	0.000
	Layer	1	465.221	106.776	0.000
	Site x Layer	4	332.281	76.264	0.000
	Plot (Site)	· 5	1.543	0.230	0.949
	Layer x Plot (Site)	5	4.357	0.648	0.663
	Error	80	6.719		
Polyphenol (mg g ⁻¹)	Site	4	0.019	17.153	0.004
	Layer	1	0.005	1.537	0.270
	Site x Layer	4	0.020	6.113	0.037
	Plot (Site)	5	0.001	0.094	0.993
	Layer x Plot (Site)	5	0.003	0.278	0.924
	Error	80	0.012		

Appendix 3.2. F statistics for ANOVA of peat fraction distribution with study sites and acrotelm layers as main effects and plots nested within study sites.

Dependent variable	Source	df	MS	. F	P
Hemic peat (kg m ⁻¹)	Site	4	1390.516	23.238	0.002
	Layer	. 1	6.086	0.367	0.571
•	Site x Layer	4	146.483	8.841	0.017
	Plot (Site)	5	59.837	7.646	0.000
	Layer x Plot (Site)	5	16.569	2.117	0.072
	Error	80	7.826		
Intact roots (kg m ⁻¹)	Site	4	157.308	11.877	0.009
	Layer	1	25.703	18.521	0.008
	Site x Layer	4	8.668	6.246	0.035
	Plot (Site)	5	13.244	6.392	0.000
	Layer x Plot (Site)	5 .	1.388	0.670	0.647
	Error	80	2.072		
Roots and chaff	Site	4	0.787	6.506	0.032
(kg m ⁻¹)	Layer	1	1.705	15.201	0.011
	Site x Layer	4	0.164	1.459	0.339
	Plot (Site)	5	0.121	5.398	0.000
	Layer x Plot (Site)	5	0.112	5.003	0.000
	Error	80	0.022		

Appendix 3.3. F statistics for ANOVAs of resource quality attributes of litter layers with study sites as main effect and plots nested within study sites.

Dependent variable	Source	df	MS	F	P
Dry mass (kg m ⁻²)	Site	4	26.415	4530.895	0.000
Dry mass (kg m)	Plot (Site)	5	0.006	0.024	1.000
	Error	40	0.000	0.024	1.000
C (mg g ⁻¹)	Site	40	14.633	17.764	0.004
C (mg g)	Plot (Site)	5	0.824	0.282	0.920
	Error	40	2.917	0.262	0.920
N (mg g ⁻¹)	Site	40	0.550	14.938	0.005
N (mgg)	Plot (Site)	5	0.037	3.531	
	Error	40	0.037	3.331	0.010
N mineral	Site			2.066	0.000
		4	1567.325	3.966	0.082
$(mg N 100 g^{-1} a^{-1})$	Plot (Site)	5	395.190	12.174	0.000
n (-1)	Error	40	32.463	15.500	0.004
P (mg g ⁻¹)	Site	4	0.208	17.528	0.004
	Plot (Site)	5	0.012	2.798	0.029
. 1	Error	40	0.004		
Solubles (mg g ⁻¹)	Site	4	649.981	326.384	0.000
	Plot (Site)	5	1.991	1.581	0.187
	Error	40	1.259		
Holocellulose (mg g ⁻¹)	Site	4	287.592	72.938	0.000
	Plot (Site)	5	3.943	0.509	0.767
	Error	40	7.739		
Lignin (mg g ⁻¹)	Site	4	583.713	166.206	0.000
	Plot (Site)	5	3.512	0.620	0.685
	Error	40	5.661		
Polyphenol (mg g ⁻¹)	Site	4	0.074	3.225	0.116
	Plot (Site)	5	0.023	0.927	0.474
	Error	40	0.025		

Appendix 3.4. F statistics for ANOVAs of resource quality attributes of litterfall with study sites as main effect and plots nested within study sites.

Dependent variable	Source	df	MS	F	P
		:			
$C \text{ (mg g}^{-1}\text{)}$	Site	4	14.623	15.059	0.005
	Plot (Site)	5	0.971	0.341	0.885
	Error	40	2.851		
N (mg g ⁻¹)	Site	4	1.648	159.999	0.000
•	Plot (Site)	5	0.010	0.932	0.471
	Error	40	0.011		
P (mg g ⁻¹)	Site	4	0.860	114.111	0.000
	Plot (Site)	5	0.008	1.001	0.429
	Error	40	0.008		
Solubles (mg g ⁻¹)	Site	4	649.981	326.384	0.000
	Plot (Site)	5	1.991	1.581	0.187
	Error	40	1.259		
Holocellulose (mg g ⁻¹)	Site	4	287.592	72.938	0.000
	Plot (Site)	5	3.943	0.509	0.767
	Error	40	7.739		
Lignin (mg g ⁻¹)	Site	4	583.713	166.206	0.000
٠.	Plot (Site)	5	3.512	0.620	0.685
	Error	40	5.661		
Polyphenol (mg g ⁻¹)	Site	4	0.074	3.225	0.116
	Plot (Site)	. 5	0.023	0.927	0.474
	Error	40	0.025		

Appendix 3.5. F statistics for ANOVAs of resource quality attributes of small roots with study sites as main effect and plots nested within study sites.

Dependent variable	Source	df	MS	F	P
Dry mass (kg m ⁻²)	Site	4	7.808	79.056	0.000
	Layer	1	2.429	77.272	0.000
	Site x Layer	4	0.284	9.022	0.017
	Plot (Site)	5	0.099	5.371	0.000
	Layer x Plot (Site)	4	0.031	1.709	0.142
	Error	80	0.018		
C (mg g ⁻¹)	Site	4	25.084	1.004	0.484
	Plot (Site)	5	24.986	4.228	0.004
	Error	40	5.909		
N (mg g ⁻¹)	Site	4	0.158	16.346	0.004
	Plot (Site)	5	0.010	0.627	0.680
	Error	40	0.015		
P (mg g ⁻¹)	Site	4	0.304	7.797	0.022
	Plot (Site)	5	0.039	9.946	0.000
	Error	40	0.004		
Solubles (mg g ⁻¹)	Site	4	455.587	86.496	0.000
	Plot (Site)	5	5.267	1.370	0.256
	Error	40	3.844		
Holocellulose (mg g ⁻¹)	Site	4	63.147	2.237	0.200
•	Plot (Site)	5	28.233	1.098	0.377
	Error	40	25.710		
Lignin (mg g ⁻¹)	Site	4	225.081	5.098	0.052
	Plot (Site)	5	44.147	1.854	0.124
·	Error	40	23.813		
Polyphenol (mg g ⁻¹)	Site	4	0.073	29.321	0.001
	Plot (Site)	5	0.002	0.149	0.979
	Error	40	0.017		

Appendix 3.6a. F statistics for ANOVAs of small root growth into buried mesh bags with study sites and acrotelm layers as main effects, and plots nested within study sites.

Dependent variable	Source	df	MS	. F	Р
g root m ⁻² 30 d ⁻¹	Site	.4	99.848	3158.744	0.000
	Layer	1	15.147	330.724	0.000
	Site x Layer	4	0.113	2.466	0.174
	Plot (Site)	5	0.032	0.220	0.953
	Layer x Plot (Site)	5	0.046	0.319	0.901
	Error	180	0.143		

Note: ANOVA based on log-transformed data.

Appendix 3.6b. F statistics for ANOVAs of small root growth into buried mesh bags with study sites, acrotelm layers and incubation periods as main effects.

Dependent variable	Source	df	MS	F	Р
g root m ⁻² 30 d ⁻¹	Site	4	99.848	690.391	0.000
	Layer	1	15.147	104.734	0.000
	Period	1	0.003	0.020	0.888
	Site x Layer	4	0.113	0.781	0.540
	Site x Period	4	0.036	0.246	0.912
	Layer x Period	1	0.001	0.010	0.922
	Site x Layer x Period	4	0.004	0.028	0.998
	Error	180	0.145		

Note: ANOVA based on log-transformed data.

Appendix 3.7. F statistics for ANOVA of leaf litter losses from mesh bags (% loss) with study sites and incubations periods as main effects, and plots nested within study areas.

Dependent variable	Source	df	MS	F	P
Leaf loss (% 90 d ⁻¹)	Site	4	1306.527	168.077	0.000
Lear loss (70 90 d)	Period	1	124.546	57.912	0.000
	Site x Period	4	948.099	440.853	0.000
	Plot (Site)	5	7.773	0.620	0.685
	Period x Plot (Site)	5	2.151	0.172	0.972
	Error	80	12.540		

Appendix 3.8. F statistics for ANOVA of leaf respiration (g CO₂ g⁻¹ 30 d⁻¹) with study sites and moisture levels as main effects, and plots nested within study sites.

Dependent variable	Source	df	MS	F	P
Leaf respiration	Site	4	405.377	64.892	0.000
$(mg CO_2 g^{-1} 30 d^{-1})$	Moisture	1	2239.731	1008.688	0.000
	Site x Moisture	4	133.813	60.264	0.000
	Plot (Site)	. 5	6.247	1.286	0.278
	Moisture x Plot (Site)	5	2.220	0.457	0.807
	Error	80	4.856		

Appendix 3.9a. F statistics for ANOVA of respiration from acrotelm peat with study sites and acrotelm layers as main effects, and plots nested within study sites.

Dependent variable	Source	df	MS	F	P
Peat respiration	Site	.4	2.655	69.733	0.000
$(mg CO_2 g^{-1} 30 d^{-1})$	Layer	1	17.550	654.357	0.000
	Site x Layer	4	0.807	30.081	0.001
	Plot (Site)	5	0.038	2.102	0.067
	Layer x Plot (Site)	5	0.027	1.480	0.198
•	Error	180	0.018		

Appendix 3.9b. F statistics for ANOVA of respiration from the top layer of acrotelm peat with study sites, acrotelm layers and moisture levels as main effects, and plots nested within study sites.

Dependent variable	Source	df	MS	F	Р
Peat respiration	Site	4	2.762	52.528	0.000
$(mg CO_2 g^{-1} 30 d^{-1})$	Moisture	1	0.117	1.474	0.279
	Site x Moisture	4	0.160	2.022	0.230
	Plot (Site)	5	0.053	2.996	0.016
	Moisture x Plot (Site)	5	0.079	4.509	0.001
	Error	80	0.018		

Appendix 3.9c. F statistics for ANOVA of respiration from the bottom layer of acrotelm peat with study sites, acrotelm layers and moisture levels as main effects, and plots nested within study sites.

Dependent variable	Source	df	MS	F	Р
Peat respiration	Site	4	0.700	56.885	0.000
(mg CO ₂ g ⁻¹ 30 d ⁻¹)	Moisture	1	0.000	0.001	0.978
	Site x Moisture	4	0.024	5.121	0.051
	Plot (Site)	5	0.012	1.675	0.150
	Moisture x Plot (Site)	5	0.005	0.630	0.677
	Error	80	0.007		

Appendix 3.10a. F statistics for ANOVA of respiration from SE6 peat with acrotelm layers and temperature levels as main effects, and plots nested within layers.

Dependent variable	Source	df	MS	F	P
Peat respiration	Layer	1	7.790	42.684	0.023
$(mg CO_2 g^{-1} 30 d^{-1})$	Temperature	1	4.648	100.322	0.010
	Layer x Temperature	1	2.100	44.986	0.022
	Plot (Layer)	2	0.183	30.518	0.000
	Temp. x Plot (Layer)	2	0.047	7.808	0.002
	Error	36	0.006		

Appendix 3.10b. F statistics for ANOVA of respiration from PI12 peat with acrotelm layers and temperature levels as main effects.

Dependent variable	Source	df	MS	F	P
Peat respiration	Layer	1	24.020	53.266	0.018
$(mg CO_2 g^{-1} 30 d^{-1})$	Temperature	1	13.263	13 961.032	0.000
•	Layer x Temperature	1	2.261	2379.505	0.000
	Plot (Layer)	2	0.451	20.051	0.000
	Temp. x Plot (Layer)	2	0.001	0.042	0.959
	Error	36	0.022		

Appendix 3.11a. F statistics for ANOVA of leaf respiration with peat extracts and study sites as main effects, and plots nested within study sites.

Dependent variable	Source	df	MS	F	P
•					
Leaf respiration	Site	1	341.007	124.812	0.008
$(mg CO_2 g^{-1} 30 d^{-1})$	Extract	2	134.256	56.567	0.001
	Site x Extract	2	3.314	1.396	0.347
	Plot (Site)	2	2.732	0.712	0.496
	Extract x Plot (Site)	4	2.373	0.619	0.651
	Error	48	3.836		

Appendix 3.11b. F statistics for ANOVA of root respiration with peat extracts and study sites as main effects, and plots nested within study sites.

Dependent variable	Source	df	MS	F	P
Root respiration	Site	1	137.441	13.072	0.069
(mg CO ₂ g ⁻¹ 30 d ⁻¹)	Extract	2	1.173	0.186	0.837
	Site x Extract	2	1.597	0.254	0.788
	Plot (Site)	2	10.514	5.787	0.006
	Extract x Plot (Site)	4	6.297	3.466	0.014
	Error	48	1.817		

Appendix 3.12. F statistics for ANOVAs of peat physical parameters with study sites and acrotelm layers as main effects and plots nested within study sites.

Dependent variable	Source	df	MS	F	P
Peat bulk density	Site	4	0.014	10.311	0.012
(g cm ⁻³)	Layer	1	0.001	1.244	0.315
•	Site x Layer	4	0.003	4.012	0.080
	Plot (Site)	5	0.001	1.031	0.405
	Layer x Plot (Site)	5	0.001	0.641	0.669
	Error	80	0.001		
Coarse fraction of	Site	4	9.050	66.709	0.000
peat (g 100 g ⁻¹)	Layer	1	2.534	36.404	0.002
	Site x Layer	4	0.116	1.661	0.293
	Plot (Site)	5	0.136	2.917	0.018
	Layer x Plot (Site)	5	0.070	1.497	0.200
	Error	80	0.047	•	